

Table 1. Summary of the results from studies on California spotted owl demographics and habitat selection.

Study	Study Location(s), Sample Size and Unit, and Period	Parameter	Habitat Selection
Blakesley et al. (2005)	Lassen Demographic Study Area, 63 territories, 11 years	Occupancy (pair or single)	The amount of nest area dominated by large trees (>24 in dbh) and canopy cover >70% was positively associated with site occupancy. The amount of nest area dominated by medium- trees (12-24 in dbh) with canopy cover >70% and the amount of area unforested or dominated by small trees (6-12 in dbh) were negatively associated with site occupancy.
		Survival	Apparent survival increased with greater amounts of forest dominated by large trees (>24 in dbh) with normal (40-70%) to good (>70%) canopy cover containing large (>30 in dbh) remnant trees.
		Reproduction	Reproduction decreased as the amount of nest area that was unforested or dominated by small trees increased.
		Nest Success	Nest success was higher when large remnant trees were present in the nest stand.
Seamans and Gutierrez (2007)	Eldorado Demographic Study Area, 66 territories, 15 years	Extinction	The amount of conifer forest dominated by medium (12-24 in dbh trees) and large trees (>24 in dbh) with >70% canopy cover was negatively correlated with the probability of territory extinction.
		Colonization	The amount of conifer forest dominated by medium (12-24 in dbh trees) and large trees (>24 in dbh) with >70% canopy cover was positively correlated with the probability of territory colonization.
Roberts et al. (2011)	Yosemite National Park, 16 burned and 16 unburned territories, 2-14 years post-fire	Occupancy (pair)	The top model suggested that nest and roost site occupancy were best predicted by the combined positive effect of basal area and the negative effect of coarse woody debris. However, there was also support for an alternative model suggesting that higher canopy closure and tree basal area were also useful predictors of nest and roost site occupancy.
Tempel et al. (2014)	Eldorado Demographic Study Area, 70 territories, 20 years	Reproduction	Reproduction was negatively related to the area of hardwood forest with <10% conifer canopy cover.
		Survival	The amount of high (>70%) canopy cover forest dominated by 12-24 in and >24 in dbh trees occurred in the top-ranked models for survival, territory extinction, and territory colonization rates, and explained more variation in population growth rate and equilibrium occupancy than other covariates. Forests dominated by trees >24 in dbh and <30% canopy cover were not associated with demographic parameters.
		Extinction	
		Colonization	
Tempel et al. (2016)	Lassen, Eldorado, Sierra, and Sequoia-Kings Canyon demographic study areas, 275 territories, 19 years	Extinction	Forests with high (>70%) and medium (40-70%) canopy cover were the only habitat covariates that were consistently identified as important for all four study areas. Occupancy reached its lowest value when high and medium canopy cover were minimized and occupancy reached its highest value when these covariates were maximized. Occupancy for the 40–49% canopy cover class was lower than occupancy for the 50–59% and 60–69% canopy cover classes. Occupancy rates are likely to be negatively affected if canopy cover is consistently reduced to 40%.
		Colonization	
		Occupancy (single or pair)	

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North et al. (2017)	Sequoia-Kings Canyon, Eldorado, and Sierra demographic study areas and Tahoe National Forest, 316 territories, sites that were occupied by an owl pair at least once between 2001 and 2013	Occupancy (pair)	Across the four study areas, the average values of total canopy cover and cover in trees >48 m (157 ft) was highest at nest sites, and consistently decreased as area expanded to PACs, territories and then the surrounding landscape. A similar trend of decreasing values from nest sites to landscape was identified for the 32–48 m (105-157 ft) strata on the three National Forest study areas but not on Sequoia-Kings Canyon. The amount of cover of trees in the 2-16 m (7-52 ft) height strata was lowest near nest sites and decreased as area expanded to PACs, territories, and then the surrounding landscape.
Jones et al. (2018)	Lassen, Eldorado, Sierra, and Sequoia-Kings Canyon demographic study areas, 275 territories, 19 years	Extinction	Extinction rates increased as the amount of forest characterized by large trees (≥ 24 in dbh) and high canopy cover (>70% cover) decreased. Median proportion of an owl site containing large trees and high canopy cover forest on national forests ranged from 0.03-0.06, corresponding with higher predicted rates of local extinction and ongoing declines in occupancy. The median proportion of forest characterized by large trees and high canopy cover in owl territories on Sequoia-Kings Canyon was 0.19, which had a lower predicted extinction rate and stable occupancy.
		Occupancy (pair or single)	
Blakey et al. (2019)	Plumas National Forest, 15 owls, 3 years	Roosting and Foraging	Owls selected against roosting and foraging sites with <50% canopy cover, selected for areas with >70% cover, and used areas with <30% cover for foraging in proportion to availability. They also selected against areas dominated by trees <12 in dbh.
Atuo et al. (2019)	Northern and Central Sierra Nevada, 53 owls, 1 year	Home Range Size	Home range sizes increased as spatial heterogeneity and elevation increased and decreased as with increasing amounts of forest with >50% canopy cover and QMD 11-13 inches.
Hobart et al. (2019a)	Northern and Central Sierra Nevada, 151 owl sites, 5 years	Occupancy	Probability of initial site occupancy increased as elevation decreased. Probability of a site being colonized or remaining occupied declined with increasing elevation, younger forest, and open area. Probability of a site being colonized or remaining occupied was lowest when previously unoccupied, and highest when previously occupied with successful reproduction.
		Reproduction	Probability of reproduction increased as elevation decreased, when territories had more north-facing slope, and more younger forest with high basal area of hardwoods.
Hobart et al. (2019b)	Across the Sierra Nevada Bioregion	Extinction	Territory extinction probability was lower when owl diets contained more woodrats and pocket gophers
		Home Range	Home range sizes decreased as the dietary proportion of woodrats and pocket gophers increased.
Tempel et al. (2022)	Southern CSO population on San Bernardino and Angeles NMS; 1991-2019; combined lower elevation oak and higher elevation pine/ MC territories.	Extinction	Extinction declined by half as tree density increased to 20 trees/ha, then extinction leveled off (large trees defined as ≥ 50 cm dbh).
		Colonization	Territory colonization increased as large tree density increased to about 20 trees/ha in low elevation sites, then declined with greater tree density in higher elevation sites. Differences between hardwood and conifer ecotypes in study were apparent in large trees associations. Positive association between occupancy and proportion of WUXI in territory was unexpected.
		Reproduction	Positive linear relationship between high canopy cover forest and reproductive output. In addition, territories located in proportionally more drainages or on northeast facing slopes also had greater reproductive output.
	Southern CSO population on San Bernardino and San Jacinto mountains; 10 breeding pairs; 2006-2020; 2,600'-8,500' elevation oak		CSO reproductive success was most strongly related to canopy cover, canopy height, and shrubby vegetation; CSO reproductive success increased with greater canopy cover and taller canopy height at the home range scale (average 85% canopy cover). CSO reproduced more successfully in areas with greater shrubby vegetation. Woodrat prey delivery model fit with greater canopy, greater canopy layers and less shrubby vegetation. (more about the prey delivery part of study in the CSO foraging study Word

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Wilkinson et al. 2023	woodland to MC;Used Tempel's 2022 data and applied 2020 vegetation descriptions from LiDAr and CSO to ten 776-acre territories; Results in foraging study summary	Reproduction	document). CSO reproductive success was unrelated to number of prey captures, and this should counter Jones et al. 2024 study which suggested woodrats are the end-all to CSO reproductive sucess.

Table 2. Summary of results from studies on the effects of logging and fuel reduction on spotted owl demographics.

Study	Study Location(s), Sample Size and Unit, and Period	Disturbance Type(s) Evaluated	Parameter	Response (Effect on Demographic Parameter)
Seamans and Gutierrez (2007)	Eldorado Demographic Study Area, 66 territories, 15 years.	High Severity Fire (including salvage), Logging	Extinction	Negative - Alteration of ≥ 50 acres of mature conifer forest was positively correlated with territory extinction probability.
			Colonization	Negative - Probability of colonization was related to the amount of mature conifer forest habitat in the territory and the alteration of such habitat reduced the probability of colonization.
Clark et al. (2013)	Southwest Oregon, 31 burned/103 unburned territories, up to 15 years pre-fire and 4-5 years post-fire.	Logging, High Severity Fire, Salvage Logging	Extinction	Negative - Probability of extinction increased due to the interactive effect of past timber harvest, high severity fire, and salvage logging.
			Colonization	Unclear - Few colonization events were observed.
			Occupancy (pair)	Negative - Declines in occupancy were driven by increases in extinction, attributable to past timber harvest, high severity fire, and salvage logging.
Tempel et al. (2014)	Eldorado Demographic Study Area, 70 territories, 20 years.	High-intensity Logging, Wildfire (including salvage), and Medium-intensity Logging.	Reproduction	Negative - "...medium-intensity timber harvests characteristic of proposed fuel treatments were [weakly] negatively related to reproduction of Spotted Owls. Reproduction appeared sensitive to modest amounts of medium-intensity harvests, and was predicted to decline from 0.54 to 0.45 when 20 ha were treated..." (p.2101)
			Survival	Neutral - No relationship in this study, however authors conclude that "we believe that the most appropriate inference about the influence of medium-intensity harvesting practices is that they appear to reduce reproductive potential, and when implemented in forests with high canopy cover, are likely to reduce survival and territory occupancy as well." (p.2103)
			Extinction	Negative - Extinction was negatively correlated with the area of high-intensity timber harvest. High intensity timber harvest occurred on 5.4% of the total area within owl territories in the study.
			Colonization	Negative - Wildfire had a strong negative effect on territory colonization, however the standard error was unestimable because of the small sample size (few territories in the study were affected by wildfire during the study). Territory colonization was positively correlated with area of vegetation class 5 and 7 (canopy cover $>69\%$ and dbh $>30.4\text{cm}$). (p. 2099) These vegetation classes associated with CSO habitat were reduced by medium intensity logging, but the authors only reported model results from wildfire impacts to colonization, not logging impacts
			Occupancy (single or pair)	Negative - Equilibrium occupancy was negatively correlated with wildfire. When fire frequency was doubled in the models then the negative association between equilibrium occupancy and area burned was greater in the model compared actual levels measured in the field study. Under future modeling scenarios, equilibrium occupancy was lower under the scenario with more wildfire.
Stephens et al. (2014)	Plumas National Forest, 8 territories, 4-5 years pre-treatment, 3-4 years post-treatment.	Group Selection and Fuels Treatments	Occupancy (single or pair)	Negative - By 3–4 years post-treatment, the number of occupied sites declined decline by 43% from the pretreatment numbers. "Our results indicate negative CSO responses to treatments, supported by the avoidance of DFPZs by foraging owls, larger owl home ranges associated with increasing amounts of treatment within the home ranges, and a 43% decline in the number of territorial CSO sites across the Meadow Valley study area within 3–4 years of the implementation of landscape treatments." (p.903).

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Tempel et al. (2015)	Tahoe National Forest, 4 territories, modeled 30 years post-treatment.	Fuels Treatment, Wildfire	Fitness	Negative - Fuels treatment had a negative effect on fitness in the absence of fire, an effect that was still present after 30 years of simulated forest growth. Negative - Simulated wildfire without fuels treatment negatively affected fitness. Negative - Fuels treatment and simulated wildfire together negatively affected fitness compared to fuels treatments without wildfire; however fuels treatment with wildfire had the least negative impact compared to no fuels treatment with wildfire.
			Occupancy (single and pair)	The general patterns for equilibrium occupancy were similar to those for territory fitness, but there was greater variation under the different scenarios.
Tempel et al. (2016)	Tahoe National Forest, 4 territories, modeled 30 years post-treatment.	Wildfire (including salvage on National Forests), Prescribed Fire, Logging	Extinction	Negative - On the ELD study area, logging less than 1% of a territory in the previous 3 years was negatively correlated with extinction. Neutral - No support for an effect of logging less than 1% of a territory in the previous 3 years was detected for the LAS or SIE study areas. Negative - On the SKC study area, wildfire was negatively related to extinction. Neutral - No support for an effect of wildfire was detected on the ELD, LAS, or SIE study areas.
			Colonization	Neutral - No support for an effect of logging less than 1% of a territory in the previous 3 years was detected for the ELD, LAS, or SIE study areas. Negative - On the SKC study area, prescribed fire was negatively associated with colonization.
			Occupancy (single or pair)	Neutral - No support for an effect of logging when less than 1% of a territory was logged in the previous 3 years for the LAS, or SIE study areas. Positive - On the ELD study area, logging less than 1% of a territory in the previous 3 years was positively associated with occupancy. Positive - medium (40-69% and high (>70%) canopy cover was consistently associated with greater territory occupancy.
Tempel et al. (2022)	Southern CSO population on San Bernardino and Angeles NMS; 1991-2019; combined lower elevation oak and higher elevation pine/ MC territories.	Small portion of fuel reduction within 10 years after fire in 40 CSO territories; 37 territories had <5% fuels treatment whereas area burned by high-severity fire was 17% of all 40 territories.	Extinction	Positive - fuel reduction treatments were correlated with increased territory extinction.
			Colonization	Neutral - no impact on colonization.
			Reproduction	Negative - fuel reduction reduced reproductive output. 19 fewer young between 2006-2019 than without fuels treatments. Fuel treatments may have caused small declines in occupancy and total reproductive output but these effects were minor compared to the effects of fire on occupancy and reproduction.
Jones et al. 2022 (2021b)	Lassen, Eldorado, Sierra, and Sequoia-Kings Canyon demographic study areas, 275 territories, modeled forward from 2035 -2064.	Wildfire and Fuel Reduction Modeling	Occupancy (single or pair)	Negative - Treatments that converted CWHR 5D to 5M negatively affected occupancy. "it is essential that large, old trees and core nesting/roosting areas within territories be maintained (Jones et al. 2018)" There were uniform benefits to midcentury occupancy when treatments were excluded from owl territories, compared to a no-treatment scenario. Benefits were greatest for CSO when treatments occurred on >40% of treatable lands including CSO territories (including PACs), but only when treatments were designed to avoid modifying large tree/high canopy cover forest in territories and PACs. More intensive treatments in CSO territories that altered CSO habitat by reducing canopy cover further reduced CSO occupancy and it took until midcentury or later for CSO population to recover.

Table 3. Summary of the results from studies on the effects of fire and salvage logging on spotted owl demographics.

Study	Study Location(s), Sample Size and Unit, and Period	Disturbance Type(s) Evaluated	Parameter	Response (Effect on Parameter)
Bond et al. (2002)	Shasta-Trinity, Klamath, San Bernardino, Coconino, and Gila National Forests, 11 burned and >300 unburned territories, 9-16 years for unburned and 1 year post-fire for burned territories.	Wildfire	Survival	Neutral - No difference in survival was detected between burned and unburned territories.
			Reproduction	Positive - Reproductive success was higher in burned territories the year following fire than in unburned territories. However these reproductive rates were well within the range of variation seen in these populations" (p. 1026).
			Fidelity	Neutral - No difference in fidelity was detected between burned and unburned territories.
Jenness et al. (2004)	Coconino, Gila, Coronado, and Lincoln National Forests, 33 burned and 31 unburned territories, 1-4 years	Wildfire and Prescribed Fire	Reproduction	Negative - Unburned territories tended to be occupied by pairs and more reproductive pairs than burned territories. Statistical significance measured at the P=0.11 level (not 0.05)
			Occupancy (single or pair)	Negative - Probability of occupancy was higher in unburned sites compared to burned sites. Statistical significance measured at the P=0.11 level (not 0.05)
Seamans and Gutierrez (2007)	Eldorado Demographic Study Area, 66 territories, 15 years.	High Severity Fire (including salvage), Logging	Extinction	Negative - Amount of mature conifer forest was negatively related to territory extinction probability, however it was not clear if this variation was due to variation among territories or to variation in mature conifer forest (Abstract).
			Colonization	Negative - Probability of colonization was related to the amount of mature conifer forest habitat in the territory and the alteration of such habitat reduced the probability of colonization. Also, alteration of ≥50 of mature conifer forest (70% canopy cover of 11" to ≥23" dbh trees) was negatively related to territory colonization (Abstract)
Clark et al. (2011)	Southwest Oregon, 23 radio-marked birds, years 3 and 4 post-fire.	Wildfire (including salvage)	Survival	Negative - Average annual survival of owls living inside burn perimeters (also salvage logged) was lower than outside the burn perimeters and was lower than survival rates of spotted owls in all other areas with survival estimates at the time of the study.
Roberts et al. (2011)	Yosemite National Park, 16 burned and 16 unburned territories, 2-14 years post-fire.	Wildfire and Prescribed Fire	Occupancy (pair)	Neutral - Fire did not reduce the probability of occupancy.
Lee et al. (2012)	Sierra Nevada-wide, 41 burned/145 unburned territories, up to 7 years post-fire.	Wildfire (including salvage)	Extinction	Neutral - No significant difference between burned and unburned sites in probability of local extinction.
			Colonization	Neutral - No significant difference between burned and unburned sites in probability of colonization.
			Occupancy (single or pair)	Neutral - No significant effect of high severity fire on occupancy.
Clark et al. (2013)	Southwest Oregon, 31 burned/103 unburned territories, up to 15 years pre-fire and 4-5 years post-fire.	Logging, High Severity Fire, Salvage Logging	Extinction	Negative - Probability of extinction increased due to the interactive effect of past timber harvest, high severity fire, and salvage logging.
			Colonization	Unclear - Few colonization events were observed.
			Occupancy (pair)	Negative - Declines in occupancy were driven by increases in extinction, attributable to past timber harvest, high severity fire, and salvage logging.
			Extinction	Positive - Average annual extinction probability was higher in burned territories, increased as the amount of habitat that burned at high severity increased, and increased as the amount of habitat that was salvage logged increased.

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Study	Study Location(s), Sample Size and Unit, and Period	Disturbance Type(s) Evaluated	Parameter	Response (Effect on Parameter)
Lee et al. (2013)	San Bernardino National Forest, 78 unburned/58 burned territories, 9 years for unburned and 8 years post-fire for burned territories.	High Severity Fire, Salvage Logging	Colonization	Negative - Mean annual probability of colonization was lower in burned sites than unburned sites, but was not affected by salvage logging.
			Occupancy (single and pair)	Negative - When >50 ha of forested habitat burned at high severity, site occupancy probability decreased by 0.003 for every additional hectare of forested habitat severely burned and post-fire salvage logging exacerbated the effect by decreasing occupancy probability an additional 0.05.
Tempel et al. (2014b)	Eldorado Demographic Study Area, 70 territories, 20 years.	High-intensity Logging, Wildfire (including salvage), and Medium-intensity Logging	Reproduction	Negative - Medium-intensity timber harvests were negatively related to reproduction. Reproduction was sensitive to modest amounts of medium-intensity harvests. This relationship was not statistically significant.
			Survival	Negative - Medium-intensity logging, when implemented in high canopy cover forests, was associated with reductions in survival.
			Extinction	Negative - Extinction was negatively correlated with the area of high-intensity timber harvest.
			Colonization	Negative - Medium-intensity logging, when implemented in high canopy cover forests, were associated with reductions in colonization.
			Occupancy (single or pair)	Negative - Equilibrium occupancy was negatively correlated with wildfire. This effect was stronger with future models consisting of increased fire intensity.
Lee and Bond (2015a)	Stanislaus National Forest, 45 territories, 1 year post-fire.	High Severity Fire	Occupancy (single and pair)	Neutral - Probability of occupancy of a single individual 1 year post-fire was relatively high, compared to other studies on the species in burned or unburned forest in the Sierra Nevada, with most sites being occupied by pairs.
Lee and Bond (2015b)	San Bernardino National Forest, 76 unburned/52 burned, 9 years for unburned and 4-8 years post-fire for burned territories.	High Severity Fire, Salvage Logging	Reproduction	Neutral - No significant effect of fire or logging on reproduction were detected.
			Occupancy (single or pair)	Negative - Occupancy was lower in burned vs. unburned sites and was further reduced by the amount of salvage logging that occurred.
Tempel et al. (2016)	Lassen, Eldorado, Sierra, and Sequoia-Kings Canyon demographic study areas, 275 territories, 19 years.	Wildfire (including salvage on National Forests), Prescribed Fire, Logging	Extinction	Negative - On the ELD study area, logging less than 1% of a territory in the previous 3 years was negatively correlated with extinction. Neutral - No support for an effect of logging less than 1% of a territory in the previous 3 years was detected for the LAS or SIE study areas. Positive - On the SKC study area, wildfire was negatively related to extinction. Neutral - No support for an effect of wildfire was detected on the ELD, LAS, or SIE study areas.
			Colonization	Neutral - No support for an effect of logging less than 1% of a territory in the previous 3 years was detected for the ELD, LAS, or SIE study areas. Negative - On the SKC study area, prescribed fire was negatively associated with colonization.
			Occupancy (single or pair)	Neutral - No support for an effect of logging when less than 1% of a territory was logged in the previous 3 years for the LAS, or SIE study areas. Positive - On the ELD study area, logging less than 1% of a territory in the previous 3 years was positively associated with occupancy.
	Eldorado demographic study area, 15 unburned/30 burned	High Severity Fire	Extinction	Negative - Probability of extinction increased as the proportion of high-severity fire increased and extinction was 7 times more likely in territories that burned with >50% high severity.

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Study	Study Location(s), Sample Size and Unit, and Period	Disturbance Type(s) Evaluated	Parameter	Response (Effect on Parameter)
Jones et al. (2016)			Colonization	Negative - Sites that burned at <50% high-severity were more likely to be colonized after the fire than unburned territories or territories that burned with >50% high severity.
			Occupancy (single or pair)	Negative - Probability occupancy was nine times lower for territories that burned with >50% high-severity fire effects than unburned sites.
Rockweit et al. (2017)	Klamath Province, 24 burned/70 unburned territories, 26 years for unburned and 4-26 years post-fire for burned territories.	Wildfire	Survival	Negative - As the total amount of high severity and moderate severity fire effects increased, apparent survival decreased.
			Recruitment	Neutral or Positive - There was no significant difference between post-fire recruitment rates and the control group, except for owls affected by wildfire in 2008, where recruitment rates increased.
Jones et al. (2019)	Simulated model of fuel reduction impacts to both extreme fire behavior and CSO demography across entire Sierra Nevada.	Simulated fuel treatments on public lands without operational constraints, about 35% of entire Sierra Nevada. Total treatment extent varying by 18%, 36%, 54%, 72% and 90%.	Severe Fire Area	Negative - Treatments reduced predicted severe fire area by 1.6% to 30.5% from 2035-2064, depending on treatment extent, treatment location, and climate scenario.
			Regional CSO Population with HRCA and PAC treatments	Weak Positive - There was a benefit to treating owl territories (HRCA and PACs) rather than excluding them from fuel reduction, but this regional population benefit was modest. *** FUEL TREATMENTS KEPT LARGE TREES/LARGER QMD ; QMD over 61cm and reduced existing high canopy cover to between 40-70% cover post-treatment.
			Regional CSO Population without HRCA or PAC Treatments	Positive - At the individual territory scale, treatments that avoided territories benefitted these territories to mid-century. These effects varied spatially according to G.Jones pers.comm with TNF 2/27/23; These benefits grew when fuel treatments included surface and ladder fuel treatments in HRCAs and PACs, but did not reduce habitat quality.
Jones et al. (2020)	ENF and TNF demographic study areas including 2014 King Fire. 23 owls tracked with backpack GPS units over 3 years post-fire.	Severe Wildfire and Salvage Logging	Population-Level Habitat Selection	Neutral - Severe fire (>75% canopy mortality) and pyrodiversity (mix of low, moderate and high severity fire) did not explain population-level habitat use. Weakly Negative - Effect of severe fire on foraging was negative, but confidence intervals included zero; effect of pyrodiversity was slightly positive but included zero with high degree of variability among individuals. Population-level habitat use was best explained by two factors: 1) distance to activity center and 2) avoidance of habitat with sparse cover pre-fire (<40% cc).
			Individual Habitat Selection	Variable and Scale-Dependent - Individual owls selected severely burned habitat only when it represented a small proportion of their home range (<5%) but avoided severely burned forest when it was more prevalent. Individual owls tended to select larger patches of severe fire when the average patch size was smaller than 115 ha. Owls selected smaller patches of severe fire when their home ranges contained larger patches severe fire. Individual response to severely burned forest varied significantly depending on individual level habitat availability (aka. functional availability of habitat). Forays into severely burned areas occurred at distances < 100 m. Salvage Logging Negative - Owls avoided post-fire logged areas, especially in large patches. Negative response to salvage logged areas was stronger than for just patches of severely burned forest alone.
			Occupancy	Neutral or Negative - Individual owls continued to occupy territories where <40% of territory was burned by severe wildfire. Territories were abandoned after that threshold.

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Schofield et al. (2020)	YNP 27 CSO territories: 12 within and 15 outside 2013 Rim Fire. 4 years of post-fire monitoring.	Wildfire	Occupancy	Negative Beyond a Threshold- Territories with greater than 30% severe fire were unoccupied post-fire. Maximum percent of occupied territory with high severity burn was 27%. Neutral- mean RdNBR (quantified burn severity) did not predict post-fire CSO occupancy. The only predictor of post-fire occupancy was a high pre-fire canopy cover at territory scale (similar to PAC ie.153 ha). Change in canopy cover or NDVI did not predict post-fire occupancy (NDVI is normalized difference vegetation index derived from LANDSAT). "Additional habitat variables [such as prey availability] may be important in mediating the consequences of high severity fire on owl persistence."
			Nesting	Neutral- mean RdNBR (quantified burn severity) did not predict post-fire CSO nesting rates. CSO nested after fire in similar numbers to before even though canopy cover and NDVI were lower. CSO nests or roosts (core areas) shifted from historical sites after fire, but there was little distinction between recent territories and the surrounding landscape.
Jones et al. (2021)	ENF and TNF demographic study areas including 2014 King Fire that burned 34 out of 83 owl sites. 6 ys post-fire monitoring at 4 spatial scales (nest 300m/ PAC 700m/ territory 1100m/ home range 1500m).	Wildfire and Salvage Logging	Site Persistence	Negative- Severe wildfire (>50% severe fire, defined as >75% canopy mortality) reduced probability of owl site persistence across all 4 spatial scales; strongest negative effect was at territory scale; odds of site persistence decreased for every 10ha increase in severely burned area. Positive or Neutral- a mosaic of burn intensity (<50% severe fire aka. pyrodiversity) increased probability of site persistence at 2 finer spatial scales, but had no effect on owl site persistence at 2 largest spatial scales. Salvage Logging Neutral- no effect of salvage logging on site persistence across all 4 scales.
			Colonization	Negative- Extensive severe fire reduced the probability of site colonization at all 4 spatial sales; strongest negative effect was at territory scale; odds of site colonization decreased as severely burned area increased. Mixed-Severity Fire Neutral- no effect on site colonization regardless of scale. Salvage Logging Neutral- no effect on site colonization across all 4 scales.
			Occupancy	Negative- Occupancy dropped sharply in the year after severe fire and then dropped again to near zero for next 5 years of study at home range scale. Neutral- sites that burned less severely had slight decrease in colonization probability the first year then stable for the next 5 years following burn. Neutral- site occupancy of unburned sites remained stable or slightly increased compared to 25-year pre-fire decline in occupancy in demography study.
Wood et al. (2021c)	Statistical power analysis of remote monitoring as a tool to detect hypothetical population impacts from simulated wildfire events using 72 remote monitoring scenarios.	Remote Monitoring After Wildfire Event	Ability to Detect an Effect of Fire on Occupancy (hypothetical species)	Positive- Statistical power to not underestimate the effect of a megafire on site occupancy was fairly high overall. Negative- statistical power to accurately identify the correct population response was low. Power to correctly estimate site occupancy was also low.
			Ability to Detect Effect of Fire on BBWP and CSO Populations	Positive- Case-study simulations based on existing ARU (autonomous recording unit) monitoring in the Sierra Nevada indicate that there are enough sampling stations to accurately detect an impact of wildfire on populations of CSO or BBWP. Negative- Existing ARUs are inadequate to describe any nuance in population level impacts or accurately detect trends in site occupancy for CSO or BBWP.
Tempel et al. (2022)	Southern CSO population on San Bernadino and Angeles NFs: 1991-	High severity fire burned 17% of 40 CSO territories	Occupancy (single or pair)	Negative- High severity fire accounted for 9.6% decline in long term occupancy. Additional causes of decline should be investigated. Low to moderate severity fire impacts were drawn from a small sample size (6 territories), so caution should be taken in interpreting the results, however low to moderate severity fire had an unexpected negative impact on initial probability of occupancy. This may be related to prey availability if dusky footed woodrat in this study were impacted they way desert woodrat were by fire in southern CA woodlands in another study.

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	Angies Mts, 1991-2019	territories combined.	Colonization	Negative - As area burned by severe fire approached 40%, territory occupancy was reduced to zero.
			Reproduction	Low-moderate Severity Fire Negative - 141 fewer young in territories that experienced low to moderate severity fire in past 10 years. This data was from a small sample size of 6 territories.

Literature Cited

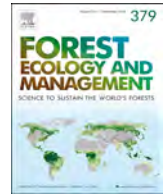
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Resource selection by GPS-tagged California spotted owls in mixed-ownership forests



Fidelis A. Atuo^{a,*}, Kevin Roberts^b, Sheila Whitmore^a, Brian P. Dotters^b, Martin G. Raphael^c, Sarah C. Sawyer^d, John J. Keane^e, R.J. Gutiérrez^a, M. Zachariah Peery^a

^a Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA

^b Sierra Pacific Industries, PO Box 496014, Redding, CA, USA

^c USDA Forest Service, Pacific Northwest Research Station, Olympia, WA, USA

^d USDA Forest Service, Pacific Southwest Region, Vallejo, CA, USA

^e USDA Forest Service, Pacific Southwest Research Station, Davis, CA, USA

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ABSTRACT

The relative contribution of private and public forest to the conservation of species in mixed-ownership landscapes has often been contentious because management goals vary among owners. This tension can be exacerbated by a lack of understanding about how wildlife use habitats managed by different landowners and the relative value of habitats in having different structures, configurations, and management histories. To address this knowledge gap and enhance science-based conservation planning among different ownerships, we analyzed habitat selection by 53 GPS-tagged California spotted owls across multiple temporal scales within mixed-ownership landscapes in the Sierra Nevada. At a fine temporal scale, step-selection function analysis of hourly locations collected by GPS tags suggested that foraging spotted owls selected closed-canopy, larger-tree forest (Quadratic Mean Diameter [QMD] ≥ 33 cm, canopy cover $\geq 60\%$). Point selection function (PSF) analysis based on single nightly locations suggested that spotted owls selected a broader range of forest conditions including selection of forests having intermediate sized trees and intermediate canopy cover (QMD 28–33 cm, canopy cover $\geq 50\%$), and the strength of selection for these forest conditions increased in the less frequently used areas of home ranges. The PSF also suggested that spotted owls selected areas with relatively high cover type heterogeneity that included a mix of seral stages, except in the core of their home range where they selected relatively spatially homogenous forests characterized by large trees and closed canopy. Spotted owl home ranges increased in size with increasing elevation and cover type heterogeneity, and decreased in size with forest characterized by intermediate-sized trees. Collectively, these results indicate that landscapes having forest patches characterized by either intermediate or large-sized trees, both with high canopy cover, likely constitute the important foraging habitat for California spotted owls in Sierra Nevada mixed conifer forests. However, selection for any one particular cover type was not sufficiently strong for us to infer selection of individual landownership types, in spite of differences in forest conditions among ownerships. Collectively, our findings suggest that privately-owned lands used in our study may harbor more suitable spotted owl foraging habitat than previously recognized. Finally, given the importance of understanding the relationship between landowner management priorities and the resultant pattern of vegetation on lands with different ownerships, the development of forest management strategies relevant for broad-scale conservation of the Sierra Nevada forest will benefit from effective collaboration between forest managers, landowners, and research organizations.

1. Introduction

Balancing forest resource use and species conservation objectives has become a dominant theme in forest science and management (Chaudhary et al., 2016; Heikkala et al., 2016; Moussaoui et al., 2016).

Achieving these sometimes conflicting objectives can be difficult in mixed-ownership (private and public) landscapes because forests are managed according to different priorities, silvicultural practices, and regulatory mechanisms (Thomas, 1990; Christensen et al., 1996; Bergmann and Bliss, 2004). Typically, publicly-owned forests are

* Corresponding author.

E-mail address: atuo@wisc.edu (F.A. Atuo).

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managed for a suite of objectives such as timber production, species conservation, watershed integrity, fuels management, and recreation, whereas privately-owned industrial forests are more often managed with an emphasis for commercial timber production. Spatial pattern of landownership can further challenge conservation when, for example, private lands occur in close proximity to public lands such that species use both ownership types. Despite such patterns, the relatively large global expanse of privately-owned forestlands suggests that conservation focused solely on habitat protection on public lands may be insufficient in many places to achieve species conservation objectives (Chaudhary et al., 2016). Therefore, encouraging and incentivizing private, industrial forest owners to promote species conservation during commercial timber management is considered a key component in maintaining global biodiversity (Knight, 1999).

The contribution of privately-owned forests to biodiversity conservation depends on timber management strategies that retain contributions to habitat quantity, quality, and connectivity for species of concern. Effective conservation planning in such landscapes requires an understanding of: (1) how species use different landownerships to meet their life-history requirements, and (2) what constitutes high-quality habitat in forests that are often markedly different in species composition, structure, and management histories. Addressing these questions can provide a strong scientific basis for cooperative forest management in mixed-ownership landscapes that leads to both species conservation and economic opportunities. Effective species conservation in mixed-ownership forests, however, is often hampered by a lack of research on private lands stemming from landowner concerns about regulatory actions that might result from research findings (Dale et al., 2000; Norton, 2000; Mir and Dick, 2012). Therefore, effective conservation efforts among private landowners, government agencies, and researchers will benefit from being both transparent and collaborative (Selin and Chevez, 1995; Wondollick and Yaffee, 2000).

The California spotted owl (*Strix occidentalis occidentalis*) is one of the three subspecies of spotted owls recognized by the American Ornithologists' Union (1957). It occurs primarily in mature closed-canopy forests that are multistoried or complex in structure with abundance of large trees and large coarse woody debris (Gutiérrez et al., 1995; Verner et al., 1992a; Roberts, 2017). In the Sierra Nevada, most spotted owls are concentrated in mid-elevation mixed-conifer forests, but they also occur at lower density in lower and higher elevation forests (Gutiérrez et al., 1992; Roberts, 2017). Although the California spotted owl is not listed as a threatened/endangered species at the federal level, it is a “species of special concern” at the state level, and has experienced a steady population decline on demographic study areas within national forests over the last 20 years (Gutiérrez et al., 2017). Habitat loss and fragmentation from forest management and high-severity fire and competition with the barred owl (*Strix varius*) have been identified as threats to the owl (Eyes et al., 2017; Jones et al., 2016; Keane, 2017).

Until recently, it has been assumed that successful conservation planning for the California spotted owl hinged primarily on management within national forests, whereas private lands were believed to make a relatively modest or unknown contributions to its population viability (Verner et al., 1992a; Peery et al., 2017). However, early studies demonstrated that spotted owls selected public lands over private lands for both nesting and roosting in a mixed-ownership in the central Sierra Nevada (Bias and Gutiérrez, 1992; Gutiérrez, 1994) and owls had a 15% higher probability of using publicly- than privately-owned lands for foraging (Williams et al., 2014). By contrast, a recent study found that California spotted owl had relatively high occupancy rates and crude densities in a set of landscapes composed primarily of private lands (Roberts et al., 2017). Therefore, we studied resource selection and space use by California spotted owl during putative foraging activities in a landscape containing public and private lands to understand the contributions of mixed-ownership forests to spotted owl conservation in the Sierra Nevada. Previous studies have characterized

foraging habitat and space use by California spotted owls (Call et al., 1992; Williams et al., 2011, 2014; Eyes et al., 2017; Gallagher et al., 2018), but our study represents an important advance in the understanding of spotted owl habitat selection in several respects. First, we characterized habitat selection patterns using a sample size of individuals that was considerably greater than prior studies and included individuals distributed across relatively broad environmental gradients (e.g., latitude, elevation, forest types, and landownerships). Second, individuals were marked with GPS tags capable of collecting multiple locations per night, whereas VHF radio-telemetry requires physically tracking individuals in rugged terrain and typically yields fewer locations. By collecting several locations per night, we are able to characterize fine-scale (within-night) habitat selection patterns for the first time in this species, an important advance given that the ecological factors that modulate organisms' habitat choices are often structured across ecological scales that vary in space and time (Turner, 1989; Kotliar and Wiens, 1990; McGarigal et al., 2016). Third, GPS tags typically yield more precise locations compared to VHF telemetry, which is particularly important when studying habitat selection in landscapes characterized by fine-scale heterogeneity in habitat and landownership conditions, as is the case in the Sierra Nevada. Finally, habitat selection was inferred based on a vegetation map that we developed using a combination of dense vegetation sampling and high resolution aerial imagery that provided a highly accurate depiction of habitat conditions within owl home ranges. Hence, these advances should provide novel insights into habitat selection and thus allow a stronger scientific basis for spotted owl conservation planning in mixed-ownership landscapes.

2. Materials and methods

2.1. Study area description

Our study areas occurred in the Sierra Nevada in Tehama, Eldorado, Butte, Plumas, Yuba, Sierra, Nevada, Placer, Amador, and Calaveras counties and included the Tahoe, Eldorado, Plumas, and Stanislaus National Forests. Mixed conifer was the primary forest type on all study areas, which had a dominant tree canopy of Douglas fir (*Pseudotsuga menziesii*), ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), black oak (*Quercus kelloggii*), live oaks (*Quercus chrysolepis* and *Q. wislizeni*), Pacific madrone (*Arbutus menziesii*), and incense-cedar (*Calocedrus decurrens*) (Mayer and Laudenslayer, 1988). Elevations ranged between 400 and 2200 m. The climate was Mediterranean with an average of 1182 mm of precipitation most of which fell as snow (Tempel et al., 2015). These landscapes contained a mosaic of publicly-owned national forests managed by the US Forest Service, large privately-owned forests managed for commercial timber production, and smaller privately-owned parcels managed for other uses (Fig. 1). Sierra Pacific Industries (SPI) was our cooperating private landowner and managed 49% of the area encompassing the owl home ranges we used in this study. The US Forest Service managed 40% of these areas with the remaining 11% managed by small private landowners. Logging began in the Sierra Nevada in the late 19th century and involved the selective removal of large, commercially valuable trees. Recent logging has emphasized “diameter-limited thinning from below” on national forests while even-aged management practices such as clear-cutting and groups selection is predominant on private lands (North et al., 2017). Timber harvesting and fire suppression on national forests have resulted in spatially homogenous forest cover with high tree densities and a “large-tree deficit” (Jones et al., 2018), whereas timber harvesting on privately-owned lands typically has resulted in a mosaic of different-aged forest stands (Baker, 2014; North et al., 2017; Jones et al., 2018). Clear-cuts often result in abrupt successional differences between regenerating forest stands on private and more mature – albeit spatially homogeneous forest cover on public lands (Bias and Gutiérrez, 1992; Fedrowitz et al., 2014; Williams et al., 2014). Finally, wildfires have affected forest structure on some of these areas, particularly the 2014

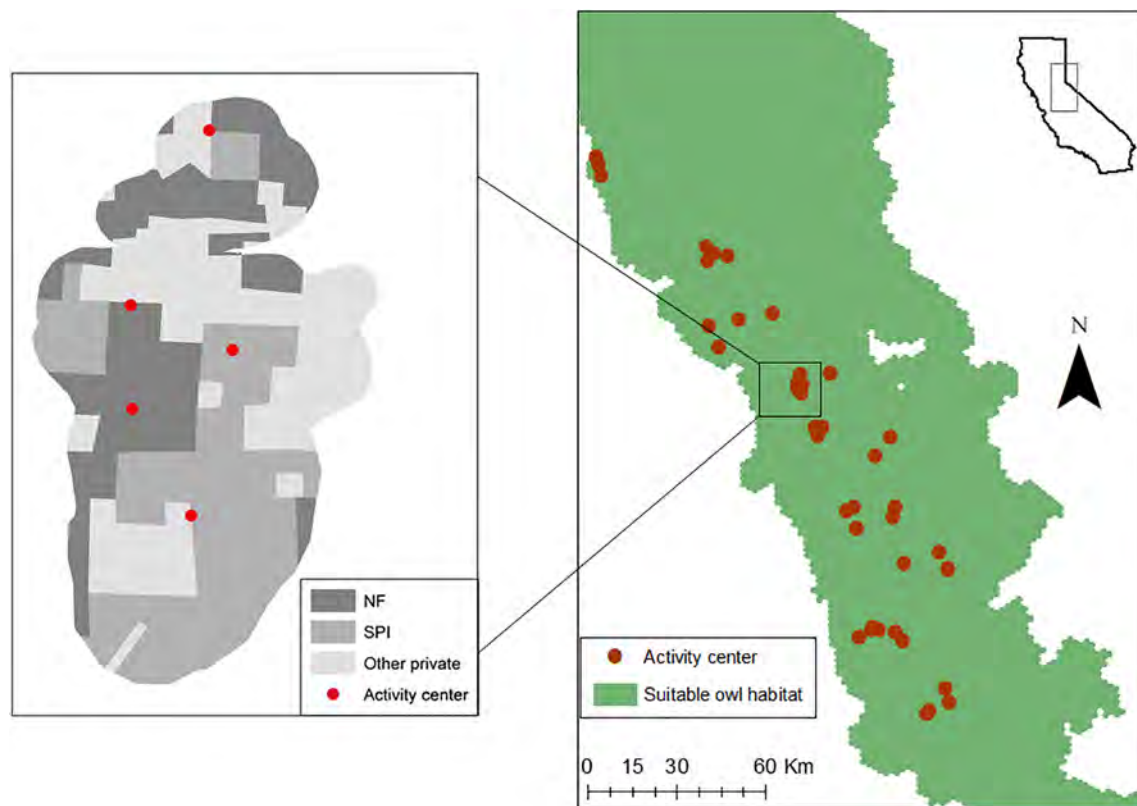


Fig. 1. California spotted owl study area showing activity centers of 53 GPS tagged owls in the Sierra Nevada, California, USA. Study area boundary was based on the 95% kernel home ranges of 53 individual owls. The suitable owl habitat (area in green) is based on the U.S Forest Service, Pacific Southwest Research Station's delineation (Keane unpublished data). The insert illustrates patterns of landownership in the study area.

King Fire that severely burned parts of several owl sites included in this study (Jones et al., 2016; see below).

2.2. Owl captures and monitoring

We captured and monitored 53 GPS-tagged California spotted owls during the breeding season (April–July) of 2017 (Fig. 1). Territories in which owls were selected for telemetry monitoring were chosen opportunistically but spanned a broad range of elevation, landownership, and vegetation conditions, which we believed represented conditions used by owls throughout the ecoregion (Fig. 2). We captured owls by hand and with snare poles as described by Franklin et al. (1996) prior to or early in the nesting season and fitted them with remotely-downloadable GPS tags (Lotek Wireless, model Pinpoint VHF 120) weighing approximately 10 g (< 2% of average California spotted owl body mass). Tags were either attached using a backpack harness or as tail mounts and were either retrieved by recapture at the end of the study or expected to be shed during molt, respectively. Tags were programmed to obtain hourly locations from 22:00 to 02:00 every night. Spotted owls are nocturnal predators that forage by moving from perch to perch (Forsman et al., 1984; Delaney et al., 1999) and we therefore assumed that most GPS fixes represented foraging locations, acknowledging that owls engage in other activities at night including resting, territory defense, and prey delivery to nests. We remotely downloaded data from GPS tags every 3–4 weeks. We removed all locations with a DOP (dilution of precision) score > 5 (resulting from poor satellite signals) prior to analysis to avoid potential erroneous inference about space use and movement. We defined activity centers for each GPS-tagged owl, in order of priority, based on the location of a (i) nest and (ii) the geometric center of all daytime (i.e., roosting) locations obtained as part of capture attempts and GPS data retrieval.

2.3. Cover type mapping

We mapped cover types within the 95% kernel home range (see home range estimation below) of each GPS-tagged owl (10,165 km²) to determine conditions within home ranges rather than broader, landscape-scale mapping of areas outside of home ranges. Thus, our habitat analyses corresponded to a third-order habitat selection by owls (sensu: Johnson, 1980). To take advantage of the extensive and fine-scale habitat information collected regularly by SPI for timber management purposes, we delineated and classified homogeneous patches of forest cover according to SPI's systematic forest inventory protocols (SPI's Cruise Manual available upon request from SPI), with cover types defined based on tree size (quadratic mean diameter; QMD) and canopy cover (see Table 1). We mapped seven cover types, but only retained four (HF1, HF2L, HF2H, HF4; see Table 1 for definitions and Fig. 2a–d) for resource selection and space use analysis because the other three cover types (HF0, HF3, and HF5; see Table 1 for definitions) comprised a small fraction (< 3%) of the landscape and are less frequently used by spotted owls (Jones et al., 2016; Robert, 2017). We classified areas severely burnt by the King Fire (Jones et al., 2016), early seral forest with QMD < 13 cm in replanted clear-cuts, and smaller unmapped patches of residual large trees serving as habitat retention areas within owl home ranges were included in the HF1 cover type (Table 1). HF1 comprised 13% of the landscape, with 91% of that being open areas and 9% high-severity burn areas within the King Fire perimeter. The proportion of the four cover types we used in our analyses varied among landownerships. HF4 was the dominant cover type in the landscape, respectively accounting for 58%, 45%, and 57% of national forests, SPI-owned lands, and other privately-owned lands (Fig. 2e). Other cover types also differed among landownerships with the proportion of HF1 and HF2L being greatest on SPI-owned lands (Fig. 2e).

On SPI-owned lands, a variable-radius vegetation plot was sampled

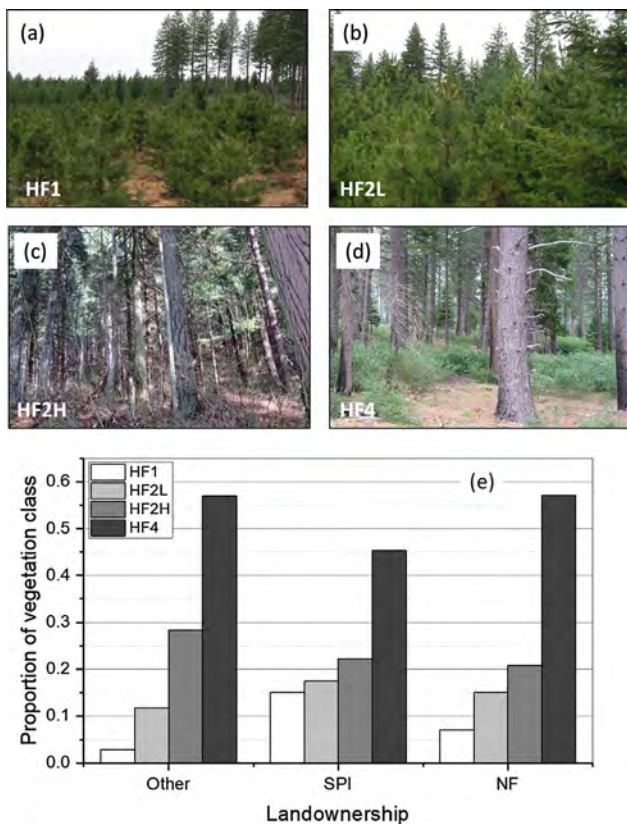


Fig. 2. (a–d) Primary cover types present in the study area, with definitions provided in Table 1. Photos were taken in spring of 2017. (e) Proportion of study areas in different cover types and landownership categories.

approximately every 1.6 ha in which the diameter at breast height (dbh) of trees was measured using Basal Area Factor forestry prisms (Monserud and Sterba, 1996; Burkhart et al., 2018). We used similar approaches on national forests, but tree estimates were based on lower density of sample of plots ~1 every 8 ha ($n = 587$). Plots were randomly selected but restricted to areas having road access. Therefore, sampling plots on private lands were more evenly distributed compared to public lands. We estimated canopy cover based on tree species and diameters calculated from crown diameter measurements of

trees ≥ 13 cm dbh. We then modeled the vertical projection of stand canopy cover using the inventory plot tree list and the canopy index (SPI unpublished data). Additionally, we used drone flights to gather local aerial imagery and videography of the land to estimate canopy cover on national forest lands and ensure that habitat typing from the most recent ortho-photos (2016 National Agriculture Imagery Program imagery) was accurate. We extrapolated forest stand information from the aggregate of 10 sampling points in a 16-ha vegetation polygon. When ownership fell on private lands outside SPI ownership and plot data was unavailable, we relied on ortho-photo interpretation, and visual assessments when possible, to classify cover types.

We developed topographical variables using 30-m resolution Land Management Unit (LMU) layers that were developed for the Sierra Nevada using the LMU Tool version 2 (North et al., 2012), which is a raster-based GIS tool that partitions a landscape into basic topographic categories. We identified six categories: (i) ridge; (ii) canyon/drainage bottom; (iii) NE midslope $< 30\%$; (iv) NE midslope $> 30\%$; (v) SW midslope $< 30\%$; and (vi) SW midslope $> 30\%$. We obtained data on the distribution of roads and streams from the United States Forest Service data portal (<https://www.fs.usda.gov/main/r5/landmanagement/gis>) and calculated their proximity to owl locations and random locations within 95% kernel-defined home ranges.

2.4. Resource selection and space use

We analyzed resource selection and space use at three different temporal scales using locations derived from GPS-tagged spotted owls. For our “fine” scale, we characterized patterns of selection for various habitat characteristics based on all locations (~5 per night collected at hourly intervals) obtained by the GPS tags. We used integrated Step Selection Analysis (iSSA; Avgar et al., 2016) to compare habitat characteristics at used and available locations when the individual animal’s “choice” of habitats is conditional on where it previously occurred on the landscape. At an intermediate scale, we used a Point Selection Function (PSF) approach (Manly et al., 2007; Zeller et al., 2012) to assess selection of putatively independent foraging locations obtained on different nights given that hourly locations used in the iSSA may or may not be an appropriate time interval to capture independent foraging decisions made by spotted owls as they leave their daytime nesting and roosting sites to engage on nocturnal foraging activities (see Thurfjell et al., 2014). At the broadest scale, we related the size of home ranges during the breeding season home ranges to spatial forest conditions, with the expectation that larger home ranges are indicative of lower

Table 1

Descriptions of variables used to model resource selection by California spotted owls in the Sierra Nevada, California, USA, 2017. QMD = quadratic mean diameter and CC = percent canopy cover.

Variable	Definition
HF0	Lakes, marshlands, and wide streams
HF1	Early seral with QMD < 13 cm or severely burned forests with smaller unmapped patches of residual large trees
HF2L	Forests with small trees (QMD: 13–28 cm) and CC $\geq 40\%$
HF2H	Forest with intermediate trees (QMD: 28–33 cm) and CC $\geq 50\%$
HF3	Forest with various tree size (QMD ≥ 13) and CC $< 40\%$
HF4	Forests with large trees and high canopy cover: QMD ≥ 33 cm, CC $\geq 60\%$, > 22 tree per hectare > 56 cm DBH
HF5	Bare (exposed rock, cliffs, quarries)
NF	Publicly-owned land managed by the US Forest Service
SPI	Land owned and managed by Sierra Pacific Industries
Other	Land owned and managed by other private landowners
LMU	Land Management Unit. A categorical variable with 6 levels: (i) ridge, (ii) canyon/drainage bottom, (iii) NE midslope $< 30\%$, (iv) NE midslope $> 30\%$, (v) SW midslope $< 30\%$, and (vi) SW midslope $> 30\%$.
Hindex	Shannon-Wiener index of the proportion of habitat form (HF) in a 100-m radius centered on a used or available point
Elev	Elevation gradient associated with a relocation or available point
dist.stream	Euclidian distance from a relocation or random available point to the nearest stream
dist.road	Euclidian distance from a relocation or random available point to the nearest road
dist.edge	Euclidian distance from a relocation or random available point to the nearest hard edge
Hab	A categorical variable containing HF1, HF2L, HF2H, and HF4
Own	A categorical variable with 3 landownership variables: NF, SPI, and other

habitat quality (e.g., lower prey density) than smaller home ranges (Zabel et al., 1995; Glenn et al., 2004). Collectively, this multi-scale approach was expected to yield insights into how forest conditions influence spotted owl foraging activities across several temporal scales.

2.5. Data analysis

In our iSSA analysis, we tested for patterns in resource selection with a use-versus-available study design where available habitat associated with a given owl location was conditional on where the individual occurred at the time of the previous GPS location in the same night. For available locations, we generated 10 random steps for each observed hourly step made by owls. We randomly generated turn angles (in radians) for available steps from a uniform distribution of $-\pi$ and π (corresponding to non-directional random walks; Prokopenko et al., 2017). We generated step lengths by randomly drawing lengths from a frequency distribution derived from observed hourly steps made by GPS-tagged owls using the package *amt* 0.0.4.0 (Signer et al., 2018) in program R version 3.4.1 (R Core Team, 2015). We estimated the probability of selection using conditional logistic regression analyses with owl location (coded as “1”) versus available location (“0”) as the response using the package *survival* 2.41-3 (Therneau, 2015). The conditional logistic regression approach provided maximum likelihood estimates of resource selection coefficients and their sampling errors (Fortin et al., 2005; Hooten et al., 2017). We treated each cover type and landownership category (i.e., each of the four cover types and the three landownership categories listed in Table 1) as binary variables in the iSSA model (Stockwell and Peterson, 2002). Specifically, we set the value of the cover type or landownership category to 1 when the used or random point occurred within the cover type or landownership category in question, and 0 if not. We also included the following variables in conditional logistic regression models: (i) distance to streams and roads as linear or logarithm Euclidian measurements from the owl or random location; (ii) linear or logarithmic distance to a hard edge (defined as a boundary between HF2H or HF4 and any other habitat class; and (iii) landownership (national forest, SPI, or other). We ranked a set of 12 *a priori* models based on different combinations of these variables according to their AIC values adjusted for small sample size (Burnham and Anderson, 2002) using the MuMIn package (Bartoń, 2016). We considered a model to be competitive for explaining resource selection if $\Delta AIC < 2$, providing its parameters were not simply variants of those in the best model plus one or more uninformative parameters (Arnold, 2010). Following Cade's (2015) criticisms of model averaging, we avoided averaging model parameter estimates to reduce uncertainties that may arise from correlations among independent variables. Indeed, for compositional analysis, independent variables are often correlated such that the behavior of one variable may be dependent on other variables present in a model biasing parameter interpretations (Cade, 2015; Banner and Higgs, 2017). We evaluated the influence of individual predictors within the best supported models by examining predictor effects sizes and their 95% confidence limits (Burnham and Anderson, 2002; Arnold, 2010). We considered a predictor variable as having a strong effect if its 95% confidence interval did not overlap zero.

In our PSF analysis, we also quantified resource selection using a use-versus-availability study design (Manly et al., 2007), but randomly selected one GPS location per individual per night, such that dependence of locations was reduced. We stratified our random points such that the number of random points was equal to the number of owl locations within each quantile of the owl's fixed kernel home range (see home range estimation below) and conducted selection analyses for both the entire dataset and for individual utilization distribution categories (see below) to examine how habitat selection patterns varied among more- vs less-frequently used areas of the home range. We used the same cover types, landownership categories, and proximity variables as in the fine-scale analysis above, but we also included the

categorical topographic variable LMU and an index of cover type heterogeneity. We used the Shannon-Wiener Index to estimate heterogeneity based on the proportion of each cover type within a 100-m circular buffer centered on each selected owl location and each randomly generated location (reported as Hindex in tables). Thus, our heterogeneity measure was restricted to the major vegetation cover types in our study system and did not account for possible within-stand variation in forest structure. We chose 100-m radius as being sufficiently broad to capture the diversity of vegetation cover type around a used or available location, but still sufficiently small to capture movement patterns. In this analysis, we treated cover type, landownership category, and LMU as categorical variables with multiple levels. For ease of interpretation, we avoided the conditional logistic regression approach required in the iSSA modeling approach as it does not allow for the estimation of an intercept and makes interpretation of categorical effects greater than two difficult (Agresti, 2003). Rather, we fitted PSFs using a Generalized Linear Mixed Model (GLMM) framework treating the response variable as binomially distributed and individual owl as a random effect. We then conducted model selection in the same manner as for the iSSA analysis.

For analyses of spotted owl home range size, we calculated 95% kernel home ranges for each owl based on GPS data using the package ‘adehabitatHR’ (Calenge, 2006) in Program R as well as the 0–10%, 11–25%, 26–50%, 51–75%, 76–95% isopleths of kernel density for use in the analyses described above. The choice of a suitable bandwidth (smoothing factor) is a key consideration when applying the kernel method (Silverman, 1986) so we used the reference bandwidth because our data distribution was bivariate normal (each owl had single centers of activity). This bandwidth minimizes discrepancy between true and estimated utilization distribution (Seaman and Powell, 1996). To examine variation in spotted owl home range size as a function of habitat conditions within the home range, we fitted GLMs with the size (ha) of the 95% kernel home range as the dependent variable and proportional landownership, cover type variables (i.e., the proportion of each cover type in home ranges), and elevation as independent variables in candidate models. We computed elevation of an individual home range as the mean elevation associated with all owl locations within the home range. We also estimated the Shannon-Weiner Index using cover type classes within the home range and included this index as a variable in our model to evaluate the potential benefits of habitat heterogeneity to owls (Table 1). At all scales, we performed Pearson correlation analyses to identify and remove highly correlated variables ($|r| \geq 0.6$) from the same model.

3. Results

We captured and tracked the movements of 53 individual California spotted owls between April–July during 2017. The activity centers of 23 individuals were located on national forests, 29 were on lands owned by SPI, and 1 was on other privately-owned lands. We collected 10,651 locations (median = 213, range 17–267) over an average 58-day individual-owl monitoring period (range: 16–85). We collected a median of 4 (range: 0–5) locations per night and a median of 87 nights with at least one location.

3.1. Fine-scale resource selection based on conditional selection (iSSA)

We obtained 4278 steps for 51 individuals (median = 85; range = 36–112) for our iSSA analysis after removing two individuals that had insufficient locations (i.e., 19 and 17) for analysis. Table S1 provides summary statistics for all covariates considered in this study. Based on the iSSA, spotted owls selected forests with larger trees and high canopy cover (i.e., HF4) and national forest lands (iSSA coefficient NF: 0.14, 95% CL: 0.01–0.26; HF4: 0.12, 95% CL: 0.05–0.19; Table 2). Lands owned by SPI were also in this top model with owls exhibiting positive selection for this landownership (Table 2), but the 95%

Table 2
Rankings of iSSA models of fine-scale habitat selection by California spotted owl in the Sierra Nevada, USA.

Model	df	logLik	ΔAIC	ω
HF4 + NF + SPI	3	−14392.80	0.00	0.41
HF4	1	−14395.18	0.76	0.28
HF4 + NF + SPI + dist.edge	5	−14391.62	1.63	0.18
HF4 + HF2L + HF1	3	−14394.59	3.57	0.07
HF4 + HF2L + HF1 + HF2H + dist.edge + dist.road + dist.stream + NF + SPI	8	−14390.85	6.09	0.02
dist.edge + NF + SPI + HF2H	4	−14395.58	7.55	0.01
dist.edge + SPI + HF2H + other	4	−14395.58	7.55	0.01
HF1	1	−14398.81	8.02	0.01
dist.edge + SPI + HF2H + other + NF + dist.road	5	−14395.19	8.78	0.01
dist.road	1	−14399.42	9.24	0.00
NF	1	−14399.66	9.72	0.00
dist.edge + NF + other + dist.road + dist.stream	5	−14396.08	10.55	0.00
Null	0	−14401.27	10.94	0.00

Starting AICc value = 28791.60.

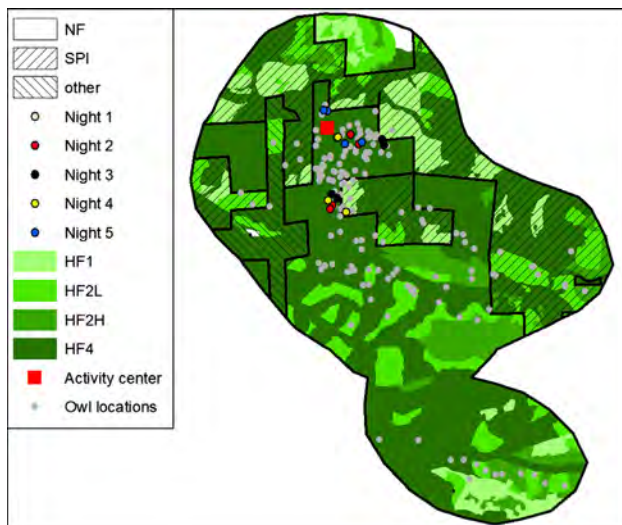


Fig. 3. Distribution of GPS locations within 95% kernel home range across different cover types and landownership categories. Circular symbols of the same color indicate locations collected on a single night for five different nights and grey symbols represent locations from all other nights.

confidence intervals associated with this parameter estimate overlapped zero (0.10, 95% CL = −0.03 to 0.23). Fig. 3 shows GPS locations of an adult male California spotted owl within 95% kernel home range across difference cover types and landownership categories.

3.2. Intermediate-scale resource selection based on point selection function (PSF)

We used 2938 putatively independent nightly locations among 53 individuals for our PSF analysis. Spotted owls selected forests with large trees and intermediate-sized trees (HF2H and HF4), lands owned by SPI, and locations that had high spatial heterogeneity in cover type composition (Table 3). This model had an AIC weight of 0.57 and there were no competing models. Based on this model, odds ratios indicated that cover types HF4 and HF2H were 1.94 and 1.67 times more likely to be selected than HF1, respectively. Moreover, selection coefficients for both of these classes were greater than the coefficients associated with HF1 and HF2L (Fig. 4a). We conducted a *post-hoc* analysis where we treated each cover type as a binary variable (i.e., we set the value of the cover type to 1 when the used or random point occurred within the cover type in question, and 0 if not) in a separate model. This model indicated selection for HF4 and HF2H (HF4: 0.60, 95% CL: 0.40–0.80; HF2H: 0.47, 95% CL: 0.27–0.67); HF2L was selected in proportion to availability (0.05, 95% CL: −0.19 to 0.29), and HF1 was selected

Table 3

Rankings of PSF models of intermediate-scale habitat selection by California spotted owl in the Sierra Nevada, USA. Variable abbreviations are explained in Table 1.

Model	df	logLik	ΔAICc	ω
hab + Hindex + own	8	−5598.29	0.00	0.57
dist.edge + dist.stream + hab + Hindex + own	10	−5597.47	2.37	0.18
dist.edge + hab + Hindex + LMU	12	−5595.57	2.58	0.16
dist.edge + dist.stream + Hindex	8	−5601.19	5.80	0.03
dist.edge + hab + LMU	11	−5598.36	6.16	0.03
hab + LMU	10	−5599.90	7.23	0.02
hab	5	−5605.27	7.96	0.01
dist.edge + dist.stream + hab + LMU	12	−5598.36	8.16	0.01
dist.edge + dist.stream + dist.road	5	−5641.24	79.88	0.00
Null	2	−5645.30	82.00	0.00

Starting AIC value = 11212.60.

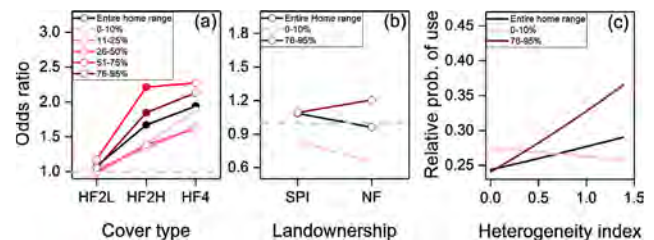


Fig. 4. Odds ratios from California spotted owl resource selection function models (a) for three cover types relative to HF1, (b) two landownership categories relative to “other”, and (c) relative probability of use as a function of habitat heterogeneity. Plotted are odds ratios for selection patterns across the entire home range and for individual utilization distributions when effects were supported in PSF models. The dashed lines at a value of 1 indicate equal odds of selecting a cover type or landownership category relative to the reference level. A closed circular symbol for a given cover type or landownership category indicates that the associated coefficient is significantly greater than the coefficient for the preceding coefficient (e.g., a closed circular symbol for HF4 indicates that the coefficient for this level is significantly greater than the coefficient for HF2H).

against relative to availability (−0.50, 95% CL: −0.68 to −0.32). Although the top model indicated selection for SPI-owned land, selection coefficients did not differ significantly between SPI-owned lands and national forests (Fig. 4b). Finally, spotted owls appeared to select areas with greater cover type heterogeneity as the relative probability of use increased with the heterogeneity index (0.17, 95% CL: 0.04–0.30; Fig. 4c).

Resource selection patterns among the five utilization distribution categories reinforced the importance of cover type as this variable was present in the top model for each category (Table S2). As was the case

when the entire home range was considered, odds ratios for HF4 and HF2H – relative to HF1 – exceeded 1 for all home range distribution categories (Fig. 4a). Notably, odds ratios were greatest for these two cover types in the 51–75% and 76–95% utilization distribution categories and reached as high as 2.21 and 2.27 for HF2H and HF4, respectively. Thus, in these categories, spotted owls were almost two and half times more likely to select these two cover types than HF1. Odds ratios for HF2L – relative to HF1 – were low and always ≤ 1.18 . Landownership was present in the top model for both the 0–10% and 76–95% utilization distribution categories (Table S2), although odds ratios indicated that patterns of selection for the three landownerships were inconsistent and selection coefficients were not significantly different (Fig. 4b). The heterogeneity index was present in the top model for both the 0–10% and 76–95% utilization distribution categories (Table S2). The relative probability of use tended to decrease with increasing cover type heterogeneity in the 0–10% category, although confidence intervals overlapped zero (-0.06 , 95% CI: -0.36 to 0.22), and increased with increasing cover type heterogeneity in the 76–95% category (0.43 , 95% CI: 0.10 – 0.76 ; Fig. 4c).

3.3. Correlates of home range size

Median home range size was 931.6 ha (range = 195.1–4280.7; $n = 53$) with males (1206.8 ha; range = 273.7–4280.7; $n = 33$) having larger home ranges than females (median 659.1 ha; range = 195.1–1828.5; $n = 20$; $F_{(1, 51)} = 7.7$, $p = 0.007$). Home range size increased with spatial heterogeneity and elevation, and decreased with the amount forest with intermediate-sized trees (HF2H; AIC model weight = 0.51; Table 4, Fig. 5). The only competing model contained all these variables plus one uninformative variable – national forest lands (Table 4). Parameter estimates associated with all three variables in the top model had 95% confidence intervals that did not overlap zero (HF2H: -0.24 , 95% CI: -0.41 to -0.06 ; elevation: 0.17 , 95% CI: 0.01 – 0.33 ; heterogeneity index: 0.35 , 95% CI: 0.18 – 0.52), and were thus considered important in explaining variation in spotted owl home range size.

4. Discussion

We did not observe strong patterns of selection for different landownerships by spotted owls in this study. While the landownership covariate was present in the top intermediate-scale PSF model (for the entire home range), odds ratios indicated there were no substantive difference in owl use among landownerships. In the fine-scale iSSA analysis, selection coefficients for national forest and SPI-owned lands were similar in magnitude (0.14 and 0.10 , respectively), suggesting

Table 4

Rankings of models of home range size for California spotted owls in the Sierra Nevada forests, USA. Variable abbreviations are explained in Table 1.

Model	df	logLik	Δ AICc	ω
Hindex + Elev + HF2H	5	−41.93	0.00	0.51
Hindex + Elev + HF2H + NF	6	−41.35	1.40	0.25
Hindex + Elev + HF2H + SPI	6	−41.91	2.51	0.14
Hindex + HF2H + SPI	5	−44.06	4.27	0.06
Hindex + Elev + NF	5	−45.11	6.36	0.02
Hindex + Elev + HF1 + HF2L	6	−45.38	9.45	0.00
Hindex + Elev + HF1 + SPI	6	−45.56	9.81	0.00
Hindex + NF	4	−48.29	10.28	0.00
Elev + HF2H + HF4	5	−47.46	11.06	0.00
Elev + HF2H + HF4 + HF1 + HF2L	7	−45.22	11.79	0.00
Elev + HF2H + HF4 + HF1	6	−47.38	13.46	0.00
Elev + HF2H + HF4 + HF1 + HF2L + NF	8	−44.90	13.93	0.00
HF1 + SPI	4	−51.65	17.00	0.00
Null	2	−54.41	17.93	0.00

Starting AICc values: 95.

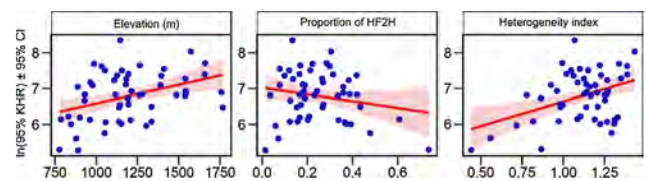


Fig. 5. Relationships between 95% kernel home range (KHR) size (km^2) and elevation, proportion of HF2H in the home range, and habitat heterogeneity for California spotted owls in the Sierra Nevada, USA. Data are plotted on a log scale and the shaded areas around fitted regression lines represent 95% confidence intervals (CI).

little difference in selection for these two landownerships. Moreover, we suspect that spotted owls tended to exhibit selection for national forests and SPI-owned lands over other privately-owned lands in the fine-scale iSSA analysis because only one owl had an activity center occurring on other private lands. As such, used steps may have been more likely to occur on national forests and SPI-owned lands when owls returned to their activity centers (e.g., to deliver prey to nest sites), whereas random (available) steps were generated without this tendency. Thus, we infer that national forests, SPI-owned, and other privately-owned lands provided foraging habitat to spotted owls in an approximately equal manner. Differences in selection patterns observed in our study and those reported in previous studies such as Williams et al. (2014) could be the result of either differences in sample sizes (53 owls in our study vs 13 owls in their study), differences in transmitters (GPS vs VHF), or differences in management strategies between private lands in the two studies. Thus, despite differences in cover types, forest structure, and management priorities among landownerships, privately-owned forests can provide more foraging habitat for California spotted owls than previously believed – although it is important to note that previously reported differences in selection between landownerships was modest (Williams et al., 2014).

We also found that spotted owls selected forests with intermediate- and large-sized trees and canopy cover $> 50\%$, and areas with high heterogeneity in cover type composition. Thus, both vegetation and cover type composition appeared to influence foraging decisions by California spotted owls. However, the strength of selection we observed for the cover types considered in this study was modest given that odds ratios for forests with large- and intermediate-sized trees and high canopy cover relative to early seral stages were < 2 at the home-range scale (Fig. 4a) and differences in the proportion of used versus available points among cover types were also not large (Fig. 6). Indeed, the modest level of selection we observed among cover types may be the

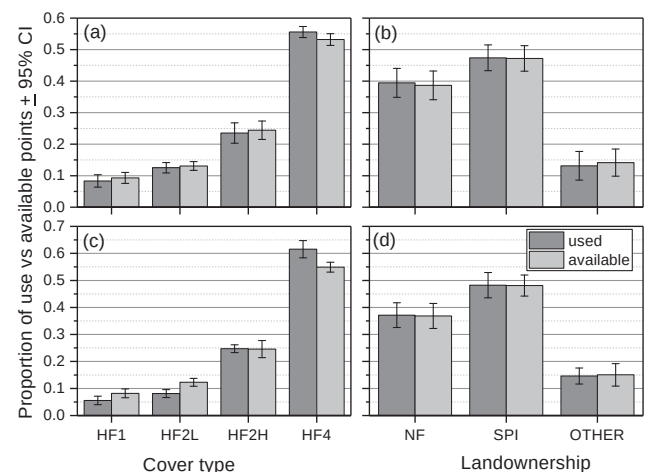


Fig. 6. Proportion of used and available points for (a) cover types and (b) landownership categories in the iSSA analysis, and points for (c) cover types and (d) landownership categories in the intermediate-scale PSF analysis.

reason differences in forest conditions between public and private lands (e.g., greater prevalence of large-tree high canopy-cover forest on public lands) may not have resulted in strong foraging preferences for any single landownership.

4.1. Hourly vs. nightly foraging patterns

Consistent with previous studies, California spotted owls in our area selected resources non-randomly and exhibited differential selection patterns depending on behavior and the scale of observation (Gutiérrez et al., 1992; Call et al., 1992; Williams et al., 2014). However, our conditional analysis (hourly movement data) was novel and corroborated selection analyses done by a more recent study of California spotted owl habitat selection (Blakey et al., 2019) as well as earlier studies of other spotted owl subspecies (e.g., Carey et al., 1990; Ganey and Balda, 1994). However, our PSF analysis based on putatively independent nightly locations suggested that spotted owls used cover types characterized by both intermediate- and large-sized trees and higher canopy cover (i.e., trees > 28 cm QMD and ≥50% canopy cover). Therefore, the use of the intermediate-sized tree cover types supported what has long been known about spotted owls (i.e. they expand their cover type use when foraging; Call et al., 1992; Irwin et al., 2007; Williams et al., 2011), while the analysis based on conditional use suggests that spotted owls might spend more time in forests having larger trees. The contrast in selection between the iSSA and PSF analyses (mainly the lack of selection for intermediate-sized trees in the iSSA analysis) might be attributed to the fact that some movements in the iSSA relates to central place foraging by owls where owls return frequently to centers of activity centers such as nest sites (Carey and Peeler, 1995), which typically are in areas with larger trees and higher canopy cover, whereas random steps implied no central place foraging tendency. On the other hand, our analysis based on independent (once per night) observations was based on single nightly locations and may have been better positioned to capture independent foraging decisions made by spotted owls, such as the selection of intermediate-sized trees. The *post-hoc* PSF analysis, where cover types were examined independently rather than as a categorical effect, provided further insight into cover type selection. In this analysis owls selected for intermediate- and large-sized trees with high canopy cover, whereas they used forests with small trees in proportion to availability and selected against early seral cover type, which also supports the hypothesis that owls expand cover type selection when foraging. When owls occurred in open areas such as recent clear-cuts, they often used individual or groups of legacy (“leave”) trees retained as part of silvicultural prescriptions or residual survivors of fire (Fig. S1).

Overall, spotted owls selected for areas containing high heterogeneity in cover types, a relationship that was also detected at the periphery of home ranges (i.e., 76–95% utilization distribution category). Franklin et al. (2000) and Roberts (2017) suggested that different cover types and different seral stages may promote higher prey density and owl reproductive output. Spotted owls in our study likely exploited different forest conditions if they harbor a diverse prey base, suitable perch sites, and open flying space as noted by others (Gutiérrez et al., 1995; Franklin et al., 2000). However, spotted owls selected relatively homogenous forest conditions consisting mainly of large trees and closed-canopy cover in the core of their home ranges (0–10% utilization distribution category; Table S3). Although owls exploited variable forest conditions for foraging they exhibited increasing selection of cover types having intermediate- and large-sized trees with higher canopy at greater distances from core areas. This pattern in combination with patches of mature closed-canopy forests have been shown to be important characteristics of spotted owl nesting and roosting habitat in the Sierra Nevada (Bias and Gutiérrez, 1992; Williams et al., 2011).

4.2. Home range size and habitat use

Spotted owl home ranges in our study were similar to those reported previously for the northern and central Sierra Nevada (Call et al., 1992; Williams et al., 2011), but were larger than those reported for the southern Sierra Nevada (Zabel et al., 1992; Eyes et al., 2017). Home range size generally increased with cover type heterogeneity and elevation and tended to decrease when home ranges contained higher proportions of cover types with intermediate-sized trees and higher canopy cover. Fretwell and Lucas (1969) predicted that individual home range size would decline as the quality and amount of resources increased because individuals would not have to travel as far to meet their life-history requirements. Thus, the reduction in home range size associated with intermediate-sized trees and higher canopy cover suggested that this cover type may provide quality foraging for spotted owls in the area of the study. Conversely, the increase in home range size with cover type heterogeneity suggested that high heterogeneity of cover types may reduce foraging opportunities for owls by increasing travel time and distance to foraging areas. We hypothesized that these contrasting results reflected a tradeoff between the benefits that heterogeneity can provide for prey and the increased energetic costs of traveling to forage in preferred cover types more widely across home ranges when heterogeneity is high. Zabel et al. (1995), Glenn et al. (2004) suggested that smaller home ranges for spotted owls represented higher quality habitat conditions, but it is possible that elevation also plays a role in home range size because owl home ranges are smaller at lower elevations that may reflect higher woodrats (*Neotoma* sp.) abundance versus higher flying squirrel (*Glaucomys sabrinus*) abundance at higher elevations (Munton et al., 2002; Innes et al., 2007; Wilson et al., 2008). Woodrats are larger and occur in higher density than flying squirrels, which could lead to higher quality foraging habitat at lower elevations and explain smaller home range sizes in these areas (Zabel et al., 1995). Home ranges at lower elevations may also be constrained by topography because many low elevation sites are in riparian zones that are disjunct from other suitable habitats (Verner et al., 1992b). Therefore, we infer that the determination of home range size in the Sierra Nevada spotted owls is complex and likely dependent on relative distribution and abundance of prey among cover types and elevations.

4.3. Conclusions: owls in mixed-ownership landscapes

The mosaic of cover types created by the interspersed of privately-owned forests with publicly-owned forest allows foraging by spotted owls on both landownerships. However, our measure of heterogeneity in this study was compositional and measured only the diversity of some seral stages in the landscape. These types of mosaics may not be consistent with restoration goals for public lands in the Sierra Nevada landscapes intended to help reestablish low- to moderate-severity fire regimes in the mixed-conifer zone, reduce the risk of high-severity fires, and promote a heterogeneous mix of vegetation conditions more representative of the natural range of variation. Nevertheless, selection of spatially heterogeneous environments that includes documents that privately owned lands can contribute to owl conservation by, at minimum, providing owl foraging habitat. Within this context of mixed landownership patterns on large landscapes of the Sierra Nevada, it is important to develop collaborative research focused on designing economically feasible ways that private landownerships can also provide patches of suitable mature forest capable of supporting nesting to augment their existing spotted owl foraging habitat.

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Research ethics statement

Owl capture, marking, and tracking activities were performed in compliance with institutional animal care and use protocols and state wildlife research permits.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.11.011>.

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Short-term effects of wildfires on spotted owl survival, site fidelity, mate fidelity, and reproductive success

Monica L. Bond, R. J. Gutiérrez, Alan B. Franklin, William S. LaHaye, Christopher A. May, and Mark E. Seamans

Abstract The effects of wildfire on wildlife are important considerations for resource managers because of recent interest in the role of fire in shaping forested landscapes in the western United States. This is particularly true of wildfire effects on spotted owls (*Strix occidentalis*) because of the uncertainty of impacts of controlled burning within spotted owl habitat. Therefore, we documented minimum survival, site fidelity, mate fidelity, and reproductive success for 21 spotted owls after large (>540 ha) wildfires occurred within 11 owl territories in California, Arizona, and New Mexico. In each territory, fire burned through the nest and primary roost sites. Eighteen owls (86%) were known to be alive at least 1 year after the fires, which was similar to reported annual adult survival probabilities for the species. Of 7 pairs of which both members were later resighted, all were located together on the same territories during the breeding season following fires, and 4 pairs produced a total of 7 fledglings. No pair separations were observed after fire. On 8 territories where fire severities were mapped, 50% experienced predominantly low- to moderate-severity fires while 50% experienced high-severity fires that burned large (>30%) areas of the territories. We hypothesize that wildfires may have little short-term impact on survival, site fidelity, mate fidelity, and reproductive success of spotted owls. Further, prescribed burning could be an effective tool in restoring habitat to natural conditions with minimal short-term impact on resident spotted owls. While we do not advocate wholesale prescribed burning in spotted owl territories at this time, we believe our observations justify large-scale experiments on effects of prescribed burning on spotted owls to corroborate our observations and to establish cause-and-effect relationships.

Key words prescribed burning, spotted owl, *Strix occidentalis*, wildfire

Wildfire is a natural process that has shaped the character of western forests (Agee 1990). In many areas, pre-settlement fire regimes consisted of frequent low-severity fires at 5–30-year intervals (Kilgore 1973, Horton and Mannan 1988, Weather-

spoon et al. 1992, MacCracken et al. 1996). In central and southern California, the Southwest, and eastern slopes of the Cascades, low-severity fires created a mosaic of uneven- and even-aged forest stands (Kilgore 1973, Horton and Mannan 1988,

Address for Monica L. Bond, R. J. Gutiérrez, William S. LaHaye, Christopher A. May, and Mark E. Seamans: Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN 55108, USA; present address for Bond: Center for Biological Diversity, P.O. Box 493, Idyllwild, CA 92549, USA; e-mail: mbond@biologicaldiversity.org. Address for Alan B. Franklin: Colorado Cooperative Fish and Wildlife Research Unit, Department of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO 80523, USA and Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, MN 55108, USA.

MacCracken et al. 1996). In northwestern California, the xeric end of the Pacific Northwest rainforest, fire frequency occurred at about 20-year intervals and the fire regime was more similar to southwestern than other northwestern regions (Agee 1990, 1993). However, western forests were not immune to higher-severity wildfires, which occurred infrequently and were patchy in nature (Stephenson et al. 1991, MacCracken et al. 1996). Therefore, both low- and high-severity fires have had significant impacts on forest structure, composition, and distribution. Risk of high-severity wildfires associated with drought, insect and disease epidemics, and global warming has increased significantly in the western United States following decades of fire suppression (Agee 1993).

Many studies have been conducted on indirect impacts of wildfire on bird populations (e.g., Marshall 1963, Biswell 1989). Indirect impacts include changes in vegetation type, canopy closure, and relative food abundance, which influence local densities of birds (Kilgore 1973, Horton and Mannan 1988). In addition to indirect effects, direct mortality of birds due to fire has been assumed or suspected (Robbins and Myers 1992, Smith 2000). Further, avian lungs may be more susceptible to damage from smoke exposure than mammalian lungs because of an apparent inability of the avian respiratory tract to repair itself (Rombout et al. 1991). While nest destruction caused by fires has been reported for some ground-nesting birds in North Dakota (Robbins and Myers 1992), few studies have examined avian mortality and behavior directly following fire (McMahon and deCalesta 1990).

Some biologists assume that large wildfires negatively impact long-term survival of the spotted owl (*Strix occidentalis*; e.g., Weatherspoon et al. 1992, MacCracken et al. 1996), and believe catastrophic or "stand-replacement" fires, which kill all vegetation within the fire boundary, pose the greatest natural risk to spotted owl habitat (United States Fish and Wildlife Service [USFWS] 1992, 1995; Verner et al. 1992). Management plans generally recommend reducing risk of catastrophic fire in forests occupied by spotted owls (e.g., Verner et al. 1992). One method of reducing risk of wildfire is the use of prescribed fire to remove fuels that can facilitate surface fires becoming crown fires (Biswell 1989). Because northern (*S. o. caurina*) and Mexican spotted owls (*S. o. lucida*) are federally listed as threatened subspecies, prescribed fires within owl areas

require consultation with the USFWS. USFWS smoke and wildlife guidelines for prescribed burning currently exist for site-preparation of clearcut units located near northern spotted owl Habitat Conservation Areas (HCAs), but some agency biologists have proposed prescribed burns within northern spotted owl HCAs (J. Perkins, United States Forest Service [USFS], Klamath National Forest, unpublished report). Because of uncertainty over fire effects on owls, controlled burning as a habitat management tool is not conducted routinely within areas reserved for spotted owls. For example, researchers have examined occupancy of spotted owl territories in years following a wildfire (Elliot 1985, MacCracken et al. 1996, Gaines et al. 1997, Scott 1998, Jenness 2000), but short-term impacts on individuals could not be assessed because owls were not color-marked.

We describe minimum survival, site fidelity, mate fidelity, and reproductive success of color-marked spotted owls after wildfires burned nest and roost areas in northwestern California, southern California, Arizona, and New Mexico. After a fire occurred within an owl territory, we posed 4 questions:

1. Did the owl(s) survive the fire (minimum survival)?
2. If an owl survived, was it found in the same territory after the fire (site fidelity)?
3. If both members of a pair survived a fire, did they retain the same mates (mate fidelity)?
4. If both members of a pair survived a fire, did they nest successfully the year after the fire (reproductive success)?

Direct observations of fire effects on spotted owls are difficult to obtain because of the patchy and infrequent (due to fire suppression) nature of fire, and logistical or political limitations associated with conducting fire experiments on a meaningful scale. Nevertheless, we provide insight on short-term effects of fire on spotted owls by presenting observations gathered during 15 years of study throughout a large portion of the species' range.

Study areas

We recorded spotted owl responses to fires >540 ha that occurred on 4 long-term demographic study areas, representing all 3 subspecies of the owl. Study areas were located in northwestern California (292 km², 1985–2000, northern spotted owl);

San Bernardino Mountains, southern California (1,890 km², 1987–2000, California spotted owl [*S. o. occidentalis*]); Tularosa Mountains, New Mexico (323 km², 1991–2000, Mexican spotted owl); and Coconino Plateau, Arizona (585 km², 1991–2000, Mexican spotted owl).

Forests in northwestern California were primarily mixed evergreen (Sawyer et al. 1988), dominated by Douglas-fir (*Pseudotsuga menziesii*) with a hardwood subcanopy of madrone (*Arbutus menziesii*), tanoak (*Lithocarpus densiflora*), and canyon live oak (*Quercus chrysolepis*) below 1,200 m elevation. Above 1,200 m, forests were mainly subalpine forests (Sawyer and Thornburgh 1988) dominated by white fir (*Abies concolor*) and pines (*Pinus* spp.). Forests in the San Bernardino Mountains consisted of mixed evergreens (Sawyer et al. 1988) below 1,500 m, and ponderosa pine (*P. ponderosa*) and white fir-sugar pine (*P. lambertiana*) forests (Thorne 1988) above 1,500 m. Forests consisted of various combinations of white fir, ponderosa pine, sugar pine, incense-cedar (*Calocedrus decurrens*), and black oak (*Q. kelloggii*) at higher elevations, and canyon live oak and bigcone Douglas-fir (*Pseudotsuga macrocarpa*) at lower elevations. Forests in the Tularosa Mountains were primarily mixed-conifer and pine-oak. Douglas-fir and white fir were the dominant species in mixed-conifer forests. Pine-oak forest was dominated by ponderosa pine and Gambel oak (*Q. gambelii*). Piñon-juniper woodland, dominated by piñon pine (*P. edulis*) and alligator juniper (*Juniperus deppeana*), was an extensive community within the mountain range. Forests on the Coconino Plateau were pine-oak dominated by ponderosa pine and Gambel oak (Peet 2000). Other communities on the plateau included mixed-conifer forest having Douglas-fir, ponderosa pine, and white fir in the overstory and quaking aspen (*Populus tremuloides*) and Gambel oak in the understory; and piñon-juniper woodland dominated by piñon pine and junipers (*Juniperus* spp.; Peet 2000).

Methods

Owl surveys

We surveyed each study area annually for spotted owls during the breeding season from 1985–2001 following methods described by Forsman (1983) and Franklin et al. (1996). We captured adult and juvenile owls using snare poles, noose poles, and mist nets. All captured birds were marked with a

locking aluminum USFWS band on 1 leg and a plastic band and tab with a unique color combination on the other leg (Forsman et al. 1996). We determined the sex of owls by calls and behavior (Franklin et al. 1996). Rate of band loss for spotted owls was negligible (Franklin et al. 1996). This project was approved by the University of Minnesota's Animal Care and Use Committee (Animal Subjects Code Number: 0003A42461).

Impacts of fire

We used USFS records of severity, extent, and duration of all fires >540 ha occurring within territories of individually color-marked spotted owls. We limited our study to fires at least this large because home-range sizes of spotted owls range from 422–591 ha in northwestern California (northern spotted owl; Zabel et al. 1995), 415–810 ha in the San Bernardino Mountains (California spotted owl; Zimmerman et al. 2001), and 648 ha in Arizona (Mexican spotted owl; Ganey and Balda 1989). In each case, nest and roost areas were located within the fire perimeter, and all were burned. Detailed information about conditions (e.g., weather condition, fuel moisture, humidity, and fuel load) at owl nests and roosts was unavailable. We used available USFS data to describe the extent of each fire at the landscape and territory scales. At the landscape scale, we obtained the name, season, and year of the fire, as well as total size and duration of each fire. We addressed fire at the territory scale by estimating percent of each individual owl territory that burned, and percent of the fire-affected area in the territory that burned at high, moderate, or low severity. We defined an owl territory as a circle, with a radius of one-half the average nearest neighbor distance for each study area (see Bingham and Noon 1998) around the nest or roost site during the breeding season, at the time of or prior to the fire (northern spotted owl = 710 m [Franklin et al. 2000]; California spotted owl = 748.5 m [Smith et al. 2002]; Mexican spotted owl, AZ = 1,178 m [May 2000]; and NM = 1,060 m [Peery et al. 1999]). To estimate percent of each territory that burned and nest or roost area location within the fire, we overlaid owl territories onto digitized fire maps obtained from the USFS using ArcView GIS 3.2 (Environmental Systems Research Institute 1996).

Fire-severity classifications for each coverage were conducted by each USFS district within which the fire occurred. Coverages were classified as follows: 1987 autumn King Titus fire (24,282 ha)

in northwestern California (3 owl territories) into low (<30% canopy kill), moderate (31–70% canopy kill), and high severity (>70% canopy kill); 1995 summer HB fire (5,261 ha) in New Mexico (3 owl territories) into low (<35% canopy kill) and high (>35% canopy kill) severity; 1987 autumn Cold fire (4,876 ha) in northwestern California (1 owl territory) into high (small and subcanopy trees killed, and many to most overstory trees killed) and moderate (most small trees killed, some subcanopy trees killed or heavily damaged, and occasional mortality of overstory trees) severity; and 1996 spring Pot fire (2,833 ha) in Arizona (1 owl territory) into crown ("standing black sticks" with no live trees), high (>70% crown scorch of standing overstory trees), medium (30–70% crown scorch of standing overstory trees), and low/underburn (<30% scorch of standing overstory trees or generally on flanks or heel of fire area). Severity on the King Titus and HB fires was estimated using aerial photography; satellite imagery was also used on the HB fire. The Cold fire severity was estimated from ground surveys. The Pot fire map was developed using satellite imagery followed by ground verification. Unfortunately, USFS GIS data for the remaining 3 summer fires in southern California (Verben, 1995 [9,308 ha], Mill, 1997 [541 ha], Willow, 1999 [25,091 ha]) portrayed only boundaries. We recognized that a boundary may be over-simplified, but severity maps for these fires were unavailable. We did not include more detailed pre- and post-fire habitat information in our analysis because our study focused on short-term effects of fire on survival and movements of owls rather than long-term habitat changes. No salvage logging or other major anthropogenic changes to vegetation within owl territories occurred between the time of the fire and the time we surveyed owls the following year.

We qualitatively described impacts of fire on survival, site fidelity, mate fidelity, and reproductive success of individuals and pairs because these were opportunistic observations taken over a long period of time. We pooled data across subspecies because sample sizes for each subspecies were small (≤ 4 territories) and we were describing observational responses rather than conducting comparative statistical analyses. We defined minimum survival rate as percent of individuals resighted alive at least 1 year after the fire ($n=21$ owls). We defined site fidelity as percent of individuals resighted alive within the same territory before the fire occurred and 1 year after the fire occurred ($n=$

18 owls). We defined mate fidelity as percent of pairs that survived the fire ($n=7$ owl pairs) and both original pair members remained together (i.e., resighted in same territory as a social pair) 1 year after the fire occurred. Our evaluation of mate fidelity does not imply cause and effect if a pair-bond was broken. Rather, we interpreted it to mean only that a fire did not mediate a pair dissolution if they remained together. Reproductive success was defined as average number of fledglings per pair of owls that survived ($n=7$ owl pairs) 1 year after the fire occurred.

We compared overall estimates of annual adult spotted owl survival and reproductive success for each study area from our previous research (W. S. LaHaye, unpublished data; Seamans et al. 1999, Franklin et al. 2000) with qualitative findings from this study. Our previous survival estimates were based on mark-recapture estimators, whereas fire survival estimates were empirical estimates from a small sample size. Therefore, confidence limits for empirical estimates did not reflect uncertainty due to recapture probability. We compared short-term (1-year) reproductive success of owls surviving fires with general rates of owl reproduction. However, caution must be used when drawing conclusions about reproduction because spotted owl reproduction was more variable than survival and differences from overall averages could have been due to annual variation rather than effects of fire.

We also estimated overall annual site fidelity for each study area based on long-term data. We calculated annual site fidelity by dividing number of owls remaining on territories from year t to year $t+1$ by total number of owls surviving from year t to year $t+1$. Only banded, adult owls were used in site-fidelity calculations.

Results

Data were gathered from 4 study areas representing 38 observation years, >2,000 banded owls, >300 owl territories, and 7 wildfires. Wildfires occurred in 11 spotted owl territories (10 pairs and 1 single owl) during the period of investigation (1985–2001). Fires occurred in 4 northern, 3 California, and 4 Mexican spotted owl territories. All territories were >80% burned (83–100%). In all cases, nest and roost areas were burned. Four of 8 territories where fire severities were mapped burned primarily at low to moderate severity. However, the remaining 4 territories experienced fires

that burned 36–88% of the territory at high-severity levels.

Eighteen of 21 (86%) individual owls affected by fires were resighted at least 1 year after the fires, and 16 of the 18 (89%) resighted owls were located in the same territories in the breeding season after the fire. Among 7 owl pairs in which both members were resighted after a fire, all were site- and mate-faithful. Among 3 individuals whose mates were never resighted, 2 females were resighted after the fire on different territories with different males, and 1 male exhibited site fidelity after the fire but was found paired with a different female. Four of 7 surviving owl pairs (57%) produced 7 fledglings the year following fire.

Minimum survival of spotted owls experiencing fires was similar to overall annual survival rates reported for the 3 subspecies (Table 1). Site fidelity among fire-impacted birds was also similar to overall estimates from the 4 demographic studies (Table 1). Reproductive success of spotted owls 1 year after fire occurred was higher than overall annual rates of reproduction (Table 1).

Discussion

Results from previous studies on impacts of wildfires on spotted owls have been equivocal. In some cases, large stand-replacing wildfires appeared to have a negative impact on owl occupancy (Elliot 1985, MacCracken et al. 1996, Gaines et al. 1997). Other reports have suggested that low- to moderate-severity wildfires did not adversely impact spotted owls (Yasuda 1997, Scott 1998, Jenness 2000). Although high-severity fires may displace some owls from territories (Elliot 1985, Gaines et al. 1997), it was unknown whether birds moved or died because owls in these studies were

not marked. Since we monitored fates of color-marked owls, we could derive modest inference on effects of fire on individual survival, site fidelity, mate fidelity, and reproductive success. In our study, fates of only 3 of 21 owls exposed to fire were unknown. Relatively large wildfires that burned nest and roost areas appeared to have little short-term effect on survival, site fidelity, mate fidelity, and reproductive success of spotted owls, as rates were similar to estimates independent of fire. While post-fire reproductive rates were higher than background rates for these populations, they were well within the range of variation seen in these populations. Most (6 of 8) territories burned $\geq 50\%$ at low to moderate severity. Therefore, we hypothesize that spotted owls may have the ability to withstand the immediate, short-term (1-year) effects of fire occurring at primarily low to moderate severities within their territory.

Horton and Mannan (1988) noted that animals that occupied forests having frequent fire intervals

Table 1. Estimates (95% confidence intervals) of minimum post-fire survival, site fidelity, and average number of fledglings per pair for 21 spotted owls (*Strix occidentalis*) that experienced fire in their territories in northwestern California, southern California, Arizona, and New Mexico, compared with overall average annual survival, site fidelity, and average number of fledglings per pair for the 4 populations at the above locations, 1987–2001.

Parameter	Post-fire estimates	Estimates			
		<i>S.o. caurina</i> NWC ^a	<i>S.o. occidentalis</i> SC ^b	<i>S.o. lucida</i> NM ^c	AZ ^d
Survival	0.86 (0.71–1.00) <i>n</i> =21	0.876 (0.84–0.91)	0.79 (0.76–0.81)	0.832 (0.78–0.89)	0.814 (0.72–0.91)
Site Fidelity	0.89 (0.74–1.00) <i>n</i> =18	0.88 (0.85–0.92)	0.91 (0.88–0.94)	0.90 (0.85–0.95)	0.92 (0.85–0.99)
Average no. fledglings/pair	1.0 (0.62–1.38) <i>n</i> =7 pairs	0.62 (0.56–0.68)	0.643 (0.59–0.69)	0.77 (0.70–0.84)	0.93 (0.86–1.0)

^a Northwestern California: survival estimate from 1985–1998 (source: Franklin et al. 2000). Site fidelity estimate from 1985–2000; *n* = 42–68 owls per year for 15 years. Reproduction estimate from 1985–2001; *n* = 1019 pair observations.

^b Southern California: survival estimate from 1987–1998 (source: W. S. LaHaye, unpublished data). Site fidelity estimate from 1987–1998; *n* = 35–93 owls per year for 11 years. Reproduction estimate from 1987–1998; *n* = 840 pair observations.

^c New Mexico: survival estimate from 1991–1997 (source: Seamans et al. 1999). Site fidelity estimate from 1991–2000; *n* = 21–41 owls per year for 10 years. Reproduction estimate from 1991–2001; *n* = 203 pair observations.

^d Arizona: survival estimate from 1991–1997 (source: Seamans et al. 1999). Site fidelity estimate from 1991–2000; *n* = 19–36 owls per year for 10 years. Reproduction estimate from 1991–2001; *n* = 241 pair observations.

should be adapted to repeated fires. While pre-settlement fire regimes of western forests consisted of frequent low-intensity burns, infrequent high-severity fires also occurred and were important determinants of forest structure, composition, and distribution (Agee 1990, Stephenson et al. 1991). Given historical fire regimes within its range, the spotted owl may be adapted to survive wildfires of various sizes and severities. Therefore, prescribed burning could be an effective tool in reducing current fire risk and restoring forests to natural conditions with minimal short-term impact to owls. However, we believe that programmatic prescribed burning in spotted owl territories cannot be justified solely on the observations we report here. Experiments testing effects of fire on spotted owls are still needed to corroborate the effects we observed, establish cause-and-effect relationships, and determine long-term impacts on spotted owls.

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Monica Bond (photo) is currently a biologist with the Center for Biological Diversity. She was a research fellow in the Department of Fisheries, Wildlife and Conservation Biology at University of Minnesota (UMN) at the time of this study. She received her B.A. in biology from Duke University and her M.S. in wildlife science from Oregon State University. She has been a TWS member since 1998 and currently serves on the TWS Western Section Conservation Action Committee. **R. J. Gutiérrez** is professor and Gordon Gullion Endowed Chair in Forest Wildlife Research, Department of Fisheries, Wildlife, and Conservation Biology, UMN. He received his B.S. from Colorado State University, an M.S. from the University of New Mexico, and his Ph.D. from the University of California, Berkeley. Rocky's primary interests are forest wildlife habitat relationships, game bird ecology and evolution, and endangered species conservation. He has been a TWS member since 1967. **Alan B. Franklin** is a research scientist in the Colorado Cooperative Fish and Wildlife Unit, Colorado State University. He is also an adjunct assistant professor in the Department of Fisheries, Wildlife, and Conservation Biology, UMN. Alan received his B.S. in natural resources from Cornell University, an M.S. in wildlife from Humboldt State University, and a Ph.D. in wildlife biology from Colorado State University. Alan has worked on spotted owls since 1983 and has a primary interest in population dynamics of wildlife. He has been TWS member since 1989. **William S. LaHaye** is a research fellow, Department of Fisheries, Wildlife, and Conservation Biology, UMN. He received his B.S. in geology from Chico State University and his M.S. in wildlife from Humboldt State University. Bill has worked on spotted owls since 1983. He has been a TWS member since 1994. **Christopher A. May** is a research fellow, Department of Fisheries, Wildlife, and Conservation Biology, UMN. He received his B.S. in biology from Baylor University and his M.S. in wildlife from Humboldt State University. His research interests include habitat selection and predator-prey relationships. Outside the spotted owl field season, Chris lives in Mississippi, where he enjoys photographing wildlife and canoeing. He has been a TWS member since 1997. **Mark E. Seamans** is research fellow and Ph.D. student in the Department of Fisheries, Wildlife, and Conservation Biology, UMN. He received his B.S. in biology from California State University Sacramento, and his M.S. in wildlife from Humboldt State University. Mark's current research is focused on how temporal and spatial variability in wildlife population dynamics is related to climatic variability and habitat change. Mark has been a TWS member since 1991.

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SURVIVAL RATES OF NORTHERN SPOTTED OWLS IN POST-FIRE LANDSCAPES OF SOUTHWEST OREGON

DARREN A. CLARK,¹ ROBERT G. ANTHONY, AND LAWRENCE S. ANDREWS

Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, Corvallis, OR 97331 U.S.A.

ABSTRACT.—We estimated annual survival rates (S) of 23 radio-marked Northern Spotted Owls (*Strix occidentalis caurina*) at the Quartz and Timbered Rock burns and adjacent areas in southwest Oregon. We used known-fate models in program MARK to test for differences in survival among three groups (owls dwelling inside of burned areas, owls displaced by wildfire, and owls dwelling outside of burned areas) and to investigate the potential effects of fire severity and cover type on survival. We found that annual survival rates of Spotted Owls that maintained a territory within the burn perimeter ($\hat{S} = 0.69 \pm 0.12$) or that had been displaced by the burn ($\hat{S} = 0.66 \pm 0.14$) were lower than those of owls that had territories outside but adjacent to the burn perimeter ($\hat{S} = 0.85 \pm 0.06$). This result indicated that wildfire had a negative impact on Spotted Owl survival, at least in the short-term (i.e., 3–5 yr postburn). We were unable to identify a significant effect of fire severity or quantity of habitat on Spotted Owl survival, but this inability was likely related to our small sample size and high variability in habitat composition. We recommend long-term monitoring of survival on larger samples of owls to identify the effects of fire severity and habitat on Spotted Owl survival and to determine if wildfire poses a significant threat to the long-term persistence of Spotted Owls.

KEY WORDS: Northern Spotted Owl; *Strix occidentalis caurina*; known-fate models; post-burn survival; radiotelemetry; wildfire.

TASAS DE SUPERVIVENCIA DE *STRIX OCCIDENTALIS CAURINA* EN PAISAJES CON INFLUENCIA DE INCENDIOS EN EL SUDOESTE DE OREGON

RESUMEN.—Estimamos las tasas anuales de supervivencia (S) de 23 individuos de *Strix occidentalis caurina* marcados con radiotransmisores en las áreas quemadas de Quartz y Timbered Rock y áreas adyacentes en el sudoeste de Oregon. Usamos modelos de destino conocido en el programa MARK para determinar si existen diferencias entre tres grupos (lechuzas que habitan áreas quemadas, lechuzas que fueron desplazadas por el fuego y lechuzas que habitan fuera de las áreas quemadas) y para investigar los efectos potenciales de la severidad del fuego y del tipo de cobertura sobre la supervivencia. Encontramos que las tasas de supervivencia anuales de los individuos que mantuvieron sus territorios dentro del perímetro quemado ($\hat{S} = 0.69 \pm 0.12$) y de los individuos que fueron desplazados por los incendios ($\hat{S} = 0.66 \pm 0.14$) fueron más bajas que las de los individuos que tenían territorios adyacentes pero fuera del perímetro quemado ($\hat{S} = 0.85 \pm 0.06$). Este resultado indica que los incendios forestales tuvieron un impacto negativo en la supervivencia de *S. occidentalis caurina*, por lo menos en el corto plazo (i.e., 3–5 años después de los incendios). No fuimos capaces de detectar un efecto significativo de la severidad del fuego o de la cantidad de hábitat sobre la supervivencia de las lechuzas, pero esta inhabilidad de detectar un efecto probablemente se relacionó con nuestro pequeño tamaño de muestra y con la gran variabilidad en la composición del hábitat. Recomendamos un monitoreo a largo plazo de la supervivencia con tamaños de muestra mayores para identificar los efectos de la severidad del fuego y del hábitat sobre la supervivencia de estas lechuzas y para determinar si los incendios forestales representan una amenaza para la persistencia en el largo plazo de *S. occidentalis caurina*.

[Traducción del equipo editorial]

The Northern Spotted Owl (*Strix occidentalis caurina*; hereafter Spotted Owl) was listed as threatened by the U.S. Fish and Wildlife Service in 1990

(USFWS 1990). At that time, the primary reasons for listing included loss of habitat to timber harvest, evidence of declining populations, and lack of regulatory mechanisms to protect the owl or its habitat. In 1994, the Northwest Forest Plan (NWFP) was

¹ Email address: Darren.Clark@oregonstate.edu

adopted to protect habitat for Spotted Owls and other late-successional forest dependent species (Thomas et al. 1993) and to reduce timber harvest on federally managed lands (USDA and USDI 1994). Since the adoption of the NWFP, several Spotted Owl populations have continued to decline despite increased habitat protection and large reductions in timber harvest on public lands (Anthony et al. 2006, USFWS 2008). Ongoing population declines are thought to be related to low apparent survival (Anthony et al. 2006), competition with Barred Owls (*Strix varia*; Kelly et al. 2003, Olson et al. 2005), and habitat loss from natural disturbances, particularly wildfire (USFWS 2008).

The likelihood of stand-replacing wildfire in the dry forest physiographic provinces of the Pacific Northwest increased during the latter half of the twentieth century (Agee 1993). Increased fire frequency caused wildfire to become the leading factor contributing to loss of Spotted Owl habitat on public lands (Davis and Lint 2005). Although losses of Spotted Owl habitat to wildfire throughout the species' range equaled predicted losses (Davis and Lint 2005), loss of habitat to wildfire within the dry forest physiographic provinces exceeded predictions (Davis and Lint 2005). The increased frequency of habitat loss to wildfire caused concern for the viability of Spotted Owl populations in dry forest ecosystems (Spies et al. 2006) and contributed to the identification of wildfire as a threat to Spotted Owls (USFWS 2008).

Although the threat of wildfire to Spotted Owls has increased, little is known about the effects of wildfire on the demographic rates of Spotted Owls, particularly survival rates. Survival rates of Northern, Mexican (*S. o. lucida*) and California Spotted Owls (*S. o. occidentalis*) one year postfire were similar to rates reported throughout the species' ranges (Bond et al. 2002). Other studies indicated that occupancy of territories by Spotted Owls declined following wildfire (MacCracken et al. 1996, Gaines et al. 1997). However, it was unknown whether occupancy declines were attributable to emigration from the burned area or to decreased survival. Studies conducted in landscapes that were not recently affected by wildfire suggested that Spotted Owl survival was positively associated with increased amounts of late-successional forest (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005) and negatively associated with increased amounts of early seral forests (Dugger et al. 2005). These studies suggest that

intense wildfire that destroys or severely alters older forests may negatively impact Spotted Owl survival. Conversely, higher survival rates were observed at Spotted Owl territories that were not entirely composed of late-successional forests (Franklin et al. 2000, Olson et al. 2004), which may suggest that Spotted Owls have adapted in some ways to wildfire, which creates forest heterogeneity.

Several large wildfires in southwest Oregon during the summers of 2001 and 2002 provided an opportunity to study Spotted Owl survival in burned landscapes. Our objectives were to estimate survival rates of Spotted Owls dwelling in burned areas, those displaced by wildfire, and those dwelling outside of burned areas, and to assess the potential effects of fire severity and habitat covariates on survival rates. We predicted that survival rates of Spotted Owls inside burned areas or displaced by wildfire would be lower than those that were outside but adjacent to burned areas. We also predicted that survival rates would be positively associated with greater amounts of older forests that were unburned or burned with a low to moderate severity and negatively associated with greater amounts of high severity burns and salvage logging within individual owl's home ranges.

METHODS

Study Areas. We estimated Spotted Owl survival within and around the Quartz and Timbered Rock burns in southwest Oregon. The Timbered Rock and Quartz burns were located approximately 45 km and 21 km from Medford, Oregon, respectively. Forest types in this portion of the Spotted Owl's range were part of the mixed-conifer and mixed-evergreen vegetation zones (Franklin and Dyrness 1973). Common tree species on our study areas included ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), Oregon white oak (*Quercus garryana*), California black oak (*Quercus kelloggii*), and Pacific madrone (*Arbutus menziesii*). Prior to active fire suppression, most of southwestern Oregon was subjected to frequent low-intensity fires at low elevations and infrequent stand-replacing fires at high elevations (Agee 1993). The climate regime in this portion of Oregon is characteristically temperate with hot, dry summers and cool, moist winters. During our study, average annual rainfall was 66 cm at the Quartz burn and 88 cm at the Timbered Rock burn. The warmest and coldest average

Table 1. The percentage of area within the Quartz and Timbered Rock burns that was classified as non-habitat or Northern Spotted Owl habitat that was salvage logged or burned with a low, moderate, or high severity.

STUDY AREA	PERCENT OF STUDY AREA				
	NON-HABITAT ^b	HABITAT ^a			
		LOW SEVERITY ^c	MODERATE SEVERITY ^d	HIGH SEVERITY ^e	SALVAGE LOGGED ^f
Timbered Rock	27.10%	30.50%	12.30%	10.10%	20.00%
Quartz	28.20%	17.10%	13.40%	18.80%	22.50%

^a Forested areas that provide nesting, roosting, and/or foraging habitat for Spotted Owls.
^b Non-forested areas and early seral forests as a result of prior logging activities.
^c ≤20% of the overstory removed by wildfire.
^d >20% but ≤70% of the overstory removed by wildfire.
^e >70% of the overstory removed by wildfire.
^f Areas that received any level of postfire salvage.

daily temperatures occurred in July (21°C) and December (3°C), respectively (Oregon Climate Service, Oregon State University unpubl. data).

The Quartz Fire was ignited by lightning in August 2001 and burned 2484 ha within the Glade Creek, Little Applegate, and Yale Creek watersheds at elevations ranging from approximately 600 to 1850 m. Land ownership was a mixture of public (U.S. Forest Service [USFS], Bureau of Land Management [BLM], and Oregon Department of Forestry [ODF]) and private. The site centers of nine documented Spotted Owl territories were within the perimeter of the Quartz Fire. From 2003 to 2006, the number of territories occupied by a pair of Spotted Owls ranged from two to five. One occupied territory that was adjacent to the burn was also monitored as part of this study. The study area burned with a mosaic of low, moderate, and high severities, and substantial areas within the study area received primarily clear-cut salvage logging (Table 1).

The Timbered Rock Fire was ignited by lightning in mid-July, 2002, and burned approximately 11 028 ha within the Elk Creek watershed at elevations ranging from 450 to 1350 m. Land ownership was a checkerboard pattern of public (BLM) and private lands in the southern two-thirds of the burn and contiguous USFS-managed lands in the northern third. Twenty-two Spotted Owl territories were within the perimeter of the Timbered Rock Fire and were monitored as part of this study. From 2003 to 2006, the number of territories occupied by a pair of Spotted Owls declined from eight to three. Five additional occupied territories that were adjacent to the burn were monitored as part of this study. The study area burned in a mosaic of fire severities and

had large amounts of primarily clear-cut salvage logging (Table 1).

Owl Capture and Monitoring. Between September 2004 and June 2005 we captured and radio-marked 23 Spotted Owls in the Timbered Rock and Quartz burns and surrounding areas. We located Spotted Owls at known territory centers using acoustic surveys (Franklin et al. 1996). After locating individual owls, we captured and radio-marked owls using methods outlined by Guetterman et al. (1991). Owl capture and handling followed the guidelines of the Institutional Animal Care and Use Committee at Oregon State University (IACUC Number 3040). Of the 23 radio-marked owls, 11 were inside burned areas (five females, six males), six were displaced by the burns (three females, three males), and six were outside burned areas (three females, three males). Owls that were displaced by the burn were defined as color-banded owls that occupied a territory inside the burn for at least 1 yr postburn and established a territory outside the burn ≥2 yr postburn, where they were radio-marked. On average, owls that were displaced by the burn moved 3.4 km (range 2.3–7.0 km) from their original territory to an unoccupied territory adjacent to the burn perimeter. We fitted each owl with a 7.5-g backpack-mounted radio-transmitter equipped with a mortality sensor (Holohil Systems Ltd. Model RI-2C, Ontario, Canada). We recorded the fate (alive or dead) of individual owls from October 2004 through September 2005 by monitoring transmitter signals approximately every second day. When we could not locate an individual from the ground, we conducted aerial searches using fixed-wing aircraft. If we could not locate the owl following an aerial search, we assumed the transmitter failed or

Table 2. Description of *a priori* hypotheses and models used for testing the effects of temporal and group factors on Northern Spotted Owl survival at the Quartz and Timbered Rock burns and adjacent areas in southwest Oregon, U.S.A.

HYPOTHESIS DESCRIPTION ^a	MODEL NOTATION
TEMPORAL EFFECTS	
1. Survival rates are constant among months	S (.)
2. Survival rates differ among months	S (t)
3. Survival rates follow a linear trend	S (T)
4. Survival rates follow a log-linear trend	S (lnT)
5. Survival rates follow a quadratic trend	S (TT)
GROUP EFFECTS	
6. Owls inside the burn or displaced by the burn (Affected) have equal survival rates that are different from those of owls outside the burn (Unaffected)	S (Affected ≠ Unaffected)
7. Same as model 6, but survival also varies by sex	S (Affected ≠ Unaffected * Sex)
8. Owls inside the burn, displaced by the burn, and outside the burn have different survival rates	S (Area)
9. Same as model 8, but survival also varies by sex	S (Area * Sex)
10. Owls outside or displaced by the burn (Outside) have equal survival rates that are different than owls inside the burn (Inside)	S (Inside ≠ Outside)
11. Same as model 10, but survival also varies by sex	S (Inside ≠ Outside * Sex)
12. Survival varies by sex, but not by area	S (Sex)

^a Additive and interactive combinations of temporal and group effects were considered when appropriate.

the owl emigrated from the study area. When this happened the individual was censored during the periods of unknown fate. If the transmitter indicated a mortality (i.e., the pulse rate of the transmitter doubled), we located the carcass or remains of the owl as soon as possible to determine the cause of death. If the cause of death could not be determined in the field, we submitted the owl carcass for necropsy at the Veterinary Diagnostic Lab (VDL) at Oregon State University, College of Veterinary Medicine.

Estimation of Survival Rates. We estimated monthly survival rates (S) in program MARK using known-fate models for radio-marked individuals (White and Burnham 1999). We used a modified Kaplan–Meier (1958) estimator that allowed for staggered data entry and censoring of individuals (Pollock et al. 1989). We entered owls into the dataset during the first month they were monitored and censored owls during intervals of unknown fate. We compounded monthly survival rates over 12 mo to obtain an estimate of annual survival.

We modeled survival using a two-step process. First, we developed a set of candidate models, based on biologically plausible hypotheses to test for differences in survival among groups over time (Table 2). We used previously outlined approaches when building and naming our candidate model

set (Lebreton et al. 1992, White and Burnham 1999). We investigated models that incorporated five time effects (Table 2). In addition, we investigated candidate models based on potential differences among six groups; females and males inside burned areas, females and males displaced by the burn (color-banded owls that had a territory inside the burn 1 yr postburn and established a territory outside the burn ≥ 2 yr following the burn), and females and males outside but adjacent to the burn perimeter (Table 2). We developed seven candidate models to test for differences among these groups (Table 2). Models with ≥ 2 groups included additive (+) and interactive (*) combinations of group and time when appropriate. For example, if the linear trend (T) model ranked higher than the constant survival (.) model, the linear trend was modeled as an interactive and additive effect with the group. Second, we modeled individual covariates for habitat within each owl’s home range as an additive effect with the best model from step one.

To assess the impacts of fire severity and cover type on Spotted Owl survival, we created postfire habitat maps in ArcGIS 9.1 (ESRI, Redlands, California, U.S.A.) by merging three data layers: (1) a prefire habitat map (Davis and Lint 2005), (2) a fire severity map, and (3) the boundaries of salvage

logged areas (see Clark 2007 for additional details). We used program KERNELHR to estimate 95% fixed kernel home ranges using least-squares cross validation to select the kernel bandwidth (Seaman and Powell 1996, Seaman et al. 1998). We calculated individual covariates as the proportion of each habitat type within an individual's 95% fixed kernel home range. Due to our small sample of radio-marked owls and the large variation in covariate values (Appendix), we developed a small set of candidate models ($n = 14$) that had relatively few parameters. The two most complex covariate models we considered included four parameters [models S(LOW + MOD + HIGH + SALV) and S(RF + NRF + HIGH + SALV)]. We considered four models that included only one covariate [models S(LOST), S(LOW), S(NRF), and S(NRFL)]. The eight remaining candidate models were variations of the most complex models that had fewer parameters [e.g., models S(HIGH + SALV) and S(RF + NRF)] or combined the HIGH and SALV covariates into one parameter (LOST). Definitions for individual covariates are provided in Appendix.

We used Akaike's Information Criteria corrected for small sample sizes (AIC_c) to rank candidate models (Burnham and Anderson 2002). We used the difference between the AIC_c of the best model and the i th model (ΔAIC_c) to identify closely competing models (Burnham and Anderson 2002). Any model within 2 ΔAIC_c units was considered competitive with the best model. We used Akaike weights to evaluate the relative support for each candidate model and computed model averaged monthly and annual survival estimates (Burnham and Anderson 2002). We calculated model-averaged survival estimates using models that had summed Akaike weights of 0.95. We calculated model-averaged survival estimates and associated standard errors in program MARK. Survival estimates are reported as the mean $\pm$ SE. To determine a significant effect of various factors in the model, we evaluated whether regression coefficients (β) and their associated 95% confidence interval overlapped 0. We calculated the coefficient of variation ($CV = [SE(S)/S] \times 100$) to evaluate the precision of our estimates.

RESULTS

Causes of Mortality. We radio-marked 23 Spotted Owls, 3–4 yr postfire, at the Quartz and Timbered Rock burns and adjacent areas in southwest Oregon. From October 2004 to September 2005, five

of 23 radio-marked owls (22%) within and adjacent to the Timbered Rock and Quartz burns died. Four owl carcasses were submitted for necropsy at the VDL at Oregon State University, College of Veterinary Medicine. All four owls were severely emaciated and likely died of starvation. The VDL found no injuries attributable to the radio-transmitter package, and all owls tested negative for West Nile Virus (*Flavivirus*). One owl was not submitted for necropsy because only scattered feathers and the transmitter package were present at the recovery location, which suggested predation was the cause of death. One owl was censored from the analysis from April through May 2005 due to transmitter failure, but was reentered into the analysis in June 2005 after the transmitter was replaced.

Survival Rates. The best model from the first step of our analysis was S(Affected $\neq$ Unaffected; Table 3). Our interpretation of this model was that survival rates were constant among months but lower for owls inside or displaced by the burns (0.96 ± 0.02) compared to owls outside the burns (1.00 ± 0.00). Two models [S(.) and S(Area)] were considered competitive (i.e., within 2 ΔAIC_c units) with the best model (Table 3). Model S(.) indicated that survival rates were constant among months (0.97 ± 0.01) and that there were no differences among groups. Model S(Area) indicated that survival rates were constant among months, but owls outside, inside, and displaced by the burns had the highest (1.00 ± 0.00), intermediate (0.97 ± 0.02), and lowest (0.94 ± 0.04) monthly survival rates, respectively. There was minimal evidence that survival rates varied by sex or were variable over time, because models that incorporated sex and time effects had greater AIC_c values than the null model [S(.)] (Table 3), and their 95% confidence intervals overlapped zero considerably.

Eight models accounted for 95% of the model weight, and all eight models had ΔAIC_c values < 4.00 (Table 3). We calculated model averaged annual survival estimates using these eight models. Model averaged estimates of annual survival for owls inside the burns ($\hat{S} = 0.69 \pm 0.12$) and displaced by the burns ($\hat{S} = 0.66 \pm 0.14$) were similar but were substantially lower than owls outside burned areas ($\hat{S} = 0.85 \pm 0.06$). Likely due to our small sample sizes, our estimates of annual survival did not have a high level of precision with CV values of 17.9%, 20.9%, and 7.3% for owls inside burned areas, displaced by burns, and outside burned areas, respectively.

Table 3. Model selection results for estimation of survival rates of Northern Spotted Owls ($n = 23$) at the Timbered Rock and Quartz burns and surrounding areas in southwestern Oregon, U.S.A., from October 2004 to September 2005, using known-fates models.

MODEL ^a	AIC _c	ΔAIC _c	w _i ^b	K ^c	DEVIANCE
S (Affected ≠ Unaffected)	46.84	0.00	0.28	2	21.27
S (.)	47.60	0.77	0.19	1	24.08
S (Area)	48.42	1.58	0.13	3	20.78
S (lnT)	49.18	2.34	0.09	2	23.61
S (T)	49.48	2.64	0.07	2	23.91
S (Sex)	49.56	2.72	0.07	2	23.99
S (Inside ≠ Outside)	49.62	2.78	0.07	2	24.05
S (TT)	50.12	3.29	0.05	3	22.49
S (Affected ≠ Unaffected * Sex)	50.86	4.02	0.04	4	21.13
S (Area * Sex)	54.55	7.71	0.01	6	20.56
S (t)	58.40	11.56	0.00	12	11.01
S (Area * Sex * t) – Global	265.62	218.78	0.00	72	0.00

^a Variable definitions: . = constant survival, t = survival varies by month, T = linear trend, lnT = log-linear trend, TT = quadratic trend. Affected ≠ Unaffected = owls inside or displaced by burns have different survival than owls burns, Area = owls inside burns, displaced by burns, and outside burns have different survival, Inside ≠ Outside = owls inside burns have different survival than owls outside or displaced by burns.

^b Model weight.

^c No. of parameters.

None of the candidate models that included covariates ranked higher than the best non-covariate model (Table 4), which indicated the covariates explained little of the variation in survival rates. Furthermore, all of the regression coefficients associated with the covariates LOW, MOD, HIGH, SALV, RF, NRF, and LOST had 95% confidence intervals that broadly overlapped zero, indicating a nonsignificant effect of these covariates on survival rates. For example, the regression coefficient and the 95% confidence interval for the LOW parameter

from the best covariate model [S(Affected ≠ Unaffected + LOW)] (Table 4) was -4.11 (95% CI = -10.39 to 2.17 ; CV = 77.9%), which indicated a nonsignificant effect of this parameter on survival.

DISCUSSION

Mean annual survival rates of Spotted Owls displaced by wildfire ($\hat{S} = 0.66 \pm 0.14$) or living within burned areas ($\hat{S} = 0.69 \pm 0.12$) were lower than those outside burned areas in our study ($\hat{S} = 0.85 \pm 0.06$), which supported our initial prediction.

Table 4. Model selection results for known-fates survival estimates of Northern Spotted Owls ($n = 23$) at the Timbered Rock and Quartz burns and surrounding areas in southwestern Oregon, U.S.A., from October 2004 to September 2005, comparing the null model and the best non-covariate model to the four best ranked covariate models.

MODEL ^a	AIC _c	ΔAIC _c	w _i ^b	K ^c	DEVIANCE
S (Affected ≠ Unaffected)	46.84	0.00	0.15	2	42.77
S (Affected ≠ Unaffected + LOW)	47.23	0.39	0.12	3	41.09
S (.)	47.64	0.77	0.10	1	45.82
S (Affected ≠ Unaffected + RF + NRF)	47.68	0.84	0.10	4	39.44
S (Affected ≠ Unaffected + LOST)	48.17	1.33	0.08	3	42.03
S (Affected ≠ Unaffected + NRFL)	48.38	1.54	0.07	3	42.24

^a Variable definitions: Affected ≠ Unaffected = owls inside or displaced by the burn have different survival than owls outside the burn, LOW = suitable habitat that was unburned or burned with a low severity, RF = roosting and foraging habitat that burned with a low or moderate severity, NRF = nesting, roosting, and foraging habitat that burned with a low or moderate severity, LOST = suitable habitat that burned with a high severity or was salvage logged, NRFL = nesting, roosting, and foraging habitat that was unburned or burned with a low severity.

^b Model weight.

^c No. of parameters.

These rates were also lower than estimates of apparent survival [$\hat{\Phi}$ = true survival * (1 – the probability of permanent emigration)] of Spotted Owls in the South Cascades Demography Area ($\hat{\Phi}$ = 0.85 $\pm$ 0.01) and other areas within the subspecies range ($\hat{\Phi}$ = 0.75–0.91 $\pm$ 0.01–0.05; Anthony et al. 2006). Furthermore, annual survival estimates of owls affected by wildfire in our study were lower than apparent survival estimates of California ($\hat{\Phi}$ = 0.81–0.88 $\pm$ 0.02–0.02; Franklin et al. 2004) or Mexican Spotted Owls ($\hat{\Phi}$ = 0.81–0.83 $\pm$ 0.00–0.02; Seamans et al. 1999). Although known-fate and apparent survival estimates are not directly comparable (Φ = S only when permanent emigration is negligible), we believe the comparison is useful because permanent emigration from demographic study areas was typically <2–3% per yr (Forsman et al. 2002, Anthony et al. 2006). Consequently, Anthony et al. (2006) asserted that their estimates of apparent survival were relatively unbiased due to low permanent emigration of territorial adults.

We found no evidence for an effect of fire severity or quantity of habitat on Spotted Owl survival in our study. Consequently, we were unable to support or reject our predictions regarding the effects of these two factors on Spotted Owl survival. However, other studies indicated that Spotted Owl survival in landscapes that have not burned recently was positively associated with increased amounts of old and mature forest (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005) and negatively associated with increased amounts of early seral forest (Dugger et al. 2005). High severity fire and salvage logging removed 30% and 41% of the habitat available at the Timbered Rock and Quartz burns, respectively (Table 1), and much (27–28%) of the remaining areas within the burns were composed of non-habitat. Consequently, we suspect that past logging activities on federal and private lands plus loss of mature and older forest to high severity wildfire and salvage logging jointly contributed to the low survival rates observed in our study. Only 31% and 43% of the area within the Quartz and Timbered Rock burns were composed of habitat with low or moderate severity burns, respectively, and these amounts of habitat are below those needed for maximum survival of Spotted Owls (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). Further research is needed to clarify the relationship between wildfire and Spotted Owl survival.

In addition to habitat loss, survival rates in post-fire landscapes may be influenced by habitat degrada-

tion in stands of low to moderate severity fire due to delayed tree mortality (Gaines et al. 1997), changes in microclimate (Barrows 1981), changes in prey abundance (Lehmkuhl et al. 2006), or increased predator abundance (Carey et al. 1992). Survival of territorial raptors is often influenced by prey abundance (Wenland 1984, Steenhof et al. 1997, Brommer et al. 1998). Clark (2007) found that postfire owl diets in this study were dominated by woodrats (*Neotoma* spp.; 49% of biomass consumed), which is typical for this portion of the subspecies' range (Forsman et al. 2004). Although we did not estimate small mammal abundance following wildfire, the severely emaciated condition of owls submitted for necropsy suggested that owls struggled to obtain food resources in postfire landscapes. Furthermore, Clark (2007) found that home ranges of Spotted Owls following the Timbered Rock fire were 286 $\pm$ 105 ha larger than those of owls that inhabited the area prior to fire in the late 1980s. We suspect that owls in postfire landscapes utilized larger areas to obtain sufficient food resources, which required increased energy expenditures and ultimately influenced individual fitness (Carey et al. 1992, Ward et al. 1998). If wildfire reduced prey abundance and negatively affected Spotted Owl survival, we suspect the effects are short in duration and survival rates will increase over time as habitat and prey abundance return to prefire conditions.

Competition with Barred Owls has been identified as one of the major threats to the persistence of Spotted Owls (USFWS 2008). Barred Owls have a more generalist diet (Hamer et al. 2001) and utilize a wider range of habitats (Hamer et al. 2007) than Spotted Owls, and Barred Owls appear to decrease territory occupancy of Spotted Owls (Kelly et al. 2003, Olson et al. 2005). During our demographic surveys of nine Spotted Owl territories at the Quartz burn and 22 Spotted Owl territories at the Timbered Rock burn from 2003 to 2006, we detected only one Barred Owl (Oregon Cooperative Wildlife Research Unit unpubl. data). This indicated that Barred Owls were not abundant on our study areas and were not a potential influence on survival of Spotted Owls during our study.

Based on our results, we believe that the combination of past timber harvest, severe fire, and salvage logging were responsible for the low survival rates during our study in the short-term. Our study assessed Spotted Owl survival 3–4 yr postfire; consequently, we were unable to comment on the ability

of Spotted Owls to survive in burned landscapes over the long-term. Additional radiotelemetry studies in future years or long-term demographic studies are needed to identify the time required for Spotted Owl survival to increase to prefire levels and to assess the long-term persistence of Spotted Owls in burned landscapes.

Despite our findings of negative short-term effects of wildfire on Spotted Owl survival, we caution that the results may not be applicable to other fire-prone landscapes. The majority of our sample came from the Timbered Rock burn, which was dominated by a checkerboard pattern of private and federally (Bureau of Land Management) administered lands. Most of the private lands were logged previously and salvage logged after the fire. In addition, federally managed lands were subjected to considerable timber harvest prior to the fires; all of these influences led to high levels of fragmentation and large areas of forest unsuitable for Spotted Owls throughout the landscape. This undoubtedly exacerbated or confounded our ability to assess the effects of wildfire on survival rates in this study. Given the large degree of variability in forest types, fire hazards, and intensities throughout the species range, additional studies are needed before definitive conclusions can be reached. Therefore, we urge caution when applying our findings to forest management or recovery planning for Spotted Owls.

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Appendix. The mean proportion of cover types or length (km) of edge between suitable and unsuitable habitat within 95% fixed kernel home ranges of Northern Spotted Owls inside and outside the Timbered Rock and Quartz burns in southwestern Oregon, U.S.A.

GROUP	HABITAT TYPE								
	LOW ^a	MOD ^b	HIGH ^c	SALV ^d	LOST ^e	RF ^f	NRF ^g	NRFL ^h	EDGE ⁱ
Inside Burn (<i>n</i> = 11)									
Mean	0.41	0.14	0.08	0.11	0.18	0.15	0.39	0.31	25.7
SD	0.13	0.07	0.04	0.09	0.09	0.07	0.11	0.11	12.7
Range	0.24–0.66	0.04–0.31	0.02–0.13	0.01–0.27	0.04–0.32	0.09–0.27	0.18–0.52	0.14–0.49	9.8–58.2
Outside Burn (<i>n</i> = 12)									
Mean	0.71	0.01	0.00	0.02	0.02	0.21	0.50	0.49	15.3
SD	0.13	0.01	0.00	0.02	0.03	0.09	0.13	0.13	10.0
Range	0.52–0.89	0.00–0.04	0.00–0.02	0.00–0.07	0.00–0.08	0.14–0.41	0.34–0.73	0.33–0.72	1.8–38.1

^a LOW—Suitable habitat that was unburned or burned with a low severity.
^b MOD—Suitable habitat that burned with a moderate severity.
^c HIGH—Suitable habitat that burned with a high severity.
^d SALV—Suitable habitat that received any level of postfire salvage logging.
^e LOST—Suitable habitat that burned with a high severity or was salvage logged.
^f RF—Roosting and foraging habitat that burned with a low or moderate severity.
^g NRF—Nesting, roosting, and foraging habitat that burned with low or moderate severity.
^h NRFL—Nesting, roosting, and foraging habitat that was unburned or burned with a low severity.
ⁱ EDGE—The length of edge habitat (m) within the home range, defined as the interface between suitable and unsuitable habitats.



Research Article

Relationship Between Wildfire, Salvage Logging, and Occupancy of Nesting Territories by Northern Spotted Owls

DARREN A. CLARK,¹ Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

ROBERT G. ANTHONY, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

LAWRENCE S. ANDREWS, Oregon Cooperative Fish and Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, OR 97331, USA

ABSTRACT The northern spotted owl (*Strix occidentalis caurina*) is one of the most intensively studied raptors in the world; however, little is known about the impacts of wildfire on the subspecies and how they use recently burned areas. Three large-scale wildfires in southwest Oregon provided an opportunity to investigate the short-term impacts of wildfire and salvage logging on site occupancy of spotted owls. We used Program MARK to develop single-species, multiple-season models of site occupancy using data collected during demographic surveys of spotted owl territories. In our first analysis, we compared occupancy dynamics of spotted owl nesting territories before (1992–2002) and after the Timbered Rock burn (2003–2006) to a reference area in the south Cascade Mountains that was not affected recently by wildfire. We found that the South Cascades had greater colonization probabilities than Timbered Rock before and after wildfire ($\hat{\beta} = 1.31$, 95% CI = 0.60–2.03), and colonization probabilities declined over time at both areas ($\hat{\beta} = -0.06$, 95% CI = -0.12 to 0.00). Extinction probabilities were greater at South Cascades than at Timbered Rock prior to the burn ($\hat{\beta} = 0.69$, 95% CI = 0.23–2.62); however, Timbered Rock had greater extinction probabilities following wildfire ($\hat{\beta} = 1.46$, 95% CI = 0.29–2.62). The Timbered Rock and South Cascades study areas had similar patterns in site occupancy prior to the Timbered Rock burn (1992–2006). Furthermore, Timbered Rock had a 64% reduction in site occupancy following wildfire (2002–2006) in contrast to a 25% reduction in site occupancy at South Cascades during the same time period. This suggested that the combined effects of habitat disturbances due to wildfire and subsequent salvage logging on private lands negatively affected site occupancy by spotted owls. In our second analysis, we investigated the relationship between wildfire, salvage logging, and occupancy of spotted owl territories at the Biscuit, Quartz, and Timbered Rock burns from 2003 to 2006. Extinction probabilities increased as the combined area of early seral forests, high severity burn, and salvage logging increased within the core nesting areas ($\hat{\beta} = 1.88$, 95% CI = 0.10–3.66). We were unable to identify any relationships between initial occupancy and colonization probabilities and the habitat covariates that we considered in our analysis where the β coefficient did not overlap zero. We concluded that site occupancy of spotted owl nesting territories declined in the short-term following wildfire, and habitat modification and loss due to past timber harvest, high severity fire, and salvage logging jointly contributed to declines in site occupancy. © 2012 The Wildlife Society.

KEY WORDS colonization, extinction, northern spotted owl, occupancy, salvage logging, site occupancy, southwest Oregon, *Strix occidentalis caurina*, wildfire.

Northern spotted owls (*Strix occidentalis caurina*, hereafter spotted owl) are a medium sized, forest-dwelling owl with high levels of mate and site fidelity (Forsman et al. 1984, 2002; Thomas et al. 1990; Zimmerman et al. 2007). Nesting territories of spotted owls have greater proportions of mature and older forest than surrounding landscapes (Ripple et al. 1991, 1997; Meyer et al. 1998; Swindle et al. 1999). Forest

stands used by spotted owls have large proportions of downed woody debris and snags, high canopy closure, and high structural diversity (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000). The features that provide structural complexity within spotted owl habitat also serve as ladder fuels that increase the likelihood of stand-replacing wildfire (Agee 1993, Wright and Agee 2004). As a result, forest stands that provide favorable habitat conditions for spotted owls within dry forest ecosystems are at risk of stand-replacing wildfire (Agee 1993, Agee et al. 2000). Presently, wildfire is the leading cause of spotted owl habitat

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¹E-mail: darren.clark@oregonstate.edu

modification on federally administered lands, and the rate of habitat modification due to wildfire within dry forest ecosystems has exceeded predictions (Davis and Lint 2005). Consequently, the viability of owl populations in dry forests has been questioned (Spies et al. 2006), and wildfire has been identified as a threat to the persistence of spotted owls occupying dry forest ecosystems (U.S. Fish and Wildlife Service [USFWS] 2011).

Despite the perceived threat of wildfire, little is known about the effects of wildfire on spotted owls, and the hypothesized effects come from research conducted in unburned landscapes. Numerous studies have documented that spotted owl survival, reproduction (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005), and territory occupancy (Blakesley et al. 2005, Dugger et al. 2011) were positively associated with increased amounts of late-successional forest within their core use areas or home range. Furthermore, owl territories with large reductions in the amount of older forest will have low reproduction or be abandoned (Bart and Forsman 1992, Bart 1995). These studies suggest that loss of older forests negatively affects spotted owls; however, the response of spotted owls to high severity fire and subsequent harvest of dead standing trees is unknown. Conversely, survival rates of spotted owls were greater at territories that were not entirely composed of late-successional forests (Franklin et al. 2000, Olson et al. 2004), which suggests that spotted owls may be adapted to natural disturbances such as wildfire that create a mosaic of forest conditions. Territory occupancy and nest success of spotted owls decreased as the amount of the territory composed of clear-cuts increased (Thraill et al. 1998), which suggests widespread post-fire salvage logging may negatively affect spotted owls.

The few studies that have been conducted on spotted owls in burned landscapes have provided equivocal results regarding the effects of wildfire on the species. Lack of consensus between studies may be owing to the confounding effects of salvage logging, the short-term nature of studies, small sample sizes from which to draw inference, treating the effect of fire as a binomial variable (i.e., burned or unburned), or potentially different responses of the 3 subspecies of spotted owls to wildfire. Radio-marked northern and California spotted owls (*Strix occidentalis occidentalis*) used forest stands that burned with low to high severities (Clark 2007, Bond et al. 2009); however, survival rates of radio-marked northern spotted owls occupying a burned area that was subsequently salvage logged were less than others reported throughout the subspecies' range (Clark et al. 2011). Conversely, short-term (<1 yr) survival rates of northern, Mexican (*Strix occidentalis lucida*), and California spotted owls in burned landscapes that were not subjected to post-fire salvage logging were similar to annual survival rates (Bond et al. 2002). The number of reproductive spotted owl pairs and the number of occupied spotted owl territories declined 1 year post-fire on the eastern slope of the Washington Cascade Range (Gaines et al. 1997); however, only 6 territories were surveyed in this study, 1 of which had a large amount of stand-replacing fire. Other studies indicate low and moderate severity burns may have

minimal impacts on spotted owls. Territory occupancy of Mexican spotted owls in burned areas was similar to unburned areas (Jenness et al. 2004). Probability of territory occupancy for California spotted owls in the Sierra Nevada Mountains of California were similar between randomly selected burned and unburned sites (Roberts et al. 2011).

Because spotted owls are territorial and have high site fidelity (Forsman et al. 2002, Zimmerman et al. 2007), occupancy of nesting territories is essential for successful survival and reproduction. Occupancy models (MacKenzie et al. 2003, 2006) are well suited for investigating territory occupancy by spotted owls because the structure of existing spotted owl surveys (Franklin et al. 1996) fits the model framework well. Furthermore, occupancy models allow the inclusion of site-specific covariates, which allows the investigation of fire severity and habitat influences on site occupancy dynamics (i.e., extinction and colonization rates). The Biscuit, Quartz, and Timbered Rock burns in southwest Oregon provided an opportunity to investigate the impacts of wildfire and subsequent salvage logging on site occupancy by spotted owls. Our first objective was to determine if occupancy rates changed substantially following wildfire and subsequent salvage logging when compared to pre-burn occupancy rates and to occupancy rates in a landscape that had not been recently affected by wildfire. We met this objective by comparing occupancy rates of spotted owls before (1992–2002) and after (2003–2006) the Timbered Rock burn to an adjacent unburned landscape in the southern Oregon Cascades. We predicted that occupancy rates of spotted owls would be similar between study areas prior to the Timbered Rock burn but occupancy rates would decline substantially following the Timbered Rock burn in response to modification and loss of owl habitat from wildfire and subsequent salvage logging. Our second objective was to model the impacts of fire severity, salvage logging, and habitat characteristics on site occupancy of spotted owls at the Biscuit, Quartz, and Timbered Rock burns from 2003 to 2006. We predicted that extinction probabilities would increase as the amounts of past timber harvest, high severity burn, and salvage logging within a territory increased. We also predicted that initial occupancy and colonization probabilities within the 3 burned areas would be greater at territories with decreased levels of disturbance. In particular, we predicted that initial occupancy and colonization probabilities within the 3 burned areas would be greater at territories that had more intermediate-aged and older forest that burned with low or moderate severities.

STUDY AREA

We studied site occupancy by spotted owls at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon. Each burn was located within a distinct geographic region: the mid-Coastal Siskiyou Mountains (Biscuit burn), the Siskiyou Mountains (Quartz burn), and the southern Oregon Cascades (Timbered Rock burn). We also analyzed site occupancy of spotted owls at the South Cascades Demographic Study Area, which was adjacent to the

Timbered Rock burn and was not affected by a large scale wildfire within the last 100 years. Consequently, site occupancy by spotted owls in this area served as a reference for comparison to the Timbered Rock study area.

Common tree species within our study areas included ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), Douglas-fir (*Pseudotsuga menziesii*), incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), California red fir (*A. magnifica*), mountain hemlock (*Tsuga mertensiana*), Oregon white oak (*Quercus garryana*), California black oak (*Q. kelloggii*), tanoak (*Lithocarpus densiflorus*), and Pacific madrone (*Arbutus menziesii*). Prior to the implementation of active fire suppression policies by state and federal agencies, most of southwest Oregon was characterized by frequent low-intensity fires and occasional stand-replacing fires at higher elevations (Agee 1993, Taylor and Skinner 1997, Heyerdahl et al. 2001). After active fire suppression policies were implemented, fire frequencies declined and high-intensity wildfires became more common (Agee 1993, Agee and Skinner 2005). The climate regime in southwest Oregon is characteristically temperate with hot, dry summers and cool, moist winters. During our study, the warmest and coldest average daily temperatures occurred in July (21° C) and December (4° C), respectively. Average annual rainfall was lowest at the Quartz burn (66 cm) and highest at the Biscuit burn (113 cm; Oregon Climate Service, Oregon State University, unpublished data).

The Biscuit burn originated from several lightning strikes in July 2002. The small fires eventually merged into a complex fire that covered 201,436 ha. Land ownership within the burn was predominantly public (U.S. Forest Service [USFS], Bureau of Land Management [BLM], Oregon Department of Forestry [ODF], and Josephine County). Fifty documented spotted owl territories were within the burn. We non-randomly selected a sample of 9 territories on the eastern side of the burn to include in our study that were in xeric forest types and provided reasonable access. The 9 territories included in this study were located within the Briggs Creek, Silver Creek, Deer Creek, and Illinois River watersheds, ranging in elevation from 300 to 1,400 m. The remaining 41 territories were not included in our study because of logistical concerns or because they were located in mesic forest types on the western side of the burn. The 9 study territories were surveyed annually from 2003 to 2006. The area within 2.2 km of the 9 study territories burned with a

mixed severity and received the least amount of salvage logging of the 3 burns (Table 1).

The Quartz burn was ignited by lightning in August 2001 and burned 2,484 ha of public (USFS, BLM, and ODF) and private (primarily industrial forest) lands. The fire burned portions of the Glade Creek, Little Applegate, and Yale Creek watersheds at elevations ranging from 600 to 1,850 m. The fire completely or partially burned (i.e., burned the majority of a 2.2-km buffer around the territory center) 9 spotted owl territories. All 9 territories were surveyed annually from 2003 to 2006. The study area burned with a mosaic of fire severities and was subjected to substantial amounts of salvage logging, primarily on private lands (Table 1).

The Timbered Rock burn was ignited by lightning in July 2002 and burned 11,028 ha of land within the Elk Creek watershed at elevations ranging from 450 to 1,350 m. Land ownership was dominated by a checkerboard pattern of public (BLM) and private industrial forest lands in the southern two-thirds of the burn and contiguous USFS managed lands in the northern third. Twenty-two spotted owl territories were within the burn perimeter and were surveyed annually from 2003 to 2006. These 22 territories were also surveyed prior to the burn from 1992 to 2002. The study area burned with a mixed severity and much of the private land was salvage logged (Table 1).

The South Cascades Demographic Study Area (South Cascades) is 1 of 8 study areas included in the range-wide monitoring program for spotted owls (Lint et al. 1999, Anthony et al. 2006) and it served as a reference area for our analyses. From 1992 to 2006, surveys to locate spotted owls were consistently conducted on an annual basis at 103 spotted owl territories by the Oregon Cooperative Fish and Wildlife Research Unit (OCFWRU). The South Cascades area encompasses approximately 223,000 ha of lands managed by the USFS at the southern terminus of the Oregon Cascades and at elevations ranging from 900 to 2,000 m. No large-scale wildfires occurred within the study area from 1992 to 2006. Forest conditions have been influenced historically by mixed-severity wildfire and more recently by forest management, livestock grazing, and fire suppression. Forest management has included individual tree selection, stand thinning, and even-aged management (U.S. Department of Agriculture [USDA] 1997, 1998). Current management activities are guided by the objectives set forth by the Land-use Allocations of the Northwest Forest Plan.

Table 1. The percentage ($\pm$ SE) early seral, intermediate-aged, and older forest that burned with a low or moderate severity or was salvage logged within 2,230 m of 40 northern spotted owl territories at the Biscuit, Quartz, and Timbered Rock burns in southwest, Oregon, USA from 2003 to 2006.

Study area	Non-forest or early seral	Intermediate-aged or older forests			
		Low severity ^a	Moderate severity ^b	High severity ^c	Salvage logged ^d
Biscuit	27.2 $\pm$ 6.1	40.5 $\pm$ 6.7	13.6 $\pm$ 1.8	17.1 $\pm$ 3.6	1.6 $\pm$ 0.7
Timbered Rock	27.8 $\pm$ 1.6	35.9 $\pm$ 4.1	10.1 $\pm$ 0.7	9.3 $\pm$ 1.4	16.9 $\pm$ 3.2
Quartz	21.7 $\pm$ 1.5	48.5 $\pm$ 4.4	6.6 $\pm$ 1.5	10.0 $\pm$ 2.3	13.2 $\pm$ 2.7

^a $\leq$ 20% of the forest canopy removed by wildfire.

^b 21–70% of the forest canopy removed by wildfire.

^c $>$ 70% of the forest canopy removed by wildfire.

^d Areas that were intermediate-aged or older forest prior to the burn that were salvage logged.

The main purpose of matrix lands is timber production, whereas the late-successional reserves are for conservation of older forests and silvicultural treatments are intended to promote forest stand structures similar to historical conditions or old forest characteristics (USDA and U.S. Department of the Interior [USDI] 1994).

METHODS

Data Acquisition and Preparation

To assess the effects of wildfire on occupancy of spotted owl territories, we created post-fire habitat maps in ArcGIS 9.1 (ESRI, Redlands, CA) by merging 3 data layers: 1) a pre-fire habitat map (Davis and Lint 2005), 2) a fire severity map, and 3) the boundaries of salvage logged areas (see Clark 2007 for additional details). The final map output had 8 distinct habitat classes (Table 2) and a minimum mapping unit of 2 ha. We used ground plot data to calculate map accuracies, which we estimated to be 68% for the Timbered Rock burn, 69% for the Biscuit burn, and 75% for the Quartz burn. Seventeen of 20 (85%) classification errors at the Biscuit burn, 10 of 15 (67%) at the Quartz burn, and 11 of 22 (50%) at the Timbered Rock burn were within 1 habitat or fire severity class of the correct classification. Based on these estimates, overall map accuracy within 1 habitat or fire severity class was 95% at the Biscuit burn, 92% at the Quartz burn, and 84% at the Timbered Rock burn (Clark 2007).

We conducted annual surveys between 1 March and 31 August to determine the occupancy of spotted owls on nesting territories according to established survey protocols (Franklin et al. 1996) and Oregon State University, Institutional Animal Care and Use Committee guidelines (IACUC Number 3040). Post-fire surveys were conducted as a collaborative effort between the OCFWRU, the BLM, the USFS, and private timber companies. From 1992 to 2006, we surveyed 22 and 103 territories at the Timbered Rock and South Cascades study areas, respectively. We also surveyed 9 territories at both the Biscuit and Quartz burns from 2003 to 2006. The average number of visits conducted varied by study area and year (range: 1.9 [Timbered Rock 2002]–5.8 [Timbered Rock 1994]). The maximum number of surveys at individual spotted owl territories ranged from 7 to 9

depending on the year. The variability in survey effort was a function of occupancy and nesting status (i.e., territories that were occupied by a pair of non-nesting owls were visited less). Occasionally, some territories were not surveyed every year, which was most often because of limited access during years of high snowfall. Fortunately, differences in survey effort and missing observations can easily be accounted for in open population models if you assume that occupancy dynamics are the same at territories that are and are not surveyed (MacKenzie et al. 2006), which is a reasonable assumption as long as survey effort is unbiased.

We used results from demographic surveys to create site-specific detection histories for owl pairs. Owl pairs represent the appropriate ecological unit of interest when modeling site occupancy. Protocols for adapting survey data from spotted owls using methods outlined in Franklin et al. (1996) to fit an occupancy modeling framework were established by Olson et al. (2005). These protocols were used in subsequent occupancy analyses for spotted owls (Kroll et al. 2010, Dugger et al. 2011) and this analysis. If a pair of owls was detected, we coded the visit as a 1 and if 1 or no owls were detected, we coded the visit as a 0. However, if 1 owl was detected and the owl exhibited nesting behavior (e.g., the owl was observed on a nest) or if young were observed with an adult owl, we coded the visit as a 1. If a survey was not conducted, we coded the visit as a missing observation (·). A hypothetical detection history of 10.1 would indicate that a pair of owls was detected on the first and fourth surveys, no owls or a single owl was detected on the second survey, and the territory was not visited during the third survey.

Data Analyses

Basic modeling procedures.—We estimated site occupancy in Program MARK (White and Burnham 1999) using single-species, multiple-season models (MacKenzie et al. 2003, 2006). This analysis generated estimates of 4 parameters: Ψ , the probability that a site is occupied in the first year of the study (initial occupancy); ϵ , the probability an occupied site became unoccupied the subsequent year (extinction); γ , the probability an unoccupied site was occupied the subsequent year (colonization); and P , the probability of detection (detection). In our analyses, primary sampling occasions were years and secondary sampling occasions were visits to

Table 2. Definitions of habitats used in the assessment of the impacts of wildfire and salvage logging on northern spotted owl site occupancy at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon, USA, from 2003 to 2006.

Habitat class	Description
Early seral	Non-forested areas, early seral and pole sized conifer stands
Intermediate forest ^a —low severity burn	Intermediate-aged conifer stands with ≤20% of the canopy removed by fire
Intermediate forest—moderate severity burn	Intermediate-aged conifer stands with 21–70% of the canopy removed by fire
Older forest ^b —low severity burn	Older conifer forest with ≤20% of the canopy removed by fire
Older forest—moderated severity burn	Older conifer forest with 21–70% of the canopy removed by fire
High severity	Intermediate-aged and older conifer forests with >70% of the canopy removed by fire
Salvage	Intermediate-aged and older conifer forests that were salvage logged
Edge	The interface between the combined area of intermediate-aged and older forest that burned with a low or moderate severity and all other habitat types

^a Forest stands that provide suitable roosting and foraging habitat for spotted owls.

^b Forest stands that provide nesting habitat for spotted owls.

territories within years. This modeling framework was flexible and allowed for time-specific parameter estimates, inclusion of site-specific covariates, the ability to include missing observations, the direct estimation of colonization and extinction, and it assumed detection probabilities were <1 (MacKenzie et al. 2003, 2006).

We modeled the 4 occupancy parameters using a step-wise approach (Olson et al. 2005, MacKenzie et al. 2006, Dugger et al. 2011). We first determined the most parsimonious model for within year detection probabilities followed by among year detection probabilities, retained that model, and then proceeded to model initial occupancy. We then retained the most parsimonious model for initial occupancy and proceeded to model colonization and extinction parameters. We followed the conventions of Lebreton et al. (1992) and White and Burnham (1999) when developing and naming models. We considered several possible temporal effects on detection probabilities both within and among years that included constant detection ($\cdot$), linear (T), log-linear ($\ln T$), and quadratic (TT) trends. We did not evaluate time-specific models (t) within years because they required estimation of too many parameters to obtain reasonable estimates (Olson et al. 2005); however, we considered models that included time-specific effects among years (year). We also considered models that included differences in detection probabilities between study areas, because experience and effort of survey personnel may have differed. We considered 2 initial occupancy models that contrasted differences between study areas (area) and constant initial occupancy ($\cdot$). When modeling extinction and colonization parameters, we considered models that compared differences between study areas (area) and no differences between areas ($\cdot$), and we considered several biologically plausible temporal effects including constant rates among years ($\cdot$), variable rates among years (t), and linear (T), log-linear ($\ln T$), and quadratic (TT) trends over time. Models that included ≥ 2 study areas included additive and interactive effects between study area and temporal effects, where appropriate.

We used Akaike's Information Criterion corrected for small sample sizes (AIC_c) and the difference between the AIC_c value of the best model and the i th model (ΔAIC_c) to rank and compare candidate models at each step of the analysis. We used Akaike weights to evaluate the strength of evidence for 1 model versus another model (Burnham and Anderson 2002). We considered models that were ≤ 2.0 AIC_c of the best model as competitive. We used estimates of regression coefficients ($\hat{\beta}$) and their 95% confidence intervals to evaluate the relative effect and measure of precision of various covariates in our models. Following the approach outlined by Anthony et al. (2006), we used 95% confidence intervals for the coefficients as a relative measure of support for observed relationships rather than a strict test of the hypothesis that $\beta = 0$. Covariates whose 95% confidence intervals did not overlap 0 had strong evidence for an effect, those that narrowly overlapped 0 had some evidence for an effect, and those that broadly overlapped 0 had little or no evidence for an effect on the parameter of interest. We used this approach because significance testing is not valid under

an information theoretical approach (Burnham and Anderson 2002) and it is best to present estimates of effect size and precision under this analysis paradigm (Anderson et al. 2000).

Comparison of South Cascades and Timbered Rock.—We compared occupancy at Timbered Rock and South Cascades from 1992 to 2006. Our objective was to determine if extinction and colonization probabilities following the Timbered Rock burn were different from unburned landscapes in the South Cascades (i.e., the control) during the same time period. In this analysis, we considered all study area and temporal effects on site occupancy parameters that are outlined above in the basic modeling procedures. In addition, we considered 10 models for colonization and extinction that were modifications of common study area and time effect models (Fig. 1). We considered these models because they may identify distinct changes in extinction and colonization rates following a disturbance such as wildfire and subsequent salvage logging. We predicted that under model [Pre-burn($\cdot$)Post-burn(area)] the South Cascades and Timbered Rock would have similar, constant extinction probabilities prior to the Timbered Rock burn, but extinction probabilities would be greater at Timbered Rock following the burn. In contrast, we predicted the opposite for colonization probabilities (e.g., under model [Pre-burn($\cdot$)Post-burn(area)], colonization rates would be equal at Timbered Rock and South Cascades prior to the Timbered Rock burn, but colonization rates would be lesser at the Timbered Rock study area following the burn). We retained the best ranked initial occupancy, extinction, colonization, and detection probability models and combined them to determine our best overall model. We used the best overall model to calculate estimates of year-specific probabilities of site occupancy in Program MARK using the equation from MacKenzie et al. (2003):

$$\hat{\Psi}_t = \hat{\Psi}_{t-1}(1 - \hat{\varepsilon}_{t-1}) + (1 - \hat{\Psi}_{t-1})\hat{\gamma}_{t-1}$$

Relationship between wildfire, salvage logging, and spotted owl site occupancy.—We modeled occupancy of nesting territories after fires from 2003 to 2006 at the Biscuit, Quartz, and Timbered Rock burns. Our objective was to model the potential influence of fire severity, salvage logging, and habitat covariates on site occupancy of spotted owls. In this analysis, we used a multiple step approach outlined in previous occupancy analyses for the species (Olson et al. 2005, Dugger et al. 2011). This approach included 3 steps: 1) determine the occupancy model that best described temporal and study area effects, 2) retain the best model from step 1 and model individual covariates to determine the best spatial scale and relationship of the covariate, and 3) retain the best model from step 1 and the best spatial scale and relationship of covariates from step 2 to test specific hypotheses regarding the effects of covariates on site occupancy.

Our first step was to determine the best model that only included study area and temporal effects by following the methods outlined in the basic modeling procedures. Our

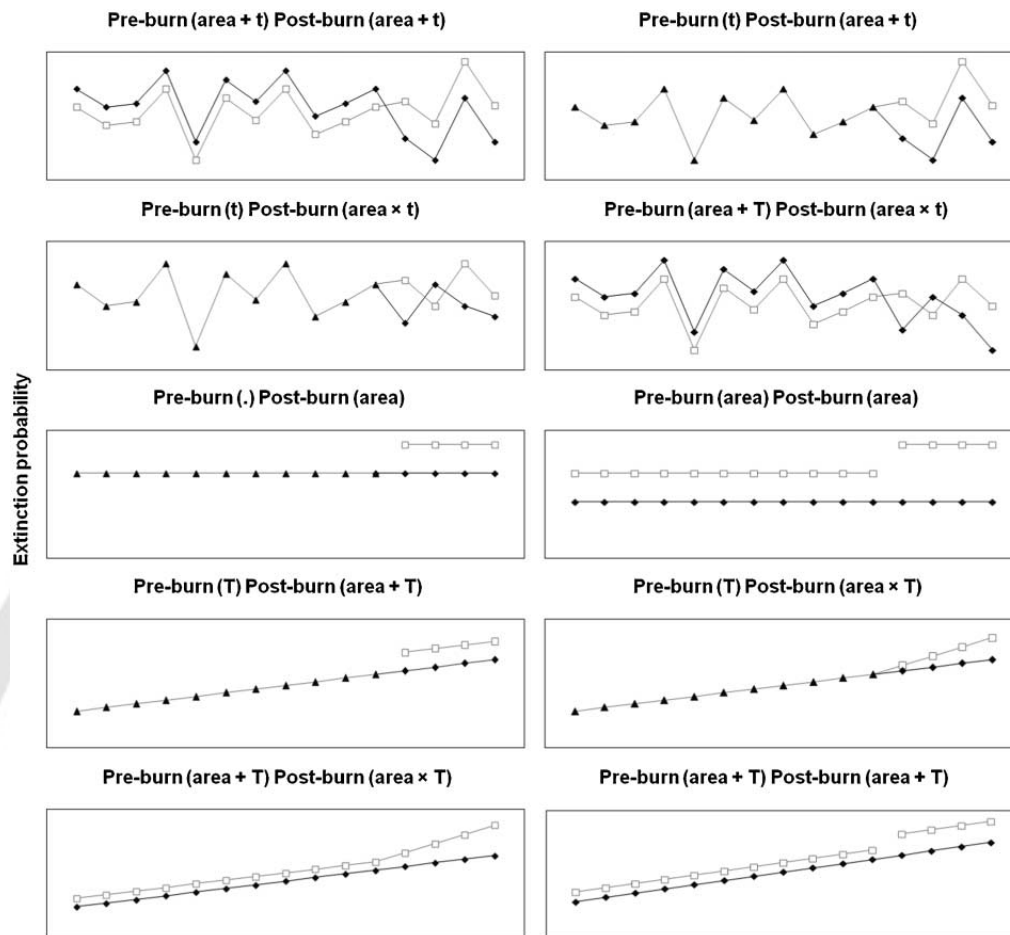


Figure 1. Visual representation of 10 hypothetical models comparing extinction rates of northern spotted owl territories at the Timbered Rock burn and South Cascades Demographic Study Area. We considered models that compared differences between study areas (area) and no differences between areas ($\cdot$), and we considered several biologically plausible temporal effecting including constant rates among years ($\cdot$), variable rates among years (t), and linear (T) trends over time. The last 4 intervals represent the predicted changes in extinction probabilities following the Timbered Rock burn. The opposite relationship was predicted for colonization rates. Grey lines with open boxes represent the Timbered Rock study area, black lines with black diamonds represent the South Cascades Demographic Study Area, and gray lines with black triangles represent no differences between study areas.

objective in this step, was to develop a base model upon which we modeled the effects of covariates. We considered all models outlined in the basic modeling procedures and 3 additional study area covariates for initial occupancy, extinction, and colonization models that incorporated various study area combinations including, 1) the Quartz and Timbered Rock burns would have similar occupancy dynamics because they include large amounts of private land ($BIS \neq TR = Q$), 2) the Timbered Rock and Biscuit burns would have similar occupancy dynamics because they occurred 1 year after the Quartz burn ($BIS = TR \neq Q$), and 3) the Quartz and Biscuit burns would have similar occupancy dynamics because they are both located in the Siskiyou Mountains ($BIS = Q \neq TR$). Our primary objective during this portion of the analysis was to develop a parsimonious model on which to model covariates; consequently, we did not consider competing models in this step of the analysis. After determining the best study area and temporal effects model, we retained this model and proceeded to the second step of the analysis.

In the second step of this analysis, our objective was to determine the spatial scale and relationship that best

explained the effect of various covariates on initial occupancy, extinction, and colonization probabilities. We calculated site-specific covariates at 2 spatial scales (territory and core area) and with 2 relationships (linear and log-linear), which represented 4 possible models for each covariate. We calculated covariate values in ArcGIS 9.1 from post-fire habitat maps as the percent of each cover type within a 2,230-m radius (1,560 ha; territory scale) and a 730-m radius (167 ha; core area scale) of the territory center. We selected these spatial scales because they were used to model spotted owl survival and reproduction in the same geographic region (Dugger et al. 2005).

For initial occupancy and colonization probabilities, we modeled 9 covariates (Table 3) to determine the best spatial scale and relationship of the covariate. All of the covariates we modeled on initial occupancy and colonization parameters were thought to represent the quality of habitat remaining at the territory and were based on biologically meaningful relationships. Forested areas that burned with a low or moderate severity likely had minimal changes in the amount of canopy cover, snags, and downed woody debris, which are all critical components of spotted owl habitat (Hershey et al.

Table 3. Candidate model sets for initial occupancy, extinction, and colonization parameters in the analysis of covariate effects on site occupancy of northern spotted owls at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon, USA, from 2003 to 2006.

Initial occupancy (Ψ) and colonization (γ) ^a	Extinction (ϵ) ^b
INTL + INTM + OLDL + OLDM	EARLY + HIGH + SALVAGE
INTL + OLDL	HIGH + SALVAGE
INT + OLD	HARVEST + HIGH
OLDL + OLDM	EARLY + HISALV
OLDL	HISALV
OLD	HARVEST
LOW + MOD	SALVAGE
LOW	HIGH
EDGE	EARHISALV
	EDGE

^a INTL, intermediate-aged forest that burned with a low severity; INTM, intermediate-aged forest that burned with a moderate severity; OLDL, older forest that burned with a low severity; OLDM, older forest that burned with a moderate severity; INT, intermediate-aged forest that burned with a low or moderate severity (combined area of INTL and INTM); OLD, older forest that burned with a low or moderate severity (combined area of OLDL and OLDM); LOW, intermediate-aged and older forest that burned with a low severity (combined area of INTL and OLDL); MOD, intermediate-aged and older forest that burned with a moderate severity (combined area of INTM and OLDM); EDGE, the interface between forested areas that burned with low or moderate severity and areas that were early seral stands, burned with high severity, or were salvage logged; EDGE was modeled as an additive effect with the best ranked covariate model to determine if it improved model fit.

^b EARLY, non-forested areas early seral stands that burned with any severity; HIGH, the combined area of intermediate-aged and older forest that burned with a high severity; SALVAGE, any intermediate-aged or older forest that was salvage logged; HARVEST, any forested area, that was harvested before or after the burn (combined area of EARLY and SALVAGE); HISALV, any forested area, excluding early stands, that burned with a high severity or was salvage logged (combined area of HIGH and SALVAGE); EARHISALV, any early seral stand or forested area that burned with high severity or that was salvage logged (combined area of EARLY, HIGH, and SALVAGE).

1998, North et al. 1999, Irwin et al. 2000). Intermediate-aged forests contribute to landscape heterogeneity, which influenced spotted owl survival in other studies (Franklin et al. 2000, Olson et al. 2004), so we hypothesized that it would also influence site occupancy by the subspecies. Spotted owl territories usually have high proportions of mature and older forests (Ripple et al. 1991, 1997; Meyer et al. 1998; Swindle et al. 1999), so we expected that initial occupancy and colonization probabilities would be influenced by the amount of older forest within the territory.

We elected to use a different set of covariates on extinction probabilities because of the highly correlated nature of extinction and colonization probabilities (MacKenzie et al. 2006). Modeling the same set of covariates on extinction and colonization parameters can result in counter-intuitive results. This is because sites that went extinct are the sites available for colonization. As a result, factors that contribute to increased extinction probabilities could also contribute to increased colonization probabilities. For extinction models, we modeled 7 covariates (Table 3) to determine the best spatial scale and relationship of the covariate. All of the covariates considered for extinction were thought to be

related to the impacts of habitat loss and modification attributable to past timber harvest, high severity fire, and salvage logging. We hypothesized that all 3 of these factors would negatively affect site occupancy. Spotted owl territories that had increased amounts of clear-cut timber harvest had decreased occupancy (Thraillkill et al. 1998^{Q1}). Timber harvest and post-fire salvage commonly results in large-scale clear-cuts, as a result, site occupancy by owls should be negatively affected by these factors. High severity fire removes downed woody debris and reduces canopy cover and structural diversity. All of these factors influence spotted owl habitat selection (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000), so we hypothesized that increased amounts of high severity fire may increase extinction probabilities.

We considered the effects of the amount of edge habitat on initial occupancy, extinction, and colonization probabilities because we suspected edge could have positive or negative impacts on site occupancy. Greater amounts of edge habitat may increase site occupancy by increasing prey availability, particularly woodrats (*Neotoma* spp.), which are common in edge habitats (Zabel et al. 1995, Ward et al. 1998) and are a primary prey item in this portion of the spotted owl's range (Forsman et al. 2004). In contrast, increased amounts of edge habitat may decrease the amount of interior forest available to owls, which has been associated with decreased spotted owl survival (Franklin et al. 2000). To avoid the potential correlation between extinction and colonization parameters (MacKenzie et al. 2006), we only used edge in 1 of the parameters, not both, in the same model. We used edge as an additive effect with the best ranked covariate model for initial occupancy and extinction or colonization to determine if it improved model fit (i.e., decreased the AIC_c value).

We modeled each of the 4 possible models of each covariate individually, as an additive effect, with the best model from the first step of our analysis. We took this approach to reduce redundancy in the potential list of covariates due to spatial scales and relationships of covariates being correlated and to reduce the number of candidate models that would be considered in the final step of the analysis. We ranked each model using AIC_c values to determine the best spatial scale and relationship of each covariate.

The third step of our analysis combined the best individual covariates from the second step of our analysis into more complex models to test a specific set of biologically plausible hypotheses (Table 3). We did not use covariates on detection probabilities because they are nuisance parameters for which we had minimal interest. Our most complex initial occupancy and colonization models included 4 covariates (combinations of intermediate-aged and older forests and low and moderate burn severity; Table 3). Other models were variations of the most complex model that included a subset of these covariates or combined 2 covariates into a single covariate. Our most complex extinction model included 3 covariates (early seral stands, forests with high burn severity, and salvage logged forests; Table 3). The remaining candidate models were variations of the most complex model that had fewer covariates or combined 2 or more covariates into a

single covariate. Prior to fitting our candidate model set (Table 3), we looked for correlations between variables that may be included in the same model. We did not include candidate models with highly correlated variables ($r^2 > 0.70$). After determining the best covariate model for initial occupancy, extinction, and colonization probabilities, we retained these models and combined them to determine our best overall model.

RESULTS

Comparison of the South Cascades to Timbered Rock

The best model for detection probabilities was P (year + area + $\ln T$), and the second ranked model [P (year + $\ln T$)] was not competitive ($\Delta AIC_c = 13.18$; Table 4). The best model indicated that detection probabilities varied among, differed between areas, and followed a log-linear time trend within years. Detection probabilities were greater at South Cascades than at Timbered Rock in 10 out of 15 years. In most years (8 out of 15), detection probabilities declined over the survey season, but in the remaining 7 years, detection probabilities increased over the survey season. Detection probabilities during 1 survey over the 15 years of the study varied considerably and ranged from 0.24 to 0.82 at the South Cascades and 0.11–0.79 at Timbered Rock. The range of detection probabilities within years was less variable. The best model for initial occupancy was Ψ (area), and the second ranked model [$\Psi(\cdot)$] was not competitive ($\Delta AIC_c = 7.21$). The best model indicated that the South Cascades had greater initial occupancy ($\hat{\beta} = 2.21$, 95% CI = 0.65–3.76) than Timbered Rock. We estimated

initial occupancy probabilities in 1992 to be 0.94 (95% CI = 0.88–1.00) at South Cascades compared to 0.65 at Timbered Rock (95% CI = 0.44–0.86).

The best model for extinction probabilities was ε [Pre-burn (area + t)Post-burn(area + t)], and 2 models were highly competitive (i.e., $\Delta AIC_c < 2.0$) with the best extinction model (Table 4). However, model ε [Pre-burn(area + t)Post-burn(area + t)] had a weight of 0.42, indicating strong support for the best model. Interpretation of the best model was that extinction rates varied by year and study area, but the study areas followed the same pattern over time (Fig. 2). We found some evidence that the South Cascades had greater extinction probabilities than Timbered Rock prior to the burn because the 95% confidence interval barely overlapped 0 ($\hat{\beta} = 0.69$, 95% CI = -0.06 to 1.43). Following wildfire and subsequent salvage logging at the Timbered Rock study area, extinction probabilities were greater than at the South Cascades ($\hat{\beta} = 1.46$, 95% CI = 0.29 – 2.62 ; Fig. 2). Model ε [Pre-burn(t)Post-burn(area + t)] was the second ranked extinction probability model ($\Delta AIC_c = 1.53$; Table 4). This model suggested that extinction probabilities varied by year and the Timbered Rock and the South Cascades study areas had similar extinction probabilities prior to the Timbered Rock burn, but extinction probabilities were greater at Timbered Rock following wildfire and subsequent salvage logging. Model $\varepsilon(t)$ was the third ranked extinction model ($\Delta AIC_c = 1.84$; Table 4). This model suggested that extinction probabilities varied by year, and the Timbered Rock and South Cascades study areas had similar extinction probabilities before and after the Timbered Rock burn. We did not consider this model further, because the 2 best ranked models had similar interpretations with a combined model

Table 4. Model selection results for extinction (ε), colonization (γ), and detection (P) probability models in the analysis of site occupancy of northern spotted owls at the South Cascades Demographic Study Area and the Timbered Rock study Area in southwest Oregon, USA, from 1992 to 2006. We presented only models with an Akaike weight ≥ 0.01 . We considered models that compared differences between study areas (area) and no differences between areas ($\cdot$), and we considered several biologically plausible temporal effects including constant rates among years ($\cdot$), variable rates among years (t), and linear (T), log-linear ($\ln T$), and quadratic (TT) trends over time. For all extinction, colonization, and detection probability models, the best initial occupancy (Ψ) model was Ψ (area).

Model	AIC _c ^a	ΔAIC_c ^b	w_i ^c	K^d	Deviance
Extinction— ε					
ε (Pre-burn(area + t)Post-burn(area + t)) γ (area + T) P (year, area + $\ln T$)	8689.47	0.00	0.42	66	8552.27
ε (Pre-burn(t)Post-burn(area + t)) γ (area + T) P (year, area + $\ln T$)	8691.00	1.53	0.19	65	8555.96
$\varepsilon(t)$ γ (area + T) P (year, area + $\ln T$)	8691.31	1.84	0.17	64	8558.42
ε (area + t) γ (area + T) P (year, area + $\ln T$)	8692.58	3.12	0.09	65	8557.54
ε (Pre-burn(area + t)Post-burn(area $\times t$)) γ (area + T) P (year, area + $\ln T$)	8692.77	3.30	0.08	69	8549.08
ε (Pre-burn(t)Post-burn(area $\times t$)) γ (area + T) P (year, area + $\ln T$)	8694.30	4.83	0.04	68	8552.78
Colonization— γ					
ε (area $\times t$) γ (area + T) P (year, area + $\ln T$)	8700.13	0.00	0.43	78	8536.83
ε (area $\times t$) γ (area + TT) P (year, area + $\ln T$)	8702.15	2.03	0.16	79	8536.66
ε (area $\times t$) γ (Pre-burn (area + T)Post-burn(area + T)) P (year, area + $\ln T$)	8702.29	2.16	0.15	79	8536.80
ε (area $\times t$) γ (Pre-burn(area + T)Post-burn(area $\times T$)) P (year, area + $\ln T$)	8702.32	2.19	0.15	79	8536.83
ε (area $\times t$) γ (Pre-burn(area)Post-burn(area)) P (year, area + $\ln T$)	8703.02	2.89	0.10	78	8539.72
ε (area $\times t$) γ (Pre-burn(T)Post-burn(area $\times T$)) P (year, area + $\ln T$)	8708.47	8.35	0.01	79	8542.98
Detection probability— P^e					
ε (area $\times t$) γ (area $\times t$) P (year, area + $\ln T$)	8729.48	0.00	1.00	103	8510.61
ε (area $\times t$) γ (area $\times t$) P (year, $\ln T$)	8742.66	13.18	0.00	88	8557.33

^a Akaike's Information Criterion corrected for small sample sizes.

^b The difference between the model listed and the best AIC_c model.

^c Akaike weight.

^d No. parameters in model.

^e Detection probability modeling notation is P (among year detection, within year detection).

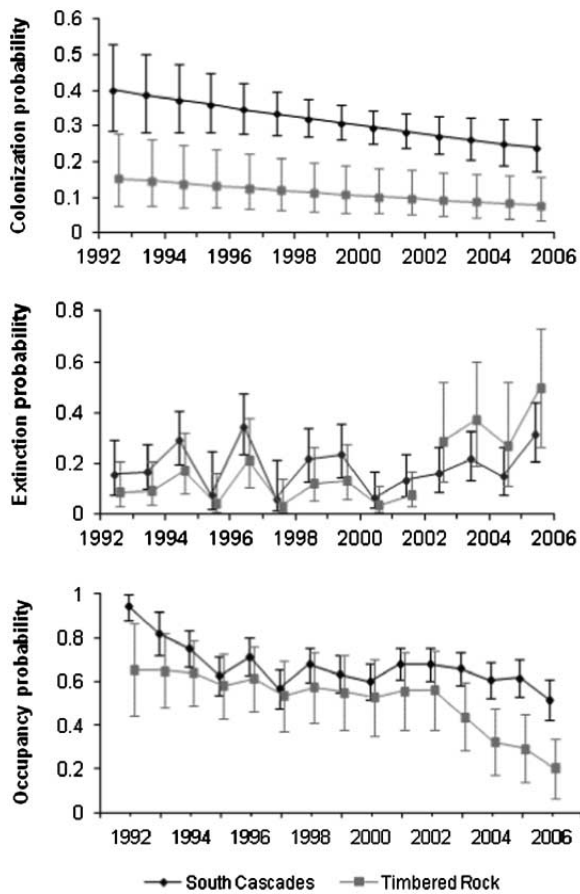


Figure 2. Estimated extinction, colonization, and site occupancy probabilities (95% CI) of northern spotted owls at the Timbered Rock and South Cascades study areas in southwest Oregon, USA from 1992 to 2006.

weight of 0.62 and indicated that post-burn, extinction probabilities were greater at Timbered Rock.

The best model for colonization was γ (area + T), and no models were within 2.0 AIC_c units of the best model (Table 4). Model γ (area + T) had a weight of 0.43 indicating strong support for this model. Interpretation of the best model was that colonization probabilities differed between study areas and declined linearly over time. Colonization probabilities were greater at the South Cascades ($\hat{\beta} = 1.31$, 95% CI = 0.60–2.03) than at Timbered Rock and declined over time ($\hat{\beta} = -0.06$, 95% CI = -0.12 to 0.00) at both areas (Fig. 2). Wildfire and salvage logging did not appear to influence post-burn colonization probabilities at Timbered Rock because models that included changes in colonization probabilities following wildfire were not competitive (i.e., $\Delta AIC_c > 2.0$) with the best model (Table 4).

We combined the best ranked models for initial occupancy, extinction, colonization, and detection probabilities to obtain our best overall model (Table 4), which we used to contrast trends in occupancy probabilities over time at the Timbered Rock and South Cascades study areas. We used the best overall model [$\Psi(\text{area})\epsilon[\text{Pre-burn}(\text{area} + t)\text{Post-burn}(\text{area} + t)]\gamma(\text{area} + T)P(\text{year} + \text{area} + \ln T)$] to calculate year-specific occupancy estimates for each study area. Site

occupancy by spotted owls at the South Cascades declined from 1992 to 1994, remained relatively stable from 1995 to 2005, and declined again in 2006 (Fig. 2). In contrast, site occupancy by spotted owls at Timbered Rock declined slightly from 1992 to 2002 and declined in an almost linear fashion from 2003 to 2006, which corresponded to the years following the Timbered Rock burn (Fig. 2). Between 2002 and 2006, the estimated proportion of spotted owl territories occupied by a pair at South Cascades declined from 0.68 to 0.51, a 25% reduction in site occupancy. In contrast, the estimated proportion of spotted owl territories occupied by a pair at Timbered Rock declined from 0.56 to 0.20, a 64% reduction in site occupancy during the same time period. This indicated that occupancy of territories by spotted owls in a recently burned landscape that was subjected to salvage logging declined at a greater rate than in a recently unburned landscape.

Relationship Between Wildfire, Salvage Logging, and Spotted Owl Site Occupancy

Our objective in this portion of the analysis was to determine the best model prior to modeling habitat covariates; consequently, we did not consider any competing models. The best model that described study area and temporal effects on spotted owl site occupancy at the Biscuit, Quartz, and Timbered Rock burns from 2003 to 2006 was $\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = Q + T)\gamma(\cdot)P(\cdot)$ (Table 5). Detection probabilities were constant within and among years, and equal between study areas. The probability of detecting a spotted owl pair on any 1 visit was 0.46 (95% CI = 0.39–0.53). The probability of initial occupancy was similar between study areas and was 0.46 (95% CI = 0.30–0.62) in 2003 at all 3 study areas. Colonization probabilities were also similar among study areas and constant over time. The probability that an unoccupied territory would be colonized the subsequent year was 0.15 (95% CI = 0.07–0.26). Extinction probabilities were greater at the Biscuit burn ($\hat{\beta} = 5.58$, 95% CI = 1.25–9.91) than the Quartz and Timbered Rock burns and increased from 2004 to 2006 ($\hat{\beta} = 2.96$, 95% CI = 0.97–4.94) at all 3 study areas. Extinction probabilities at the Quartz and Timbered Rock burns increased from 2004 to 2006 (0.11, 95% CI = 0.03–0.36; 0.72, 95% CI = 0.41–0.90, respectively). In contrast, extinction probabilities increased from 0.37 (95% CI = 0.11–0.73) in 2004 to 0.92 (95% CI = 0.58–0.99) in 2006 at the Biscuit burn. Based on the point estimates, extinction probabilities may have increased dramatically for all areas (11–92%).

We modeled individual covariates as an additive effect with the best study area and temporal effects model (Table 5) to determine the spatial scale (core or territory) and relationship (linear or log-linear) that best described the effect of the covariate on initial occupancy, extinction, and colonization parameters (Table 6). In most cases, the models for alternative spatial scales and relationships were competitive (i.e., $\Delta AIC_c < 2.0$) with the best model for each covariate; however, our objective was to reduce redundancy between models and reduce the number of models in the final step of our

Table 5. Model selection results for initial occupancy (Ψ), extinction (ϵ), colonization (γ), and detection (P) probability models in the analysis of site occupancy of northern spotted owls without site-specific covariates at the Biscuit (BIS), Quartz (Q), and Timbered Rock (TR) burns in southwest Oregon, USA, from 2003 to 2006. We presented only models with an Akaike weight ≥ 0.05 . We considered models that compared differences between study areas (area) and no differences between areas ($\cdot$), and we considered several biologically plausible temporal effects including constant rates among years ($\cdot$), variable rates among years (t), and linear (T), log-linear ($\ln T$), and quadratic (TT) trends over time.

Model	AIC _c ^a	Δ AIC _c ^b	w_i ^c	K ^d	Deviance
Extinction— ϵ					
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot, \cdot)$	476.93	0.00	0.28	6	464.38
$\Psi(\cdot)\epsilon(T)\gamma(\cdot)P(\cdot, \cdot)$	477.79	0.86	0.18	5	467.39
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + \ln T)\gamma(\cdot)P(\cdot, \cdot)$	477.94	1.01	0.17	6	465.39
$\Psi(\cdot)\epsilon(\ln T)\gamma(\cdot)P(\cdot, \cdot)$	478.65	1.72	0.12	5	468.26
$\Psi(\cdot)\epsilon(t)\gamma(\cdot)P(\cdot, \cdot)$	479.35	2.42	0.08	6	466.80
$\Psi(\cdot)\epsilon(TT)\gamma(\cdot)P(\cdot, \cdot)$	479.35	2.42	0.08	6	466.80
$\Psi(\cdot)\epsilon(\text{area} + t)\gamma(\cdot)P(\cdot, \cdot)$	480.17	3.24	0.05	8	463.21
Colonization— γ					
$\Psi(\cdot)\epsilon(\text{area} \times t)\gamma(\cdot)P(\cdot, \cdot)$	482.39	0.00	0.70	10	460.91
$\Psi(\cdot)\epsilon(\text{area} \times t)\gamma(\text{BIS} \neq \text{TR} = \text{Q})P(\cdot, \cdot)$	487.41	5.02	0.06	13	458.90
Initial occupancy— Ψ					
$\Psi(\cdot)\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	499.61	0.00	0.44	20	453.52
$\Psi(\text{BIS} \neq \text{TR} = \text{Q})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	501.12	1.51	0.21	21	452.37
$\Psi(\text{BIS} = \text{Q} \neq \text{TR})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	501.50	1.89	0.17	21	452.75
$\Psi(\text{BIS} = \text{TR} \neq \text{Q})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	502.27	2.66	0.12	21	453.52
$\Psi(\text{area})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	503.70	4.09	0.06	22	452.26
Detection probability— P^e					
$\Psi(\text{area})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\cdot, \cdot)$	503.70	0.00	0.52	22	452.26
$\Psi(\text{area})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\ln T, \cdot)$	506.28	2.58	0.14	23	452.11
$\Psi(\text{area})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(T, \cdot)$	506.44	2.74	0.13	23	452.26
$\Psi(\text{area})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(TT, \cdot)$	506.51	2.81	0.13	23	452.33
$\Psi(\text{area})\epsilon(\text{area} \times t)\gamma(\text{area} \times t)P(\text{year}, \cdot)$	507.56	3.86	0.08	25	447.79

^a Akaike's Information Criterion corrected for small sample sizes.

^b The difference between the model listed and the best AIC_c model.

^c Akaike weight.

^d No. parameters in model.

^e Detection probability modeling notation is P (among year detection, within year detection).

analysis. As a result, we did not consider competing models and assumed the highest ranked model best described the relationship of the covariate on each occupancy parameter. After determining the best spatial scale and relationship of each covariate, we looked for correlations between variables that were included in the same model. None of the variables that were included in the same model were highly correlated ($r^2 < 0.31$ in all contrasts). Consequently, we did not exclude any variables from our candidate model set because of collinearity (Table 3).

Fire severity and habitat effects.—The best model that described the relationship between site occupancy and fire severity, salvage logging, and habitat covariates at the Biscuit, Quartz, and Timbered Rock burns from 2003 to 2006 indicated that initial occupancy was best predicted by intermediate-aged and older forest that burned with a moderate severity at the core scale and amount of edge at the core scale. Extinction was best predicted by early seral stands that burned with high severity or were salvage logged at the core scale and amount of edge at the territory scale with extinction rates differing across time and at Biscuit sites. Colonization was best predicted by intermediate-aged older forests with low and moderate burn severity at the core scale and detection was constant across variables (Table 6). One model was within 2.0 AIC_c units of the best model for extinction probability (Table 6). However, this model was a slight variation of the best model and did not include the covariate

representing edge at the territory scale, so it was not considered further because the amount of edge at the territory scale improved model fit. No models competed with the best initial occupancy and colonization probability models (Table 6). The best overall covariate model ranked substantially higher (Δ AIC_c = 27.12) than the model that only included study area and temporal effects (Table 6). This indicated that the covariates used in this model explained some of the variability observed in post-fire site occupancy by spotted owls at the Biscuit, Quartz, and Timbered Rock burns.

Our best initial occupancy model included variables for the amount of low severity burn and edge (km) within the core use area (Table 6). The confidence intervals of the beta coefficients for the amount of low severity burn within the core area ($\beta = 0.52$, 95% CI = -0.22 to 1.26) and the amount of edge (km) in the core area ($\beta = -0.42$, 95% CI = -0.92 to 0.10) broadly overlapped zero, which indicated that neither of these variables influenced initial occupancy probabilities. Extinction probabilities increased as the combined area that was previously harvested, burned with a high severity, or salvage logged within the core area increased ($\beta = 1.88$, 95% CI = 0.10 – 3.66 ; Fig. 3a). We found some evidence that the amount of edge (km) within a territory had a positive effect on extinction probabilities as the 95% confidence intervals overlapped 0 slightly ($\beta = 0.18$, 95% CI = -0.01 to 0.37 ; Fig. 3b). We found weak support

Table 6. Initial occupancy (Ψ), extinction (ϵ), and colonization (γ) models in the analysis of covariate effects on site occupancy of northern spotted owls at the Biscuit (BIS), Quartz (Q), and Timbered Rock (TR) burns in southwest Oregon, USA, from 2003 to 2006. We presented only models with an Akaike weight ≥ 0.05 . For all initial occupancy, extinction, and colonization models the best detection probability model was constant detection among and within years ($P(\cdot, \cdot)$).

Model ^a	AIC _c ^b	Δ AIC _c ^c	w_i ^d	K ^e	Deviance
Best overall model					
$\Psi(\ln \text{ LOWc} + \text{EDGEc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T + \ln \text{ EARTHISALVc} + \text{EDGEt})\gamma(\text{INTLc} + \text{INTMc} + \text{OLDLc} + \text{OLDMt})P(\cdot, \cdot)$	449.81	0.00	1.00	14	418.89
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot, \cdot)$ —Base model	476.93	27.12	0.00	6	464.38
Initial occupancy— Ψ					
$\Psi(\ln \text{ LOWc} + \text{EDGEc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot, \cdot)$	473.78	0.00	0.36	8	456.82
$\Psi(\ln \text{ LOWc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot, \cdot)$	476.01	2.22	0.12	7	461.27
$\Psi(\text{INTLc} + \text{OLDLc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot, \cdot)$	476.09	2.30	0.12	8	459.13
$\Psi(\text{RFc} + \ln \text{ NRFc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot, \cdot)$	476.43	2.65	0.10	8	459.47
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot, \cdot)$ —Base model	476.93	3.15	0.08	6	464.38
$\Psi(\text{INTLc} + \text{INTMc} + \text{OLDLc} + \text{OLDMt})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot, \cdot)$	477.43	3.65	0.06	10	455.94
$\Psi(\text{OLDLc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot, \cdot)$	477.64	3.85	0.05	7	462.89
$\Psi(\ln \text{ NRFc})\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\cdot)P(\cdot, \cdot)$	477.88	4.09	0.05	7	463.14
Extinction— ϵ					
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T + \ln \text{ EARTHISALVc} + \text{EDGEt})\gamma(\cdot)P(\cdot, \cdot)$	464.61	0.00	0.60	8	447.65
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T + \ln \text{ EARTHISALVc})\gamma(\cdot)P(\cdot, \cdot)$	466.50	1.89	0.23	7	451.76
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T + \ln \text{ HARVESTc} + \text{HIGHc})\gamma(\cdot)P(\cdot, \cdot)$	469.49	4.88	0.05	8	452.53
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T + \ln \text{ EARLYc} + \text{HISALVc})\gamma(\cdot)P(\cdot, \cdot)$	469.73	5.12	0.05	8	452.77
Colonization— γ					
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\text{INTLc} + \text{INTMc} + \text{OLDLc} + \text{OLDMt})P(\cdot, \cdot)$	462.72	0.00	0.65	10	441.24
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\text{INTLc} + \text{INTMc} + \text{OLDLc} + \text{OLDMt} + \ln \text{ EDGEc})P(\cdot, \cdot)$	464.93	2.21	0.22	11	441.14
$\Psi(\cdot)\epsilon(\text{BIS} \neq \text{TR} = \text{Q} + T)\gamma(\text{OLDLc} + \text{OLDMt})P(\cdot, \cdot)$	467.27	4.54	0.07	8	450.31

^a Variables preceded by $\ln$ were modeled using a log-linear relationship, variables followed by a c were modeled at the core area scale, and variables followed by t were modeled at the territory scale. INTL, intermediate-aged forest that burned with a low severity; INTM, intermediate-aged forest that burned with a moderate severity; OLDL, older forest that burned with a low severity; OLDM, older forest that burned with a moderate severity; LOW, intermediate-aged and older forest that burned with a low severity (combined area of INTL and OLDL); MOD, intermediate-aged and older forest that burned with a moderate severity (combined area of INTM and OLDM); EDGE, the interface between forested areas that burned with low or moderate severity and areas that were early seral stands, burned with high severity, or were salvage logged; EDGE was modeled as an additive effect with the best-ranked covariate model to determine if it improved model fit; EARLY, non-forested areas early seral stands that burned with any severity; HIGH, the combined area of intermediate-aged and older forest that burned with a high severity; SALVAGE, any intermediate-aged or older forest that was salvage logged; HARVEST, any forested area that was harvested before or after the burn (combined area of EARLY and SALVAGE); HISALV, any forested area, excluding early stands, that burned with a high severity or was salvage logged (combined area of HIGH and SALVAGE); EARTHISALV, any early seral stand or forested area that burned with high severity or that was salvage logged (combined area of EARLY, HIGH, and SALVAGE); RF, intermediate-aged forest that burned with a low or moderate severity (combined area of INTL and INTM); NRF, older forest that burned with a low or moderate severity (combined area of OLDL and OLDM); T , linear time.

^b Akaike's Information Criterion corrected for small sample sizes.

^c The difference between the model listed and the best AIC_c model.

^d Akaike weight.

^e No. parameters in model.

that colonization probabilities increased as the amount of intermediate-aged forest that burned with a low severity within the core area increased ($\hat{\beta} = 0.10$, 95% CI = -0.01 to 0.38 ; Fig. 4a), as the amount of older forest that burned with a low severity within the core area increased ($\hat{\beta} = 0.10$, 95% CI = -0.01 to 0.22 ; Fig. 4b), and as the amount of older forest that burned with a moderate severity within the territory increased ($\hat{\beta} = 0.82$, 95% CI = -0.05 – 1.69 ; Fig. 4c). We found no evidence that colonization probabilities were associated with the amount of intermediate-aged forest that burned with a moderate severity within the core area ($\hat{\beta} = -1.20$, 95% CI = -3.21 to 0.80).

DISCUSSION

Comparison of the South Cascades to Timbered Rock

As predicted, the Timbered Rock and South Cascades study areas had relatively similar trends in site occupancy prior to the Timbered Rock burn. However, extinction probabilities

increased at Timbered Rock following wildfire and subsequent salvage logging, which combined with the lesser colonization rates at Timbered Rock contributed to greater declines in site occupancy than were observed in recently unburned landscapes at the South Cascades (Fig. 2). The Timbered Rock study area had an approximately 64% reduction in site occupancy following wildfire, whereas the South Cascades study area had a roughly 25% reduction in site occupancy during the same time period. This supported our prediction that occupancy rates in burned and salvage logged landscapes would decline at a greater rate than unburned landscapes. Our results contrast with those of previous studies that compared occupancy rates of spotted owls in burned and unburned landscapes. Jenness et al. (2004) found that territory occupancy of Mexican spotted owls in burned areas was similar to unburned areas. Roberts et al. (2011) found that site occupancy of California spotted owls in randomly selected burned and unburned areas were similar. Neither of these studies was affected by the high degree of salvage logging we observed following the Timbered Rock

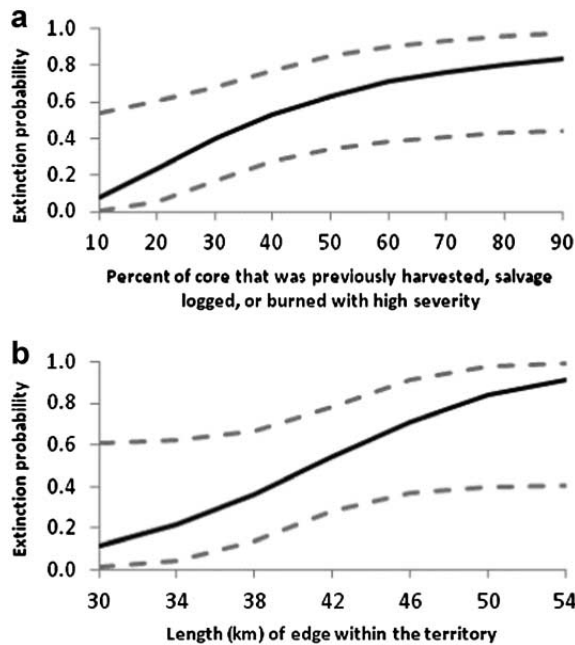


Figure 3. The estimated effects of the percent of (a) forested area that burned with a low severity and (b) forest edge on extinction probabilities of northern spotted owls at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon, USA from 2003 to 2006. The 95% confidence intervals for the estimated effects are represented by gray, dashed lines. The median values of the additional covariates in the model were held constant while varying the covariate of interest over the observed range of values.

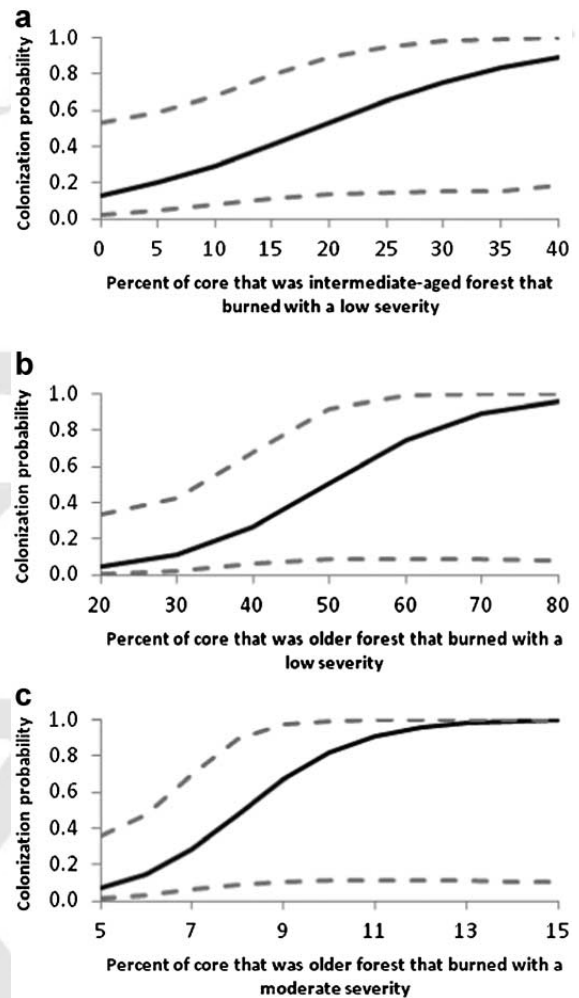


Figure 4. The estimated effects of the percent of (a) intermediate-aged forest that burned with a low severity, (b) older forest that burned with a low severity, and (c) older forests that burned with a moderate severity on colonization probabilities of northern spotted owls at the Biscuit, Quartz, and Timbered Rock burns in southwest Oregon, USA from 2003 to 2006. The 95% confidence intervals for the estimated effects are represented by gray, dashed lines. The median values of the additional covariates in the model were held constant while varying the covariate of interest over the observed range of values.

burn, which may explain the difference between our results and those of previous studies.

The approximately 25% reduction in site occupancy at the South Cascades from 2002 to 2006 was somewhat surprising given that the study area did not have any large scale disturbances during this time. However, several spotted owl populations have been declining throughout the subspecies' range (Anthony et al. 2006, Forsman et al. 2011), and declines in site occupancy at the South Cascades could be related to ongoing population declines that are unrelated to natural disturbances. Dugger et al. (2011) found that barred owls (*Strix varia*) had negative impacts on site occupancy by spotted owls by decreasing colonization rates and increasing extinction rates. This likely explains much of the nearly 25% decline in site occupancy we observed from 2002 to 2006 at the South Cascades. The 64% reduction in site occupancy at Timbered Rock from 2002 to 2006 was substantially greater than the roughly 25% decline observed at South Cascades, which suggests that wildfire, subsequent salvage logging, and past timber harvest contributed to the greater declines in site occupancy at Timbered Rock. We estimated that following the Timbered Rock burn only 46% of the area within 2,230 m of spotted owl territories were intermediate-aged or older forests that burned with a low or moderate severity (Table 1). This amount of habitat is marginal for successful reproduction (Bart and Forsman 1992) and may cause decreases in survival rates of the subspecies (Franklin et al. 2000, Dugger et al. 2005).

The large declines in site occupancy following the Timbered Rock burn are most likely explained by dispersal

out of the burn (i.e., emigration) and decreased survival of spotted owls. Several color-banded, adult spotted owls at the Timbered Rock burn (2 pairs and 1 individual, 25% of the known pre-fire population) dispersed to an unburned territory adjacent to the burn, 1–2 years post-fire (OCFWRU, unpublished data). Adult dispersal is a relatively rare occurrence in spotted owls throughout their range (Forsman et al. 2002: 5%, Zimmerman et al. 2007: 2%); however, owl territories may be abandoned when large amounts of mature and older forest are lost (Bart and Forsman 1992, Bart 1995). We believe that the relatively high rate of adult dispersal following the Timbered Rock burn suggests that insufficient habitat remained at abandoned territories to support a spotted owl pair. In addition, radio-marked spotted owls that maintained a territory within the Timbered Rock burn had lower survival rates ($\hat{S} = 0.69 \pm 0.12$; Clark et al. 2011) than reported throughout the subspecies' range ($\hat{\Phi} = 0.75$ to

0.91 $\pm$ 0.01 to 0.05; Anthony et al. 2006). Annual survival of spotted owls was positively associated with greater amounts of older forest within their home ranges or core use areas in other studies (Franklin et al. 2000, Olson et al. 2004, Blakesley et al. 2005, Dugger et al. 2005). High severity wildfire and salvage logging removed and modified 26% of the intermediate-aged and older forests within 2,230 m of spotted owl territories at the Timbered Rock burn, and 28% of the remaining area was previously harvested (i.e., early seral forest; Table 1). Consequently, the large degree of habitat loss and modification from past timber harvest, high severity fire, and salvage logging following the Timbered Rock burn likely contributed to the high levels of dispersal out of the burn, decreased survival rates and subsequent declines in site occupancy that we observed. These declines in site occupancy appear to have continued past the conclusion of our study because no spotted owls were detected during surveys conducted during the 2011 breeding season at the Timbered Rock study site (OCFWRU, unpublished data).

Increased extinction rates following the Timbered Rock burn may have been exacerbated by the checkerboard land ownership pattern of private and BLM lands (Richardson 1980). Private lands within the area of the Timbered Rock burn are managed as industrial forests and are frequently subjected to large-scale timber harvest, which creates large tracts of early seral forest. Following the Timbered Rock burn, much of the private land was salvage logged (17% of the study area), which created large clear-cuts throughout the landscape. Territory occupancy by spotted owls was negatively associated with increased areas of clear-cuts within the territory in another study (Thraillkill et al. 1998). Consequently, the large areas of clear-cuts created by salvage logging and past timber harvest (approx. 45% of the area within 2,230 m of spotted owl territories; Table 1) potentially exacerbated declines in site occupancy following the Timbered Rock burn or confounded the effects of wildfire. Declines in site occupancy may not be as large in burned areas that do not have large tracts of previously harvested areas and nor be subjected to substantial amounts of post-fire salvage logging.

Relationship Between Wildfire, Salvage Logging, and Spotted Owl Site Occupancy

Extinction.—We predicted that occupancy of nesting territories by spotted owls after fires would decline because of increased extinction probabilities attributable to habitat loss and modification from past timber harvest, high severity fire and salvage logging. Our results supported this prediction because extinction probabilities increased as the combined area of high severity burns, salvage logging, and early seral forest increased (Fig. 3a; $\beta = 1.88$, 95% CI = 0.10–3.66). This was the strongest relationship we observed in this analysis because it was the only habitat covariate where the 95% confidence interval for the regression coefficient did not overlap 0. Unfortunately, we were unable to separate the impacts of these 3 variables on extinction probabilities. When these 3 variables were included separately, the models

were not competitive with the model that combined these variables into a single covariate (Table 6). This may indicate that we lacked the precision to separate the impacts of these 3 variables or they were confounded. However, our results suggest that these 3 variables work in concert and generate synergistic effects. Any 1 disturbance event may not generate negative effects on occupancy of territories, but the combined loss and modification of habitat from these 3 factors negatively affected spotted owls in our study. The combined influence of these 3 factors may reduce spotted owl habitat to such an extent that a threshold is passed and spotted owls are no longer able to occupy the territory.

Spotted owls are associated with late-successional forests (Forsman et al. 1984, Thomas et al. 1990), and their territories have greater amounts of older forests than surrounding landscapes (Ripple et al. 1991, 1997; Meyer et al. 1998; Swindle et al. 1999). Forest stands used by spotted owls have large proportions of downed woody debris and snags, high canopy closure, and high structural diversity (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000). Timber harvest, salvage logging, and high severity fire remove or alter many of these structural characteristics associated with spotted owl habitat. As a result, we were not surprised that these factors were associated with increased extinction probabilities and declines in site occupancy. Spotted owls have high site fidelity (Forsman et al. 1984, 2002; Zimmerman et al. 2007), and survival rates are positively correlated with increased amounts of older forest in their territories (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005); consequently, owls that occupied territories with a large degree of past timber harvest, salvage logging, and high severity fire were likely forced to emigrate out of the burned area or risk decreased survival.

Radio-marked spotted owls at the Timbered Rock burn were located closer to edge habitats than at random (Clark 2007), which suggests edge habitat may provide a benefit to the subspecies. Spotted owls may prefer to forage in habitat edges because of greater densities of some prey in early seral forests (Carey and Peeler 1995, Franklin and Gutiérrez 2002), particularly woodrats in southwest Oregon and northwest California (Zabel et al. 1995, Ward et al. 1998). Our results provided some evidence that extinction probabilities increased as the amount (km) of edge increased within nesting territories increased (Fig. 3b; $\beta = 0.18$, 95% CI = -0.01 – 0.37), suggesting a negative impact of edge habitat on spotted owl territory occupancy. In our analysis, edge represented a metric of habitat fragmentation. Dugger et al. (2011) observed greater colonization probabilities at spotted owl territories when older forest was less fragmented, and our results were similar. Franklin et al. (2000) indicated that spotted owls are likely to have decreased survival at territories with reduced amounts of interior forest, suggesting that habitat fragmentation negatively affects spotted owls. The patchy nature of high severity fire and salvage logging created large amounts of edge habitat, which likely reduced the amount of interior forest available to owls and contributed to declines in site occupancy in our study. Furthermore, increases in edge may be correlated with in-

creased amounts of nonhabitat (i.e., nonforested and early seral stands) and increases in nonhabitat have contributed to declines in territory occupancy of California spotted owls (Blakesley et al. 2005) and increases in extinction probabilities in this study. Despite indications that spotted owls are negatively affected by habitat fragmentation, the mechanism of these effects is not well understood (Franklin and Gutiérrez 2002). We calculated the amount of edge as the interface between intermediate-aged and older forests that burned with a low or moderate severity and all other habitat types (Table 2). This classification of edge habitat delineated distinct boundaries between stands of larger living trees and high severity burns or early seral stands. Additional types of edge habitats exist at the interface between intermediate-aged and older forests or the interface between low and moderate severity burns, and these types of edges may provide foraging habitat for spotted owls. Additional research between the association of various edge habitats on spotted owl demography and site occupancy is needed to clarify this relationship.

Colonization.—Overall, our estimated effects of habitat covariates on colonization probabilities were relatively imprecise. We attributed this lack of precision to the fact that we observed only 6 colonization events at our 3 study areas from 2003 to 2006. Despite the fact that we observed relatively few colonization events, we were still able to document several biologically meaningful associations between post-fire habitat and colonization probabilities. We suspect that if additional colonization events had occurred during the course of our research, our estimated effects of habitat on colonization probabilities would be more precise.

We found some evidence that colonization probabilities in our study were positively associated with increased amounts of older forest that burned with a low severity within the core area (Fig. 4b; $\hat{\beta} = 0.10$, 95% CI = -0.01 to 0.22). Although this estimated effect had weak support, this finding was expected and follows the well documented association between spotted owls and older forest (Forsman et al. 1984, Thomas et al. 1990). Furthermore, previous research indicated that territory occupancy of California spotted owls was positively associated with older forest (Blakesley et al. 2005), extinction probabilities at northern spotted owl territories were greater at territories with lesser amounts older forest (Dugger et al. 2011) and site occupancy by California spotted owls in areas that primarily burned with a low and moderate severity was similar to unburned areas (Roberts et al. 2011). Older forests that burned with a low severity are likely the highest quality spotted owl habitat in post-fire landscapes. These areas likely retained much of the canopy cover, downed woody debris, snags, and structural diversity that is selected by spotted owls (Hershey et al. 1998, North et al. 1999, Irwin et al. 2000). As a result, unoccupied territories that have high quality habitat (i.e., older forest that burned with a low severity) will have the greatest probability of being colonized by spotted owls. Within the Timbered Rock burn, radio-marked spotted owls strongly selected for older forest that burned with a low severity (Clark 2007), further

demonstrating the influence of this habitat on spotted owls in post-fire landscapes.

Moderate severity burns likely remove and modify more of the forest stand features selected by spotted owls than low severity burns, yet many critical habitat features are likely retained and allow moderately burned areas to provide habitat for spotted owls following wildfire. Our analysis provided weak support that colonization probabilities were positively associated with increased amounts of older forest that burned with a moderate severity (Fig. 4c; $\hat{\beta} = 0.82$, 95% CI = -0.05 to 1.69). In addition to potentially providing many of the critical habitat features of forest stands that burned with a low severity, moderately burned stands likely have decreased risk of stand-replacement in the future because of removal of ladder fuels (Agee 1993), which likely increases the resilience of the forest stand to future disturbance. Spotted owls have been shown to disproportionately forage in habitats that have high levels of prey abundance (Carey et al. 1992, Carey and Peeler 1995, Zabel et al. 1995). Moderate severity burns may increase habitat heterogeneity and prey abundance, similar to the effects of heterogeneous thinning of young forest stands (Carey 2001). However, we did not test this hypothesis, and the potential benefits of moderate severity burns in older forests for spotted owls are unclear.

Previous studies have suggested a quadratic relationship between survival and reproduction of spotted owls and the amount of older forest surrounding nesting territories (Franklin et al. 2000, Olson et al. 2004). These studies suggest that territories that are not entirely comprised of older forests are beneficial to spotted owls and that spotted owls may be adapted to natural disturbances such as wildfire that create a mosaic of forest conditions. Our results provided weak support for this hypothesis because owl territories in our study that had increased amounts of intermediate-aged forest that burned with a low severity have a greater probability of being colonized by a pair of owls (Fig. 4a; $\hat{\beta} = 0.10$, 95% CI = -0.01 to 0.38). However, we expect a threshold exists in this relationship because spotted owls are associated with older forest (Forsman et al. 1984, Thomas et al. 1990) and spotted owls that occupy territories with insufficient amounts of older forest will have decreased survival and reproductive rates (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005). The amount of intermediate-aged forest that burned with a low severity at any 1 owl territory in our study ranged from 0% to 38%. Territories that have insufficient amounts of older forest will likely not be occupied by spotted owls, but our results provided some evidence of a benefit of habitat heterogeneity for spotted owls.

Initial occupancy.—We were unable to identify any relationships between initial occupancy probabilities and the habitat covariates that we considered in our analysis. Our best model for initial occupancy probabilities (Table 6) included variables for the amount of the core area that burned with a low severity ($\hat{\beta} = 0.52$, 95% CI = -0.22 to 1.26) and the amount of edge habitat ($\hat{\beta} = -0.42$, 95% CI = -0.92 to 0.10); however, both of these estimates were imprecise and the 95% confidence intervals broadly overlapped zero, which

suggested these relationships were not meaningful. Since these relationships were not supported by the data, additional research is needed to investigate the influence of low severity fire and edge habitat on spotted owl site occupancy.

Our analysis of site occupancy at the Biscuit, Quartz, and Timbered Rock burns identified several meaningful relationships between site occupancy and amount of post-fire habitat. All of these relationships were based on biologically plausible hypotheses and have implications for spotted owl management. However, the relationships we observed were based on small sample sizes, non-random samples at the Biscuit burn, and our estimated relationships were often imprecise. Furthermore, our study was opportunistic and observational, which prevents us from assigning cause and effect relationships. Consequently, we suggest a cautionary approach when applying our findings to future land management decisions. In particular, the relationships we observed in our analysis may not be applicable to spotted owls in post-fire landscapes that are not affected by post-fire salvage logging.

Both wildfire and barred owls have been identified as threats to the persistence of spotted owls (USFWS 2011). Barred owls have expanded throughout the entire range of the northern spotted owl (Dark et al. 1998, Pearson and Livezey 2003) and are negatively affecting spotted owls (Kelly et al. 2003, Olson et al. 2005, Dugger et al. 2011). Furthermore, barred owls have a more generalized diet (Hamer et al. 2001, Wiens 2012) and use a wider range of habitats (Hamer et al. 2007) than spotted owls, which suggests that barred owls may be better adapted to persist in burned landscapes. We only detected 2 barred owls at the Biscuit, Quartz, and Timbered Rock burns during demographic surveys conducted between 2003 and 2006, so we believe that barred owls had little to no effect on our results.

Jointly, our analyses suggest that site occupancy by spotted owls in burned landscapes is likely to decline, at least in the short-term. These declines in site occupancy are driven by large increases in extinction probabilities in post-fire landscapes and are attributable to past timber harvest, high severity fire, and salvage logging. Although territories that had increased amounts of older forest that burned with a low severity had the greatest colonization probabilities, we only observed 6 colonization events at our 3 study areas from 2003 to 2006, and this level of colonization was insufficient to offset the high extinction probabilities we observed. This suggests that insufficient habitat remained at many of the spotted owls territories included in our analyses to support a pair of spotted owls following wildfire. Site occupancy by Mexican and California spotted owls in landscapes that burned primarily with low or moderate severities was similar to unburned landscapes (Jenness et al. 2004, Roberts et al. 2011), which suggests that spotted owls may be able to persist in burned landscapes. These findings contrast our results, which suggested that spotted owl site occupancy will decline in burned landscapes; however, our results were confounded by the effects of past timber harvest and salvage logging. Additional research in post-fire landscapes that have not been impacted by past timber harvest and

salvage logging are warranted to help clarify these relationships.

MANAGEMENT IMPLICATIONS

We identified several factors that influenced occupancy of nesting territories by spotted owls in post-fire landscapes; however, the strongest association we observed was that site occupancy declined because of increased extinction probabilities. Increased amounts of past timber harvest, salvage logging, and high severity burns jointly contributed to increased extinction probabilities and subsequent declines in spotted owl site occupancy. Past timber harvest negatively influenced site occupancy in our analysis, so we recommend increased protection of older forest in dry forest ecosystems to prevent future habitat loss to timber harvest and mitigate potential losses of older forest to stand-replacing fire and subsequent salvage logging. High severity fire was 1 of 3 factors that combined to increase local-extinction probabilities of spotted owls in our study; however, we were unable to separate the impacts of wildfire from land management activities. As a result, we recommend future research to clarify the relationship between high severity fire and spotted owl site occupancy in the absence of past timber harvest and salvage logging. We believe that widespread, stand-replacing wildfires will negatively affect site occupancy by spotted owls, so we suggest efforts should be made to reduce the risk of widespread, stand-replacing wildfire in spotted owl habitat. However, a precautionary approach should be taken when implementing fuel reduction techniques that will reduce that risk of stand-replacing wildfire. Research is needed to ensure that fuel reduction techniques, particularly commercial or non-commercial thinning, are not detrimental to spotted owls, their habitat, or prey before fuel reduction techniques are implemented on a large scale. Our results also indicated a negative impact of salvage logging on site occupancy by spotted owls. We recommend restricting salvage logging after fires on public lands within 2.2 km of spotted owl territories (the median home range size in this portion of the spotted owl's range) to limit the negative impacts of salvage logging. Our results indicated a negative response of spotted owls to wildfire in the short-term, but the response is likely to vary over time; however, little is known about the long-term response of spotted owls to wildfire. As a result, long-term monitoring studies should be implemented in post-fire landscapes to determine the response of spotted owls to wildfire over time.

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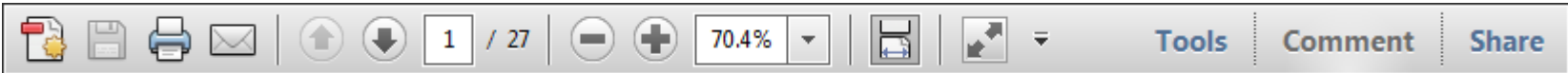
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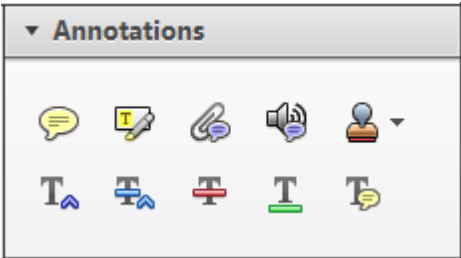
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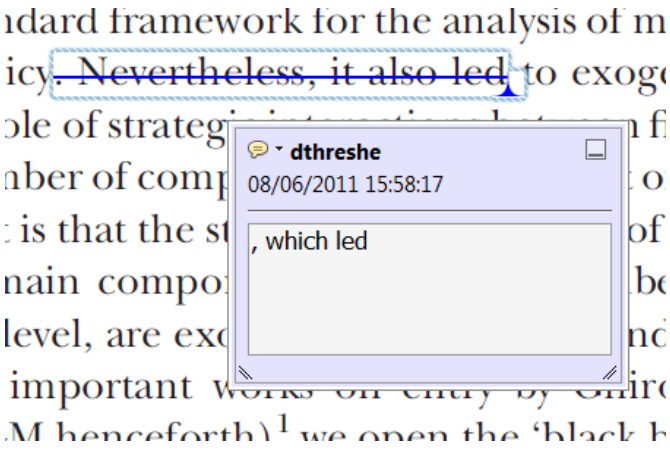
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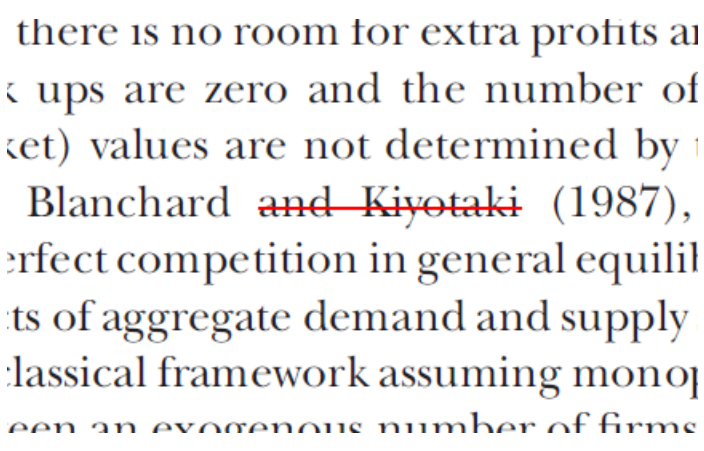
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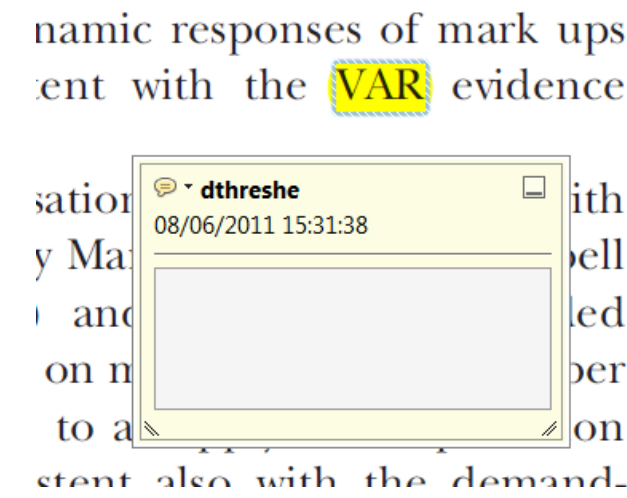
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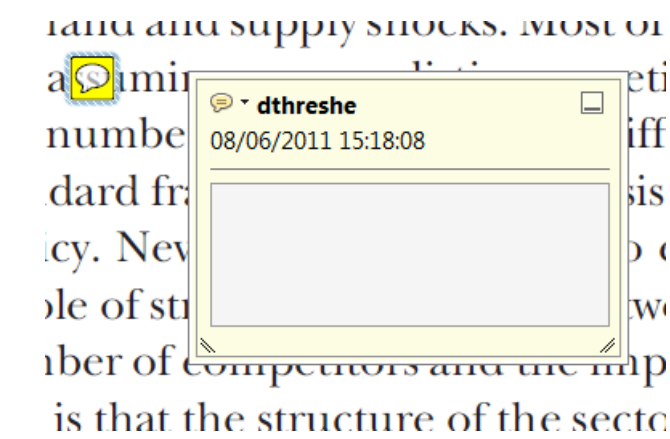
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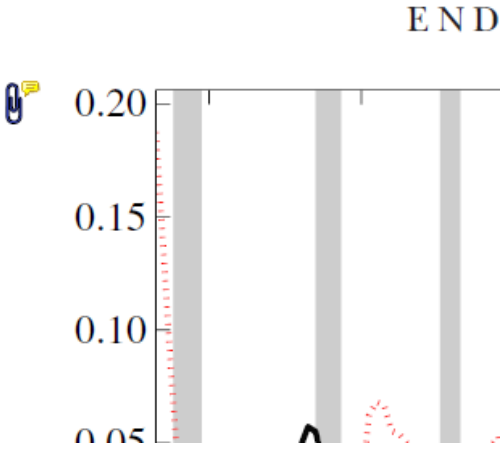


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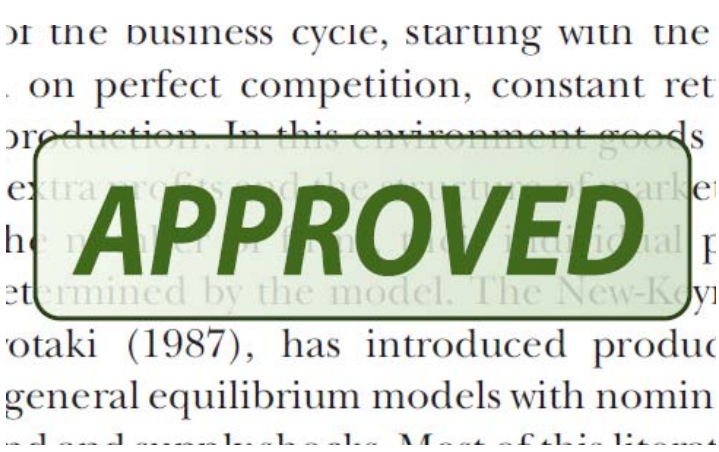


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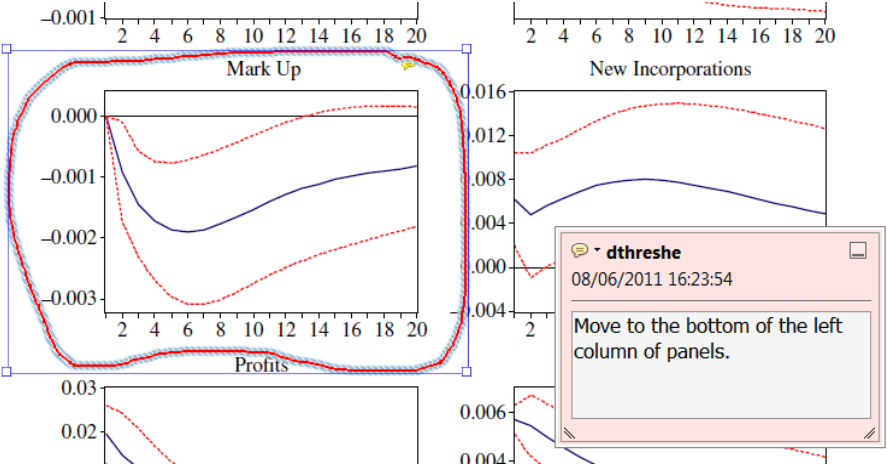


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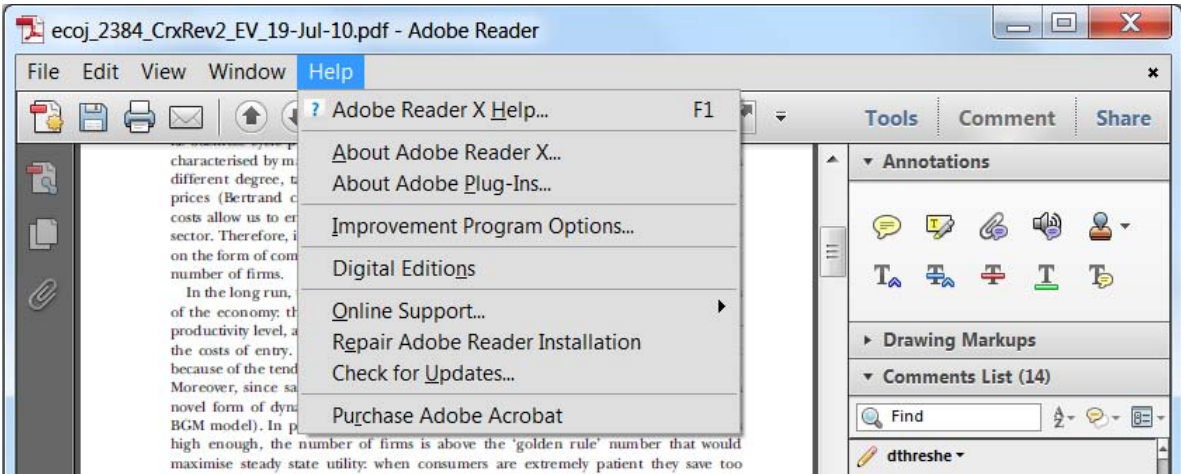
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Site occupancy and reproductive dynamics of California spotted owls in a mixed-ownership landscape

Brendan K. Hobart^{a,*}, Kevin N. Roberts^b, Brian P. Dotters^b, William J. Berigan^a,
Sheila A. Whitmore^a, Martin G. Raphael^c, John J. Keane^d, R.J. Gutiérrez^{a,e}, M. Zachariah Peery^a

^a Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA

^b Sierra Pacific Industries, PO Box 496014, Redding, CA, USA

^c USDA Forest Service, Pacific Northwest Research Station, Olympia, WA, USA

^d USDA Forest Service, Pacific Southwest Research Station, Davis, CA, USA

^e Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, MN, USA

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ABSTRACT

Biodiversity conservation in mixed-ownership landscapes often depends on contributions from privately-owned lands, where natural resource development can alter and produce novel habitat conditions for species of conservation concern. A lack of research on private lands stemming from access issues and concerns over regulatory outcomes, however, often limits evaluation of the impact of land management. The California spotted owl (*Strix occidentalis occidentalis*), for example, often occurs in mixed-ownership landscapes but research on this species has occurred primarily on public lands. Therefore, we conducted the first large-scale private-public cooperative and comparative analyses of California spotted owls inhabiting mixed-ownership landscapes in the Sierra Nevada, California, USA. We surveyed 151 spotted owl sites from 2013 to 2017 within two study systems: one comprised primarily of public lands (national forests) where the owl population has declined over the last ~20 years and a set of study areas comprised mostly of private lands on which relatively high estimates of site occupancy were recently reported. Multistate occupancy modeling indicated that the probability of occupancy and successful reproduction by owls depended on site status in the previous year, with both probabilities highest at sites where owls successfully reproduced in the previous year, intermediate at occupied sites where owls had not successfully reproduced, and lowest at previously unoccupied sites. Site occupancy probability was higher at low-elevation sites and lower at sites that contained more open area and younger forest. Successful reproduction by owls was also more likely at low-elevation sites and at sites with more north-facing slope and younger forest with high basal area of hardwoods. Study areas with more private lands tended to occur at lower elevations and have greater amounts of younger forest with high basal area of hardwoods, which may have contributed to higher occupancy and reproductive probabilities than the study area with more public land. Thus, differences in occupancy and reproductive probabilities between study areas appeared to be the result of differences in topographic and vegetation conditions that likely promote populations of key spotted owl prey species. Our results suggest that private lands in mixed-ownership landscapes may contribute to spotted owl conservation by conferring different benefits to owls than public lands and, more broadly, highlight the importance of including private lands in conservation research and planning.

1. Introduction

Privately-owned lands play an important role in biodiversity conservation (Kirby, 2003; Knight, 1999; Norton, 2000; Thomas, 2000). In the United States, about 72% of all land is private and the geographic ranges of approximately 80% of federally listed

threatened or endangered species occur at least partially on private lands (USFWS, 1997). Unlike publicly-owned lands, which are often managed for a balance of natural resource development, biodiversity conservation, and ecosystem services, resource extraction is often the priority on private lands (Bergmann and Bliss, 2004). Therefore, species conservation in mixed-ownership landscapes requires

* Corresponding author at: 1630 Linden Drive, Madison, WI 53706, USA.

E-mail address: bkhobart@wisc.edu (B.K. Hobart).

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strategies that maintain ecological integrity while allowing resource development to occur. Achieving this objective is challenging because resource development can alter habitat conditions for species of concern (Stanfield et al., 2002) and because mixed-ownership landscapes are typically characterized by complex landscape-scale patterns of landownership, habitat suitability, and species distributions (Dale et al., 2000; Mladenoff et al., 2007, 1997; Stanfield et al., 2002). Consequently, conservation success in mixed-ownership landscapes can hinge on understanding how species respond to varying and heterogeneous habitat conditions across multiple land-ownerships.

Effective conservation within mixed-ownership landscapes is often challenged by a lack of research on private lands resulting from restricted access, less funding, and landowner fear of regulatory restrictions resulting from research findings (Dale et al., 2000; Mir and Dick, 2012; Norton, 2000). Conversely, our understanding of species of conservation concern is typically based on research conducted primarily on public lands (e.g., carnivores; Peterson et al. 1998). For this reason, conservation scientists have largely focused on providing input about management issues on public lands (Knight, 1999). Nevertheless, failure to integrate private lands into conservation research and planning in mixed-ownership landscapes can lead to incorrect predictions about species responses to management, undesirable conservation outcomes, and increased tensions among stakeholders (Brook et al., 2003; Norton, 2000).

California spotted owls (*Strix occidentalis occidentalis*) occupy mixed-ownership landscapes throughout their range and have been studied extensively on public lands for decades, yet with relatively little attention paid to the influence of private lands (Stine and Manley, 2017; Verner et al., 1992). Until recently, it was assumed that the viability of this subspecies depended heavily on habitat conditions on public lands (Peery et al., 2017), whereas private lands were believed to make minimal contributions to the regional population based on studies demonstrating an avoidance of private lands for nesting, roosting, and foraging (Bias and Gutiérrez, 1992; Williams et al., 2014). Recent studies indicate that spotted owl populations are declining on three long-term national forest demographic study areas in the Sierra Nevada (Conner et al., 2016; Tempel and Gutiérrez, 2013), perhaps because of contemporary and historical loss of key nesting and roosting habitat elements (Jones et al., 2018; Tempel et al., 2014). In contrast, Roberts et al. (2017) reported high California spotted owl territory occupancy on mixed-ownership study areas (where private lands were managed primarily for timber production) relative to an adjacent national forest demographic study area. These different findings suggest that private lands, within a mixed-ownership context, may be more important for spotted owl populations in the Sierra Nevada than previously believed.

Because Roberts et al.'s (2017) comparison of spotted owl occupancy between public- and private-dominated landscapes was made in an *ad hoc* manner (e.g., potential differences in detection probabilities between study areas were not explicitly accounted for), we aimed to make comparisons among different studies more rigorous. In our study, we conducted the first large-scale, cooperative research effort between the U.S. Forest Service (USFS) and a large private landowner (Sierra Pacific Industries [SPI]) on California spotted owls inhabiting mixed-ownership landscapes in the Sierra Nevada, California, USA. By contrast, most previous studies of spotted owl populations have focused on the response of spotted owls to forest conditions without

regard to ownership (e.g., Conner et al., 2016; Tempel et al., 2016; but see Dugger et al., 2016). Our primary objectives were to: (i) estimate spotted owl occupancy and reproductive dynamics in landscapes that varied in the proportion of public and private land; and (ii) assess the extent to which differences in site occupancy and reproduction among sites were a function of forest conditions, landownership, and other environmental factors. We used multistate occupancy modeling, which offers the opportunity to relate multiple life-history traits (e.g., site occupancy and reproductive state) to environmental conditions rather than simple species presence-absence (MacKenzie et al., 2009). Indeed, including information about multiple states may provide valuable insights because habitat components on various ownerships may have contrasting effects on different life-history traits (e.g., beneficial for occupancy but detrimental or unimportant for reproduction).

2. Materials and methods

2.1. Study areas and management history

Our study areas were located in the central and northern Sierra Nevada, California, USA (Fig. 1). Historical logging and fire suppression in the Sierra Nevada have shifted tree species composition towards shade-tolerant, fire-sensitive species (e.g., White fir [*Abies concolor*]), led to a deficit of large, old trees, and an increase in surface and ladder fuels (McKelvey and Johnston, 1992). Although national forests and private forests were historically managed similarly, concern over the status of the spotted owl in the early 1990's prompted the USFS to emphasize diameter-limited logging prescriptions (North et al., 2017; Verner et al., 1992). In contrast, even-aged timber harvest on private lands has increased relative to public forests (North et al., 2017). This history has resulted in dense, spatially homogenous national forests that lack large, old trees, and private forests that contain a mix of different conditions including recent clear cuts, plantations, and forests similar to those that occur on public lands.

We used data from two sources: the USFS Eldorado Study Area (EDSA) and SPI's five Watershed Study Areas (WSAs). The EDSA was 63% national forest and 37% private (largely non-SPI) lands, which included a core 355 km² "density" area and satellite territories surrounding the "density" area (Fig. 1). Conversely, on the five WSAs private landownership predominated (overall 69%, range 48 – 94%), with lesser amounts of national forest (mean 30%, range 6 – 52%). The 549 km² (range 86 – 137 km²) WSAs spanned a 145 km latitudinal gradient (Roberts et al., 2017). The locations of all study areas were selected nonrandomly. Primary vegetation on all study areas was Sierran mixed-conifer forest, with white fir, Douglas fir (*Pseudotsuga menziesii*), incense cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), and black oak (*Quercus kelloggii*) dominating at low and intermediate elevations, while red fir (*Abies magnifica*) dominated at high elevations. Climate on the study areas was Mediterranean, with cool, wet winters and warm, dry summers. Although barred owls (*Strix varia*) are common throughout the range of the northern spotted owl (*S. o. caurina*) and are increasing in the northern Sierra Nevada, their low abundance in our study areas indicate that barred owls did not have a substantial effect on the spotted owl populations studied here (Keane, 2017; Roberts et al., 2017).

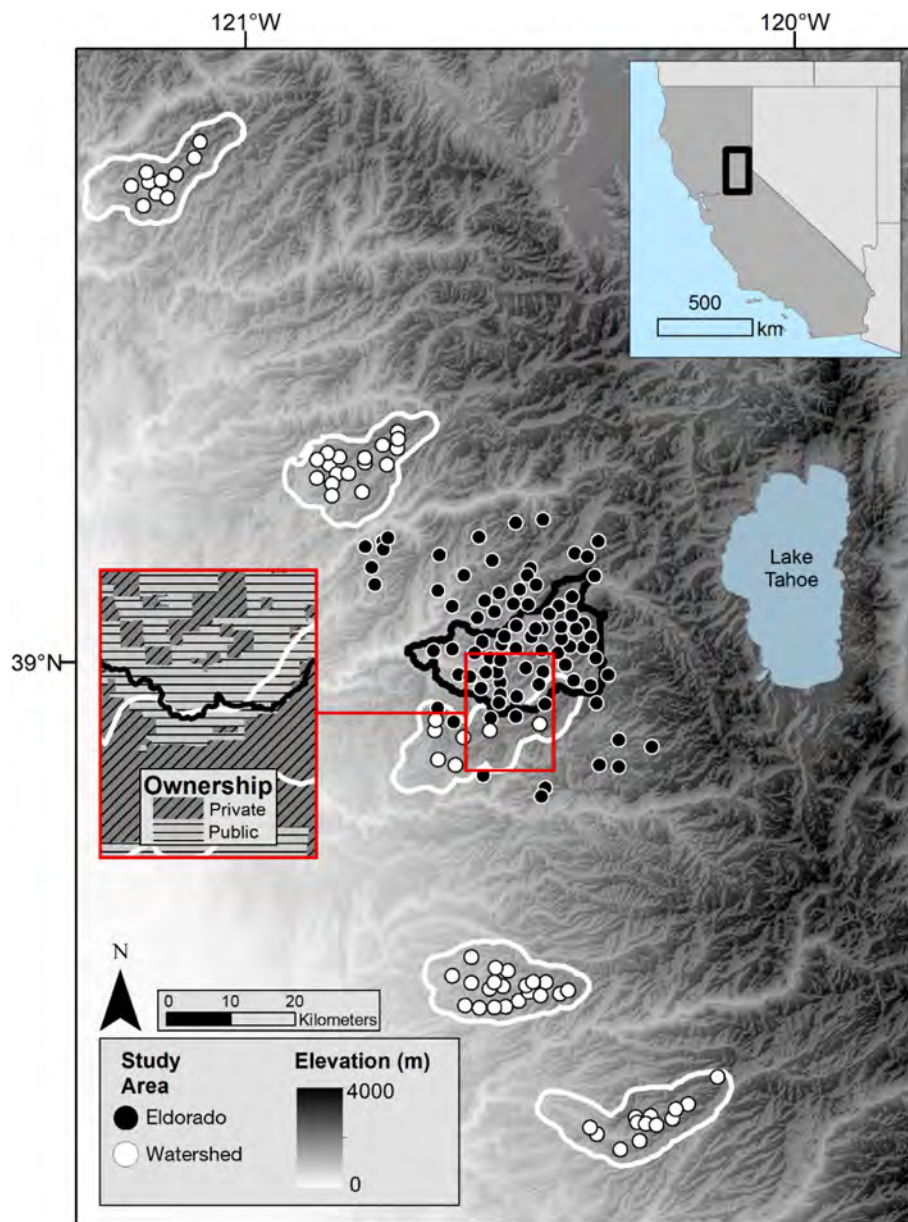


Fig. 1. Location of California spotted owl sites included in occupancy analyses. White and black shapes outline the WSAs and EDSA “density” area, respectively. Inset map displays an example of typical configuration of public and private lands on our study areas.

2.2. Owl surveys

We surveyed for owls on both study areas from March 15 to August 31, 2013–2017. Although the EDSA has been surveyed annually since 1986, we included only 2013–2017 data because we aimed to make direct comparisons to the WSAs, for which reliable data was only available 2013–2017; spotted owl occupancy and reproductive rates can vary annually (Conner et al., 2016; Franklin et al., 2000) so including data for additional years may have biased comparisons of occupancy and reproduction estimates. Territory locations on the EDSA were identified during long-term demographic research (Tempel et al., 2016), while territory locations on the WSAs were identified using records of annual owl activity centers found in the California Natural Diversity Database and from SPI’s owl surveys (Roberts et al., 2017). On the EDSA, only land within the “density” area was surveyed entirely while all WSAs were surveyed entirely.

We conducted initial early-season diurnal/twilight surveys annually to identify occupied territories on both study areas; on the WSAs, these surveys included all territories, whereas on the EDSA only territories that

were recently occupied (i.e., within the past 2–3 years) received an initial diurnal survey. We surveyed all territories at night (except those where initial surveys resulted in detections) 3–4 times per season by imitating spotted owl vocalizations for 10 min at predetermined call stations spaced 0.8–1.0 km apart or while walking routes connecting such points. When owls were detected nocturnally, we conducted diurnal follow-up surveys within 72 h to assess reproduction, locate roosts and nests, identify marked owls, and mark new owls with unique color bands. If follow-up surveys did not result in a detection, we resumed nocturnal surveys. We determined sex of detected owls by the pitch of calls, and assigned one of four age classes based on plumage characteristics (Moen et al., 1991). We determined the number of juveniles fledged by successful nests by offering live mice to adult owls, observing the delivery of mice to juveniles by parents, and counting the number of young observed outside the nest.

2.3. Modeling approach

We used multi-season multistate occupancy models to assess occupancy and reproductive dynamics that followed the conditional

Table 1

Notation and description of parameters used in multistate multi-season occupancy models employed to investigate occupancy and reproduction dynamics of spotted owls. Note that m refers to site state in year t : unoccupied (“0”), occupied without successful reproduction (“1”), or occupied with successful reproduction (“2”).

Parameter	Description
$p^{(1)}$	Probability of detecting occupancy of non-reproducing owls
$p^{(2)}$	Probability of detecting occupancy of reproducing owls
δ	Probability of correctly classifying reproduction, given occupancy
Ψ_0	Initial occupancy probability
$\Psi_{t+1}^{[m]}$	Probability of transitioning to occupied at time $t + 1$, given state m at time t
R_0	Initial reproduction probability (given occupancy)
$R_{t+1}^{[m]}$	Probability of transitioning to reproductively successful at time $t + 1$, given state m at time t

binomial parameterization initially developed by Nichols et al. (2007) for a single-season sampling design, which was later extended to multi-season designs by MacKenzie et al. (2009). In our model structure, a site’s true state was either unoccupied (“0”), occupied without successful reproduction (“1”), or occupied with successful reproduction (“2”). Thus, detection and classification parameters estimated the probabilities of detecting occupancy and reproduction, respectively (Table 1). State parameters estimated the probabilities of initial occupancy and reproduction, while a set of transition parameters estimated the probability of sites becoming occupied and reproductively successful in subsequent years (Table 1). Our notation followed MacKenzie et al. (2009) where occupancy and reproductive parameters with a superscript were transition probabilities (e.g., $\Psi_{t+1}^{[m]}$ and $R_{t+1}^{[m]}$) and those lacking a superscript were state variables (e.g., Ψ_0 and R_0).

Our sampling unit of analysis was the owl territory (hereafter site), defined here as a circle with a radius equal to $\frac{1}{2}$ nearest neighbor distance (NND) centered on a site’s activity center. One-half NND is a metric commonly used to denote areas of use for highly territorial species such as the spotted owl. We estimated site activity centers as the among-year spatial mean of nest locations when available and the within-year mean of roost locations for non-nesting years. We then calculated a single NND across all study areas (1.12 km). Although spotted owl site NND can vary with latitude (e.g., Tempel et al., 2016), the latitudinal range of our sites was relatively small, which justified the use of a single NND. We defined primary sampling periods as annual breeding seasons and secondary sampling periods as the 11 biweekly periods between March 15 and August 31. When we surveyed a site ≥ 30 min within a secondary sampling period, we assigned one of three survey results: no detection of owls, detection of at least one adult owl but no fledged juveniles, or detection of at least one fledged juvenile. We used a strict definition of “detection” to limit false-positives:

we included observations as detections only if they occurred diurnally or involved identification of known adult resident owls by resighting their uniquely-colored leg bands (Berigan et al., 2018). We defined diurnal as the time between (and including) the hours of civil twilight in the morning and civil twilight in the evening, which varied by study area and year.

In September 2014, the King Fire burned 39,545 ha in the central Sierra Nevada, including spotted owl sites on the EDSA and WSAs (Jones et al., 2016a). Jones et al. (2016a) demonstrated that owl sites that burned $> 50\%$ by area at high-severity ($> 75\%$ canopy cover loss) had significantly higher extinction probabilities following the fire, while sites that experienced $< 50\%$ high severity fire did not. Thus, to limit the potential confounding effects of wildfire on our comparisons, we censored 15 owl sites from 2015 to 2017 that experienced $> 50\%$ high severity fire (14 on the EDSA and one on the WSAs).

2.4. Site-level covariates

We included a suite of *a priori* covariates in occupancy models that fell into three broad categories: land cover, ownership, and topography (Table 2). We constructed land cover covariates using gradient nearest neighbor (GNN) forest structure maps produced by the Landscape Ecology, Modeling, Mapping, and Analysis (LEMMA) group (Oregon State University, Corvallis, OR, USA). Briefly, GNN data estimates forest conditions at 30 m resolution based on extensive forest-inventory plots and Landsat imagery (Ohmann and Gregory, 2002). We averaged 2013–2016 GNN data, except for owl sites that were severely burned $> 50\%$ in the King Fire, in which case we averaged only data from 2013 and 2014. Our three forest class covariates were open areas and sparse forests (hereafter “open areas”), younger forest, and older forest. We limited our analyses of cover classes to these three to reduce the number of models run, avoid spurious relationships, and focus on specific *a priori* hypotheses of interest. Open area was calculated as the proportion of pixels in an owl site that had canopy cover less than 40%. Younger forest was calculated as the proportion of pixels in an owl site with canopy cover greater than 40% and quadratic mean diameter of dominant and codominant trees (QMD) less than 30 cm. Older forest was calculated as the proportion of pixels in an owl site with canopy cover greater than 70% and QMD greater than 61 cm. We selected these criteria based on patterns of land cover in our study areas, previous work on spotted owl-habitat relations, and the reasonable correspondence of these classes to National Agriculture Imagery Program (NAIP) imagery (60 cm resolution; Fig. 2). Pixels with less than 40% canopy cover described low canopy cover forests and areas recently cleared as part of even-aged management practices, so we predicted that occupancy and reproduction would be lower at sites with more open area based on the importance of older forest for spotted owls (Tempel et al., 2016). Pixels with canopy cover greater than 40% and QMD less than

Table 2

Site-level covariates included in multistate models to explain variation in occupancy and reproduction dynamics of spotted owls on the EDSA and WSAs. Predicted effects were: positive (+) relationship between covariate and parameter; negative (–) relationship between covariate and parameter; and no specific prediction (x).

Covariate	Abbreviation	Description	Predicted effect on:	
			$\Psi_0, \Psi_{t+1}^{[m]}$	$R_0, R_{t+1}^{[m]}$
Open area	OPEN	Proportion of a site containing area with canopy cover $< 40\%$	–	–
Younger forest	YF	Proportion of a site containing forest with QMD < 30 cm and canopy cover $> 40\%$	+ / –	+ / –
Older forest	OF	Proportion of a site containing forest with QMD > 61 cm and canopy cover $> 70\%$	+	+
Shannon’s evenness index	EVEN	Calculated based on OPEN, YF, and OF covariates (unitless)	+	+
Diameter diversity index	DDI	Measure of forest structural diversity (unitless)	+	+
Basal area of hardwoods	BAHW	Mean live area of hardwoods (m^2/ha , divided by 25 to scale for analysis)	+	+
Study area	SA	Binary indicator: WSAs = 1; EDSA = 0	+	x
SPI-owned land	SPI	Proportion of a site with SPI-owned land	x	x
USFS-managed land	USFS	Proportion of a site with USFS-managed land	x	x
Elevation	ELEV	Elevation (km) at a site-center	x	x
North-facing slope	NFS	Proportion of a site with slope aspect within $\pm 45^\circ$ of geographic north	+	+

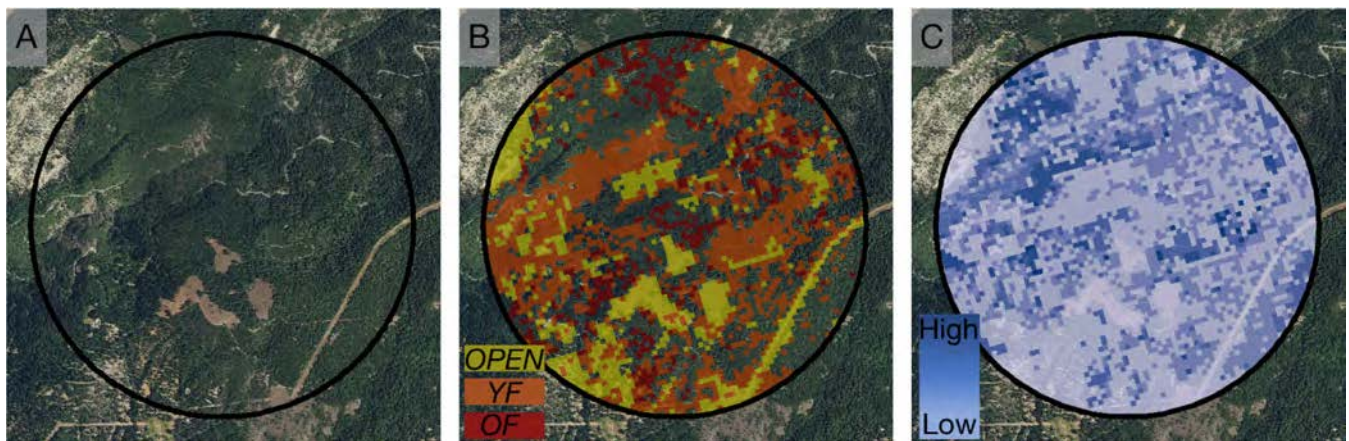


Fig. 2. Depiction of a typical spotted owl site visualized with (A) NAIP imagery, (B) GNN-derived covariates open area, younger forest, and older forest, and (C) GNN-derived basal area of live hardwoods.

30 cm typically corresponded to closed-canopy forests with sapling and pole-sized trees, which represents potential habitat for the dusky-footed woodrat (*Neotoma fuscipes*), an important spotted owl prey species (Hamm and Diller, 2009; Sakai and Noon, 1993). However, because spotted owls require older forests for nesting and roosting, we predicted that the relationship between younger forest and occupancy and reproduction could be positive or negative. Finally, forest with canopy cover greater than 70% and QMD greater than 61 cm was recently demonstrated to be strongly positively correlated with spotted owl occupancy in the Sierra Nevada (Jones et al., 2018; Moen and Gutiérrez, 1997), so we predicted that sites with more older forest would have higher occupancy and reproduction. We also included Shannon's evenness index calculated for the three preceding classes to describe site-level uniformity of forest conditions, which we predicted to be positively associated with occupancy and reproduction based on previous work demonstrating the importance of multiple forest cover types for spotted owl life-history traits (Franklin et al., 2000).

Other GNN-derived covariates included mean diameter diversity index (DDI; Spies et al., 2007) and mean basal area of hardwoods (Fig. 2). DDI is a unitless measure of stand-level forest structural diversity based on densities of different tree size classes and tends to increase with stand age. Thus, we predicted that spotted owl occupancy and reproduction would be greater at sites with higher average DDI, given the reliance of spotted owls on old forest conditions (Jones et al., 2018). We included mean basal area of live hardwoods because of the importance of hardwoods for woodrat habitat (Hamm et al., 2007) and predicted that sites with more hardwoods would have greater occupancy and reproduction, given the frequent consumption of woodrats by spotted owls (Thraill and Bias, 1989).

Our remaining covariates described study area, ownership, and topography. We specified study area as “0” for the EDSA and “1” for the WSAs. Based on Roberts et al. (2017), we predicted that occupancy would be higher on the WSAs but made no specific prediction about reproduction. We also used a proprietary ownership map (SPI, unpublished data) to estimate the proportion of owl sites on SPI and USFS ownership, each of which constituted a covariate. Finally, we included elevation (of activity centers) and north-facing slope (proportion of sites within $\pm 45^\circ$ of geographic north) as covariates because of their relationship to a suite of biotic and abiotic conditions including microclimate, mean temperature, prey availability, and forest conditions (Jones et al., 2016b). We made no specific *a priori* hypotheses regarding the relationship between elevation and occupancy and reproductive parameters. We did, however, predict that sites with more north-facing slope would have greater occupancy and reproduction because north-facing slopes create favorable microclimatic conditions for both spotted owls (Barrows, 1981; North et al., 2000) and flying squirrels (*Glaucomys oregonensis*), which are important prey (Pyare and Longland, 2002).

2.5. Model selection

We used program PRESENCE 12.6 (USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA) to fit multi-season multistate occupancy models to our detection history data in a multistage hierarchical process. We ranked models within each of seven stages using Akaike's Information Criterion (AIC; Burnham and Anderson 2002) and progressed the best model structure from each stage forward to the next stage. We did not investigate interactions between covariates as doing so would have required fitting an excessive number of models, which can result in the selection of models describing spurious relationships. Additionally, we did not include covariates in model statements together if they were highly correlated ($|r| > 0.60$; Table S1). The seven stages in our modeling framework were conducted as follows:

Stage 1. We determined the best within-year structure of $p^{[1]}$, $p^{[2]}$, and δ while holding their among-year structures fully time varying, and holding $\Psi_{t+1}^{[m]}$ and $R_{t+1}^{[m]}$ in a *state + year* structure (*state* refers to site status in the previous year). Within-year structures included: a “null” model where probabilities were constant among secondary sampling periods (“.”); a site-specific “initial” response where the probability of detection/classification varied before and after the initial detection of occupancy/reproduction; an “early” effect, where the probability of classifying sites as reproductively successful varied before and after July 1st each year; and a within-year linear time trend (“T”). Note that $p^{[1]}$ and $p^{[2]}$ were always modeled separately but with the same structure, based on strong *a priori* knowledge that spotted owls are more detectable when reproducing than when not reproducing (Tempel et al., 2016).

Stage 2. We compared among-year and among-study area structures of $p^{[1]}$, $p^{[2]}$, and δ while holding $\Psi_{t+1}^{[m]}$ and $R_{t+1}^{[m]}$ in a *state + year* structure. Among-year structures included: a “null” model where all years were given the same coefficient; a linear time trend; a log-linear time trend (“lnT”); a full time-varying year effect (“year”); and a study area effect in which probabilities varied between the EDSA, the WSAs in 2013, and the WSAs 2014–2017 (“SAdet”). Because 2013 was the first full-effort field season on the WSAs, we predicted that detection and classification may have been relatively low in that year.

Stage 3. Prior to including site-level covariates, we assessed whether $\Psi_{t+1}^{[m]}$ and $R_{t+1}^{[m]}$ depended on state in the previous year, varied annually, varied in an additive *state + year* relationship, or neither (i.e., a “null” model).

Stage 4. We modeled the effects of site-level covariates on Ψ_0 , using separate model suites for forest covariates (Stage 4.1), ownership covariates (Stage 4.2), and topographic covariates (Stage 4.3). We then compared and combined the top models from these sub-stages

Table 3

Mean values (SD) for site-level covariates used to model variability in spotted owl occupancy and reproduction dynamics.

	Overall	EDSA	WSAs
<i>OPEN</i> ^A	0.15 (0.10)	0.16 (0.12)	0.13 (0.06)
<i>YF</i> ^A	0.24 (0.09)	0.23 (0.09)	0.24 (0.10)
<i>OF</i> ^A	0.07 (0.06)	0.06 (0.05)	0.07 (0.07)
<i>EVEN</i> ^B	0.66 (0.09)	0.66 (0.09)	0.66 (0.09)
<i>DDF</i> ^B	0.49 (0.06)	0.50 (0.07)	0.49 (0.05)
<i>BAHW</i> (m ² /ha)*	7.54 (4.56)	6.81 (4.63)	8.46 (4.34)
<i>USFS</i> ^A ***	0.53 (0.37)	0.77 (0.22)	0.22 (0.27)
<i>SPI</i> ^A ***	0.31 (0.35)	0.07 (0.14)	0.60 (0.31)
<i>ELEV</i> (km) *	1.32 (0.27)	1.44 (0.22)	1.17 (0.24)
<i>NFS</i> ^A	0.27 (0.13)	0.28 (0.14)	0.25 (0.12)
<i>Post hoc covariates:</i>			
<i>YF low-BAHW</i> ^A ***	0.10 (0.05)	0.11 (0.04)	0.08 (0.05)
<i>YF high-BAHW</i> ^A *	0.14 (0.10)	0.12 (0.09)	0.16 (0.12)
<i>non-YF high-BAHW</i> ^A ***	0.30 (0.16)	0.26 (0.15)	0.37 (0.15)

Result of *t*-test comparing EDSA to WSAs: **p* < 0.05, ***p* < 0.01, ****p* < 0.001.

^A Covariate values are the proportion of an owl site.

^B Unitless index.

to determine the best model for Ψ_0 (Stage 4.4).

Stage 5. We modeled the effects of site-level covariates on $\Psi_{t+1}^{[m]}$, using separate model suites for forest covariates (Stage 5.1), ownership covariates (Stage 5.2), and topographic covariates (Stage 5.3). We then compared and combined the top models from these sub-stages to determine the best model for $\Psi_{t+1}^{[m]}$ (Stage 5.4).

Stage 6. We modeled the effects of site-level covariates on R_0 , using separate model suites for forest covariates (Stage 6.1), ownership covariates (Stage 6.2), and topographic covariates (Stage 6.3). We then compared and combined the top models from these sub-stages to determine the best model for R_0 (Stage 6.4).

Stage 7. We modeled the effects of site-level covariates on $R_{t+1}^{[m]}$, using separate model suites for forest covariates (Stage 7.1), ownership covariates (Stage 7.2), and topographic covariates (Stage 7.3). We then compared and combined the top models from these sub-stages to determine the best model for $R_{t+1}^{[m]}$ (Stage 7.4).

3. Results

3.1. Survey effort and covariate distributions

We surveyed 151 individual spotted owl sites (84 on the EDSA and 67 on the WSAs) from 2013 to 2017 (mean = 136 sites/year; range:

128 – 150). We detected occupancy at an average of 86 sites annually (range: 83 – 91) and successful reproduction at an average of 25 sites annually (range: 6 – 43). Basal area of hardwoods (*BAHW*), *USFS*, *SPI*, and *ELEV* were the only site-level covariates that differed significantly between the two study areas (all *p*'s < 0.05; Table 3). Four pairwise sets of covariates were highly correlated ($|r| > 0.60$, Table S1) and were thus only included in separate model statements.

3.2. Stagewise modeling results

Modeling stage 1 indicated that within-year detection of non-reproductive ($p^{[1]}$) and reproductive adults ($p^{[2]}$) was higher after owls were initially detected at a site ($w_i = 1.0$, Table S2, Table 4, Fig. 3A, B). Similarly, classification of successful reproduction (δ) was higher after July 1st ($w_i = 1.0$; Table S2; Table 4; Fig. 3C). Stage 2 modeling indicated that detection of non-reproductive adults ($p^{[1]}$) increased linearly among years while detection of reproductive adults ($p^{[2]}$) decreased linearly among years ($w_i = 0.42$; Table S3; Table 4; Fig. 3A, B). Classification of successful reproduction (δ) was lowest on the WSAs in 2013, intermediate on the WSAs 2014–2017, and highest on the EDSA ($w_i = 0.42$; Table S3; Table 4; Fig. 3C).

Stage 3 indicated that the probability of a site becoming or remaining occupied ($\Psi_{t+1}^{[m]}$) did not vary among years and was lowest when previously unoccupied, intermediate when previously occupied without successful reproduction, and highest when previously occupied with successful reproduction (i.e., $\Psi_{t+1}^{[0]} < \Psi_{t+1}^{[1]} < \Psi_{t+1}^{[2]}$; $w_i = 0.91$; Table S4; Fig. 4A). The probability of a site having reproductively successful owls in a given year ($R_{t+1}^{[m]}$) varied annually and followed the same previous-status relationship as occupancy (i.e., $R_{t+1}^{[0]} < R_{t+1}^{[1]} < R_{t+1}^{[2]}$; $w_i = 0.91$; Table S4; Fig. 4B).

Stage 4 indicated that initial site occupancy (Ψ_0) declined as elevation increased ($w_i = 0.33$; Table S5; Table 4; Fig. 5A). Stage 5 indicated that the probability of a site becoming or remaining occupied ($\Psi_{t+1}^{[m]}$) declined with increasing elevation, younger forest, and open area ($w_i = 0.77$; Table S6; Table 4; Fig. 5B).

Stage 6 indicated that initial reproduction (R_0) decreased as elevation increased but was higher at sites with more north-facing slope ($w_i = 0.26$; Table S7; Table 4; Fig. 6A). In modeling reproductive transitions (stage 7), two models received virtually identical support (both $w_i = 0.12$; $\Delta AIC = 0.02$; Table S8). Together, they indicated that the probability of a site having reproductively successful owls in a given year ($R_{t+1}^{[m]}$) was higher at sites containing more north-facing slope and either more basal area of hardwoods or more younger forest (Table S8; Table 4; $\beta_{YF} = 3.39$, 95% CI = -0.82 – 7.60). Note, however, that

Table 4

Beta coefficients (SE) for the top-ranked model resulting from multi-stage model selection (Table S8). Cells with “0” indicate that a covariate was not modeled for a given parameter. Parameters and covariates follow notation from Table 1 and Table 2, respectively. Bold font values indicate that the respective 95% confidence interval did not overlap zero.

<i>Detection probability parameters</i>						
	<i>initial</i>	<i>T</i>	<i>early</i> ^A	<i>late</i> ^A	<i>WSA 13</i>	<i>WSA 14–17</i>
$p^{[1]}$	1.18 (0.17)	+	0	0	0	0
$p^{[2]}$	0.91 (0.22)	+	0	0	0	0
δ	0	0	-1.63 (0.20)	1.29 (0.23)	-2.53 (0.45)	-0.55 (0.26)
<i>Detection and reproduction parameters</i>						
	<i>ELEV</i>	<i>NFS</i>	<i>OPEN</i>	<i>YF</i>	<i>BAHW</i>	
Ψ_0	-2.78 (0.96)	0	0	0	0	
$\Psi_{t+1}^{[m]}$	-1.91 (0.96)	0	-4.13 (2.42)	-7.30 (3.00)	0	
R_0	-2.62 (1.40)	4.53 (2.27)	0	0	0	
$R_{t+1}^{[m]}$	0	2.16 (1.38)	0	0	1.71 (1.06)	

+ separate beta coefficients for each year; not listed.

^A intercept term.

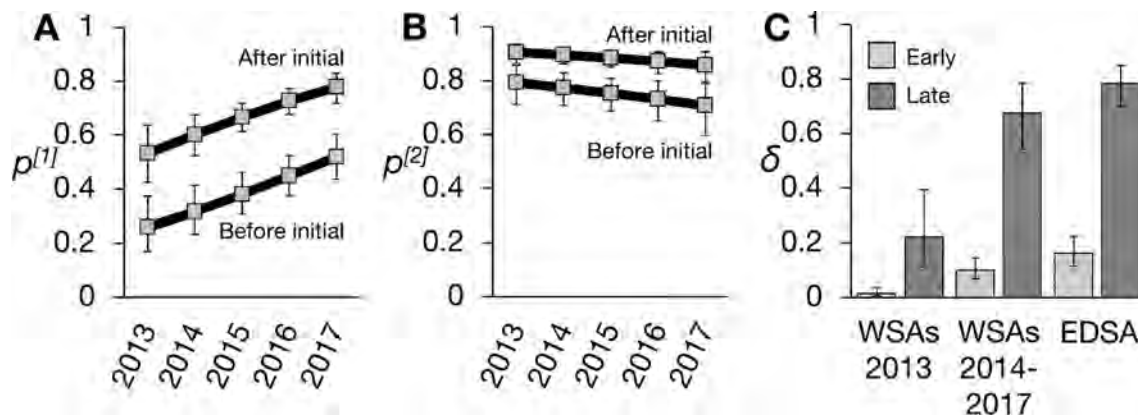


Fig. 3. Estimates of detection probabilities $p^{[1]}$ (A) and $p^{[2]}$ (B), and classification probability δ (C) for California spotted owls based on model $p^{[1]}(T, \text{initial})$, $p^{[2]}(T, \text{initial})$, $\delta(\text{SAdet}, \text{early})$ (Table S8). Error bars correspond to approximate 95% confidence intervals.

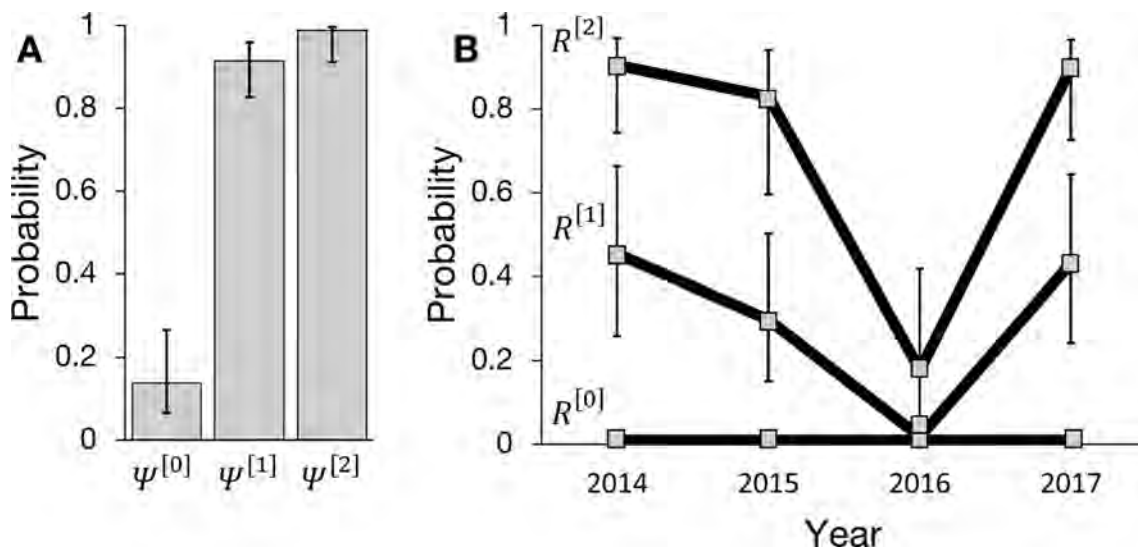


Fig. 4. Estimates of (A) occupancy and (B) reproduction transition probabilities for California spotted owls based on model $\psi_{t+1}^{[m]}(\text{OPEN} + \text{YF} + \text{ELEV} + \text{state})$, $R_{t+1}^{[m]}(\text{state} + \text{year} + \text{BAHW} + \text{NFS})$ with all site-level covariates held constant at their mean values (Table S8). Error bars correspond to approximate 95% confidence intervals and were omitted for $R_{t+1}^{[0]}$ estimates for clarity.

younger forest and basal area of hardwoods were positively correlated ($r = 0.72$; Table S1). Furthermore, all models in stage 7.4 were within 2 AIC of the top model, including the “null” model, and AIC weight was distributed relatively equally among models indicating that a considerable amount of variability in reproductive data was not described by our covariates (Table S8).

3.3. Post hoc analysis

Because younger forest and basal area of hardwoods were essentially equally supported in stage 7.4 (Table S8) and were highly correlated at the site level (Table S1), we conducted a *post hoc* analysis to assess their relative importance for spotted owl reproduction. To do so, we defined three new site-level covariates: (i) younger forest with low basal area of hardwoods (YF low-BAHW), (ii) younger forest with high basal area of hardwoods (YF high-BAHW), and (iii) non-younger forest with high basal area of hardwoods (non-YF high-BAHW). We defined younger forest using our original criteria (QMD < 30 cm and canopy cover > 40%). We used the mean value of basal area of hardwoods at the pixel scale within sites (4.5 m²/ha) to distinguish between low and high levels of hardwoods. The new covariates, then, were the proportions of pixels within sites meeting these criteria. All three covariates differed significantly between the EDSA and the WSAs (all $P < 0.05$;

Table 3) but were not significantly correlated with one another (Table S1). We proceeded to model reproductive transition probabilities ($R_{t+1}^{[m]}$) as a function of north-facing slope (which occurred in the original top model) and each of the three new covariates (in additive relationships), with all other parameters held at their previously-determined best structure. We compared these models to one another and to a null (“.”) model. Our *post hoc* analysis indicated that the probability of successful reproduction in a given year ($R_{t+1}^{[m]}$) was higher at sites containing more north-facing slope and more younger forest with high basal area of hardwoods ($w_i = 0.51$; Table S9; $\beta_{\text{YFhigh-BAHW}} = 3.07$, 95% CI = -0.72 – 6.85; Fig. 6B).

4. Discussion

4.1. State-dependency of spotted owl occupancy and reproductive dynamics

Spotted owl site occupancy and reproduction exhibited strong autocorrelation: occupancy and reproductive success in year $t + 1$ were dependent on state in year t and this structure explained a large amount of variability in the data. Specifically, occupancy was highest at sites that were occupied with successful reproduction in the previous year, intermediate at sites that were occupied without successful reproduction in the previous year, and lowest at sites that were unoccupied in the previous year. This finding supports the general understanding that

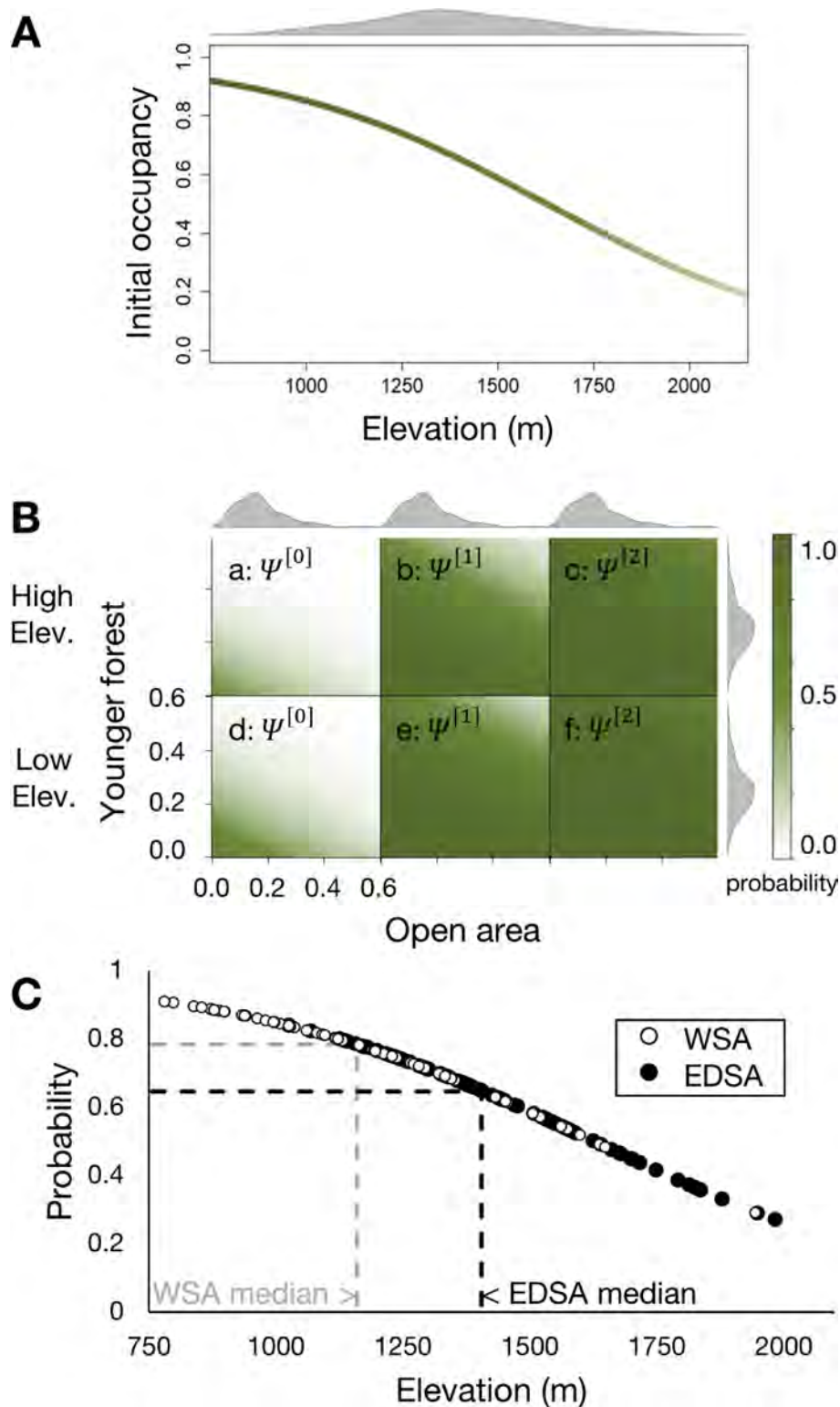


Fig. 5. A: Relationship between the probability of initial occupancy (Ψ_0) and elevation for California spotted owls based on model $\Psi_0(ELEV)$ (Table S8). The gray subplot above the main plot displays the frequency distribution of elevation of owl sites. B: Heat plots relating occupancy transition probabilities ($\Psi_{t+1}^{[m]}$; color scale) to younger forest and open area for California spotted owls based on model $\Psi_{t+1}^{[m]}(OPEN + YF + ELEV + state)$ (Table S8). Individual panels represent the probability of site occupancy at time $t + 1$, given it was unoccupied at time t (a, d), occupied without reproduction at time t (b, e), and occupied with reproduction at time t (c, f). Panels a-c represent the relationship with elevation held constant at its 3rd quartile (1.52 km) while panels d-f represent the relationship with elevation held constant at its 1st quartile (1.15 km). The gray subplots above and to right of main plots display the frequency distributions of open area and younger forest (respectively) at owl sites. C: Site-level estimates of initial occupancy probability for spotted owl sites on the EDSA and WSAs. Study area is denoted by color of points. Dashed lines indicate median elevation for each study area and corresponding initial occupancy estimates.

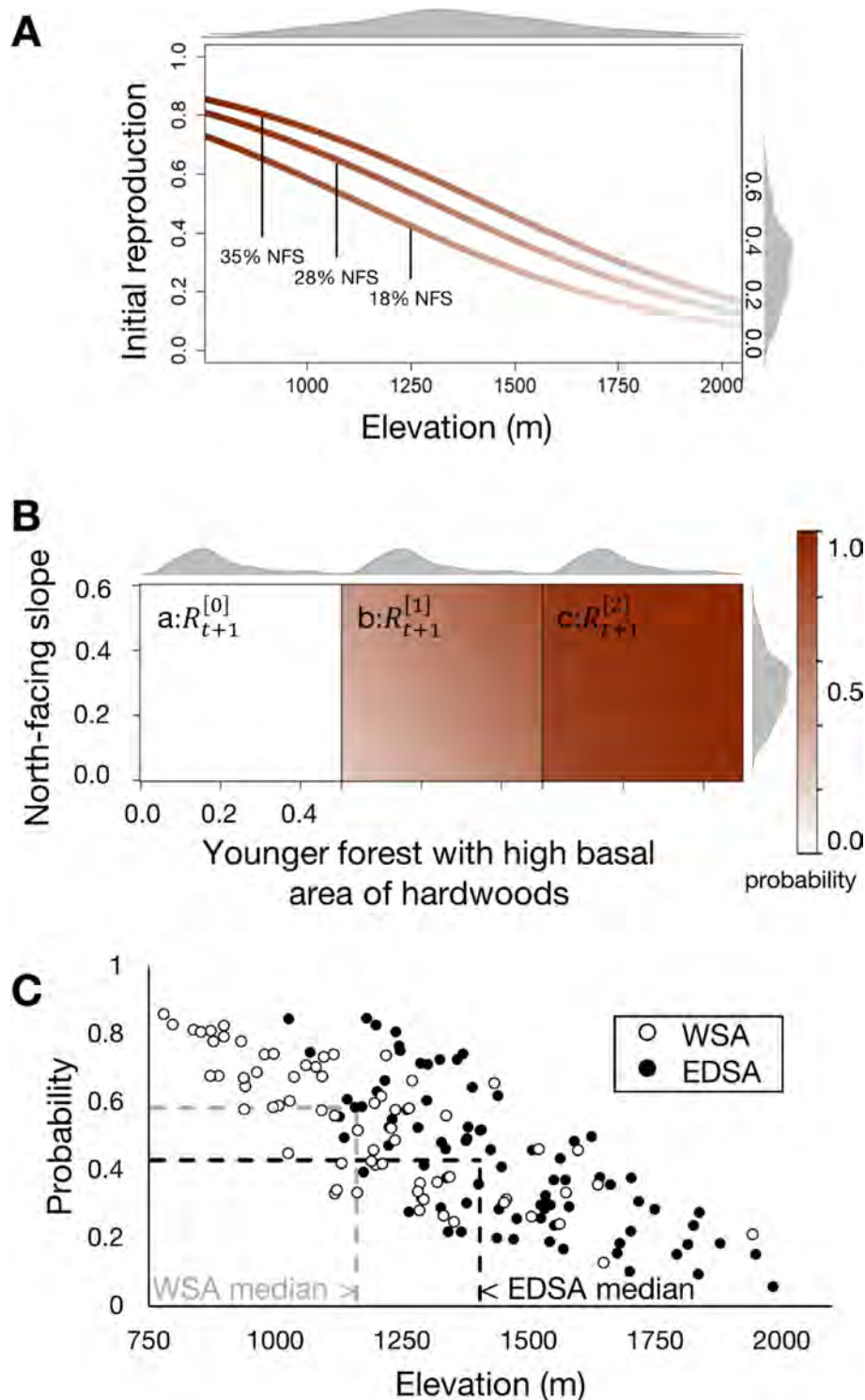


Fig. 6. A: Relationship between the probability of initial reproduction (R_0) and elevation for California spotted owls based on model $R_0(ELEV + NFS)$ (Table S8). Individual lines represent the relationship at different levels of north-facing slope (from bottom: 1st quartile, median, and 3rd quartile). Gray subplots above and to right of the main plot display frequency distributions of elevation and north-facing slope (respectively) at owl sites. B: Heat plots relating reproduction transition probabilities ($R_{t+1}^{[m]}$; color scale) to north-facing slope and younger forest with high basal area of hardwoods for California spotted owls based on model $R_{t+1}^{[m]}(state + year + YF\ high-BAHW + NFS)$ (Table S9). Individual panels represent the probability of a site successfully reproducing at time $t + 1$, given it was (a) unoccupied at time t , (b) occupied without reproduction at time t , and (c) occupied with reproduction at time t . Note that these probabilities varied annually; the relationships shown here are for the first transition (i.e., $t = 2013$, $t + 1 = 2014$). The gray subplots above and to right of main plots depict the frequency distributions of basal area of hardwoods and north-facing slope (respectively) across owl sites. C: Site-level estimates of initial reproduction probability for spotted owl sites on the EDSA and WSAs. Study area is denoted by color of points. Dashed lines indicate median elevation for each study area and corresponding initial reproduction estimates.

spotted owls have high site fidelity and the observation that California spotted owl pairs are less likely to disperse from sites at which successful reproduction occurs (Blakesley et al., 2006; Gutiérrez et al., 2011). Because others have previously reported similar patterns in state-dependency for spotted owl occupancy, these processes likely apply to the species in general (e.g., MacKenzie et al. 2009, Lee and Bond 2015). Although the probability of successful reproduction fluctuated among years, it varied by state in the same pattern as occupancy: successful reproduction in year $t + 1$ was most likely if reproduction occurred in year t . Autocorrelation in reproduction at a given site occurred despite previous evidence of the tendency for reproductive individuals to have a slightly reduced likelihood of breeding the following year (Stoelting et al., 2015). Thus, some owl sites appeared to be consistently high quality and may serve as population sources (Pulliam 1988). Predicting and identifying such high quality sites may be particularly important for prioritizing owl sites for habitat retention or forest restoration activities (Wood et al., 2018).

4.2. Associations of site occupancy and reproduction with forest conditions and topography

Spotted owl occupancy and reproductive probabilities were associated with topographic and vegetation conditions at individual sites. Occupancy and initial reproduction were greater at low elevation sites, perhaps because the dusky-footed woodrat (*Neotoma fuscipes*), an important spotted owl prey species, is more common at lower elevations in the Sierra Nevada (Roberts, 2017). Indeed, woodrats are large in size and reach high population densities, which could promote occupancy and increase the likelihood of successful reproduction by spotted owls at lower elevation sites (Smith et al., 1999). Alternatively, Jones et al. (2016b) showed that owls at high-elevation sites in the central Sierra Nevada were more adversely affected by warm summer temperatures than at low-elevation sites. They suggested that warm, drought conditions may negatively impact flying squirrels – the primary prey of spotted owls at high elevations – by reducing hypogeous fungi biomass, which is the primary summer food of flying squirrels. Because our study occurred largely under drought conditions, declines in flying squirrel populations may also have contributed to the negative relationships between elevation and owl demographic parameters. Thus, elevational patterns in spotted owl demography may be related to underlying patterns in the abundance and distribution of prey resources.

As predicted, owl sites with more north-facing slope had higher probabilities of reproduction. North-facing slopes are generally cooler than south-facing slopes and may provide thermal refugia for spotted owls, a relatively cold-adapted species with limited ability to dissipate heat (Barrows, 1981; Ganey et al., 1993; Weathers et al., 2001). Barrows (1981) suggested that spotted owls reduced heat stress by selecting for roost locations on north-facing slopes. Additionally, because north-facing slopes tend to contain relatively more old forest with complex canopy structure (North et al., 2009), they may afford juvenile spotted owls greater protection from aerial predation than the surrounding landscape, which could positively impact reproductive rates (Franklin et al., 2000; Gutiérrez and Carey, 1985). Finally, mature forests on north-facing slopes may provide favorable habitat conditions for flying squirrels (Pyare and Longland, 2002), which are consumed relatively more frequently by reproducing owls than non-reproducing individuals (Thrallkill and Bias, 1989). Further research would be required to disentangle the relative contributions of microclimatic refugia, protection from predation, and prey availability to successful spotted owl reproduction.

Spotted owl site occupancy tended to be less likely at sites that contained more open area and greater amounts of younger forests. Younger forests and open areas are warmer than neighboring mature forests (Chen et al., 1995) and are also habitats for great horned owls (*Bubo virginianus*; Johnson 1992, Gutiérrez et al. 1995), which may increase the chances of either heat stress or predation, respectively.

Although younger forests and open areas may contain high densities of potential prey, younger forests may be too densely vegetated to allow hunting by owls and open areas often lack large branches from which spotted owls perch while hunting (Gutiérrez et al., 1995). Thus, there are several ecologically plausible mechanisms that may explain the observed negative associations between occupancy and open areas and younger forests.

In contrast to our occupancy results, our *post-hoc* analysis indicated that successful spotted owl reproduction tended to be more likely at sites containing a greater area of younger forest with high basal area of hardwoods. While previous studies have shown that spotted owls selectively forage in or near forests containing hardwoods (Irwin et al., 2007; Ward et al., 1998; Zabel et al., 1995), ours is the first to report a positive association between reproduction and younger forest with high basal area of hardwoods. This relationship may have been a function of prey abundance and availability: dusky-footed woodrat densities are highest in brushy, early-seral forests with an ample supply of downed logs and in the presence of mast-producing hardwoods such as large California black oaks (Innes et al., 2007; Sakai and Noon, 1993). Thus, patches of younger forest with high basal area of hardwoods within territories may provide owls with more woodrat prey, the consumption of which is positively associated with California spotted owl reproductive success (Smith et al., 1999). The juxtaposition of younger forest with high basal area of hardwoods with other cover types is likely an important consideration (Franklin et al., 2000); spotted owls forage in younger forests in proportion to its availability but selectively forage in older forests (Atuo et al., 2019; Blakey et al., 2019) and thus may benefit from the “spillover” of small mammals from younger forests into older forests (Sakai and Noon, 1993). We did not, however, investigate the relationship between forest spatial configuration and occupancy or reproduction because fine-scale inferences based on GNN data are not appropriate (D. Bell, personal communication). Furthermore, because GNN data is remotely-sensed, we could not systematically identify the most important hardwood species. A subjective, opportunistic ground-based evaluation indicated that the younger forest with high basal area of hardwoods cover type, as we defined it based on GNN data, was both floristically and structurally variable and often included: (i) brushy openings containing a variety of species such as deerbrush (*Ceanothus* spp.), manzanita (*Arctostaphylos* spp.), and black oaks (Fig. S1A), and (ii) younger conifer forests containing a similar mix of hardwoods (Fig. S1B). Interpreting the relationship between spotted owl reproduction and younger forest with high basal area of hardwoods (as defined here) is further complicated by the fact that GNN appeared to sometimes misclassify this cover type: both our ground-based evaluation (Fig. S1C) and NAIP imagery inspection (Fig. S2) revealed that older forests were sometimes classified as younger forests with high basal area of hardwoods. Thus, additional work is required to establish which species and under what forest conditions (e.g., age) hardwoods benefit California spotted owl reproduction.

4.3. Synthesizing population-habitat linkages in California spotted owls

Our current study is one of several that relate California spotted owl demographics to environmental conditions within territories and, in general, our results corroborate other such studies. For example, previous studies have indicated that spotted owl occupancy and reproduction were higher at sites with relatively large amounts of high canopy cover and older forests (Blakesley et al., 2005; Cade et al., 2017; Jones et al., 2016b, 2018, Tempel et al., 2014, 2016). Although older forest – which on average accounted for 7% of the area in our owl sites – was not supported in our final models for occupancy or reproduction, it did have a positive coefficient when present in models and generally outperformed intercept-only models. The negative associations of occupancy and reproduction with open areas were also consistent with previous studies and indicated that such habitats are less suitable for spotted owls (Blakesley et al., 2005; Gutiérrez et al., 1995; Tempel

et al., 2014). Thus, our research was consistent with previous studies that indicated California spotted owl populations may benefit from older and closed-canopy forests and can be adversely affected by younger seral stages within their territories.

Nevertheless, remaining uncertainties – and differences in results among studies regarding associations between spotted owl demography and habitat conditions – will challenge the translation of science into effective conservation and forest management. For example, Blakesley et al. (2005) reported lower occupancy and reproduction probabilities at sites with more younger forest, but Franklin et al. (2000) found that a broad category of cover types (“other,” which included younger forest) was correlated with higher owl reproduction. Our results reflect this uncertainty given that occupancy and reproduction were negatively and positively associated with younger forest, respectively. Differences in vegetation mapping and classification may account for some variability among studies associating spotted owl demographics and young forest. Indeed, previous studies have not quantified the prevalence of hardwoods (e.g., Blakesley et al., 2005; Franklin et al., 2000) – which likely provide important food resources for small mammal populations. And, as described above, some younger forest with high basal area of hardwoods (as classified in this study) may have contained older forests; as such, it is uncertain whether hardwoods or younger forest *per se* promoted high spotted owl reproduction. Future work that incorporates rigorous, ground-based measures of vegetation conditions – and ideally experimental manipulations of the hardwood component – may help resolve this and other uncertainties regarding spotted owl habitat requirements.

4.4. Role of private lands in California spotted owl conservation

Despite decades of research, the importance of private lands for California spotted owl conservation has been uncertain. Although previous research demonstrated avoidance of private lands by spotted owls at both the territory (Bias and Gutiérrez, 1992) and foraging-site (Williams et al., 2014) scales, recent evidence suggested that landscapes containing relatively high proportions of private lands (the WSAs studied here) had higher site occupancy rates than landscapes containing more public land (the EDSA) and thus likely contribute to spotted owl conservation (Roberts et al., 2017). Here we found that spotted owl site occupancy and reproduction were best-explained by forest conditions and topography, with relatively little support for ownership covariates at either the site scale (proportion of territory in USFS versus SPI ownership) or landscape scale (EDSA versus WSAs). Yet, several important covariates differed significantly between sites occurring on the EDSA and WSAs: WSA sites, on average, occurred at lower elevations and contained more younger forest with high basal area of hardwoods (Table 3). Given our reported results for elevation and younger forest with high basal areas of hardwoods, these differences appeared to result in higher average site-level estimates of initial occupancy and reproduction probabilities on the WSAs (Fig. 5C and 6C). Of note, we observed these differences in occupancy and reproduction between study areas despite the prevalence of private lands on the WSAs, where even-aged forest management practices generate open and younger forest habitats, which our and previous work found reduced spotted owl occupancy (see above). As described below, the cause of this apparent discrepancy may hinge on the issues of cover type and prey species distributions.

A recent study indicated that GPS-tagged owls residing in the same mixed-ownership landscape studied here preferentially foraged in older forest near territory centers, but selected for diverse cover types (seral stages) at the periphery of territories (Atuo et al., 2019). These results suggest that outside of territory centers, a mix of stand conditions at fine spatial scales may provide foraging opportunities for spotted owls – even if some of those cover types are detrimental for nesting and roosting when considered at the territory scale. Given our and Atuo et al.’s (2019) results, management aimed at promoting a diversity of

cover types, maintaining adequate levels of older forest, and recruiting hardwoods (particularly mast-producing species like black oaks) following forest disturbance events (e.g., fire and harvest) may help concurrently conserve spotted owl populations and benefit forest ecosystems.

An alternative explanation for observed differences in patterns of occupancy and reproduction between study areas is that spotted owls occupying higher-elevation national forest-dominated sites (e.g., on the EDSA) may be more sensitive to forest thinning or logging that alters flying squirrels’ mature forest habitat – even when such practices retain more vertical structure than even-aged management systems (Jones et al., 2016b). By contrast, although reductions in closed canopy forests at lower elevations can also reduce spotted owl occupancy (Jones et al., 2016b), woodrats – a key spotted owl prey species at lower elevations – are less sensitive to forest management activities, particularly when some large living oaks are not harvested, hardwood regeneration is promoted, and residual snags and downed logs are retained (Innes et al., 2007). Further, differences in abundance of open and younger forests between the EDSA and WSAs – both of which contain mixed-ownership landscapes – were modest such that these habitat types did not disproportionately reduce occupancy on the WSAs relative to EDSAs (Table 3). Regardless, our results corroborate the finding of Roberts et al. (2017) that site occupancy tended to be greater on the WSAs than the EDSA and suggest that private lands like those studied here can contribute to spotted owl conservation in the Sierra Nevada depending on site conditions and management strategies/objectives.

4.5. Conclusions

Spatial heterogeneity in ecological conditions – such as the juxtaposition of older forest nesting and roosting habitat interspersed with other cover types like younger forests with high basal area of hardwoods – may create opportunities for California spotted owl conservation in mixed-ownership landscapes with relatively high proportions of private lands, particularly at low elevations. Our study, however, had several important limitations: (i) we surveyed owl sites primarily on landscapes dominated by SPI-owned and USFS-managed land, with little inclusion of either national parks or other private ownerships; and (ii) our study areas did not extend into the southern Sierra Nevada. Thus, we limit our inferences to SPI/USFS mixed-ownership landscapes in the central and northern Sierra Nevada, as conditions may differ dramatically because of natural (e.g., drought-induced tree mortality in the southern Sierra Nevada) or anthropogenic (e.g., different management regimes) factors. Further research could extend the generality of the associations we described here, and, more importantly, elucidate ecological mechanisms (e.g., prey availability, microclimate) responsible for relationships between spotted owl demographics and landscape conditions.

Our research raises several considerations related to ecology and conservation in mixed-ownership landscapes. First, this work underscores the importance of overcoming barriers to research on private lands and in mixed-ownership landscapes, which may offer novel insights into species ecology and conservation. Second, landownership is not inherently beneficial or detrimental to biodiversity conservation. Given that the distribution of ownerships across landscapes is often nonrandom with respect to topographic and ecological characteristics (Drouilly et al., 2018; Scott et al., 2001), private lands may contain ecologically important and unique portions of species’ ranges. Third, our results exemplify the context-dependent nature of conservation in mixed-ownership landscapes: habitat conditions associated with private land management may provide benefits to species of conservation concern primarily under specific ecological conditions. Thus, because public and private lands may incur different benefits to species of concern, undertaking collaborative research that considers the full breadth of ecological conditions upon which species depend is vital to the success of conservation in mixed-ownership landscapes.

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Declaration of interest

BKH, WJB, SAW, JJK, RJG, and MZP declare no conflicts of interest. KNR and BPD are currently employed by Sierra Pacific Industries, a private landowner. MGR is an ecological consultant currently contracted by Sierra Pacific Industries.

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Animal rights

All research complied with University of Wisconsin – Madison Institutional Animal Care and Use Committee guidelines.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.01.028>.

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Trophic interactions mediate the response of predator populations to habitat change

Brendan K. Hobart^{a*}, Gavin M. Jones^a, Kevin N. Roberts^b, Brian P. Dotters^b, Sheila A. Whitmore^a, William J. Berigan^a, Martin G. Raphael^c, John J. Keane^d, R.J. Gutiérrez^{a,e}, M. Zachariah Peery^a

^aDepartment of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA

^bSierra Pacific Industries, PO Box 496014, Redding, CA, USA

^cUSDA Forest Service, Pacific Northwest Research Station, Olympia, WA, USA

^dUSDA Forest Service, Pacific Southwest Research Station, Davis, CA, USA

^eDepartment of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, MN, USA

* corresponding author; email: bkhobart@wisc.edu; mailing address: 1630 Linden Drive, Madison, WI, USA 53706

AUTHOR CONTRIBUTIONS

B.K.H and M.Z.P conceived the ideas and designed the study; all authors collected the data; B.K.H., G.M.J., and M.Z.P. drafted the manuscript with inputs from all authors. All authors contributed substantially to revisions and approved the final draft of the manuscript.

1 INTRODUCTION

2 As human-driven extinctions accelerate, understanding the factors that cause population declines
3 is a central, yet challenging, goal in applied ecology (Ceballos et al. 2017). It is increasingly
4 recognized that interspecific interactions play an important role in shaping the response of
5 species to anthropogenic habitat loss and degradation (Stier et al. 2016). Trophic interactions
6 (i.e., consumer-resource relationships) in particular may affect whether and to what degree
7 habitat alterations lead to changes in population trends, given that resource consumption can
8 influence key aspects of species' life histories (Elton 1927). Indeed, resource use can modify
9 individual space-use behavior (and thus energetic budgets; Schoener 1968), fine-scale
10 demographics (Moss et al. 2016b), and broad-scale patterns in abundance (Chamberlain et al.
11 2005). Thus, understanding the interplay among habitat changes, trophic interactions, and
12 population trends may be an important prerequisite to reversing species declines, conserving
13 biodiversity, and restoring functional relationships to ecosystems (Stier et al. 2016).

14 Predators are particularly prone to diet-mediated responses to habitat change because of
15 their higher trophic position and dependence on spatially and temporally variable prey resources
16 (Elton 1927, Moss et al. 2016b). Because predator diets are often relatively plastic (Darimont et
17 al. 2009), local shifts in habitat structure and abundance that alter resource availability may lead
18 to concomitant changes in trophic interactions between predators and their prey. In some cases,
19 trophic plasticity may allow predators to exploit novel resources in highly impacted ecosystems
20 (Moss et al. 2016a). Yet, individuals may also incur fitness consequences when bottom-up shifts
21 in resource availability result in reliance on low-quality resources (Heiss et al. 2009). Thus, for
22 predators, local-scale variability in trophic interactions may cause both positive and negative
23 responses to anthropogenic habitat changes.

Local, individual-level variation in trophic interactions may have emergent consequences for predator populations at broad spatial scales (Levin 1992). In landscapes where predators consume high-quality (i.e., large-bodied and/or high-density) prey, elevated fitness can promote positive population growth (Benton et al. 2006) and smaller home ranges can increase population densities (McNab 1963). However, because consumptive patterns are logistically challenging to quantify, they are seldom evaluated alongside habitat factors as drivers of predator population change over broad extents (Rosado et al. 2016). This constraint has contributed to the viewpoint suggested by some ecologists that interspecific interactions may be unnecessary to consider at coarse grains and large spatial scales (Soberón and Nakamura 2009). Thus, despite the importance of predation to ecosystem processes (Estes et al. 2011), the role that trophic interactions play in mediating predator population response to anthropogenic habitat change is poorly understood.

Here, we assessed whether trophic interactions mediate the response of predator populations to anthropogenic habitat alteration, focusing on a territorial old-forest species, the California spotted owl *Strix occidentalis occidentalis* (hereafter “spotted owl”). In the Sierra Nevada, USA, spotted owl population status varies among forested landscapes that differ in structure owing to contrasting human land use practices on national parks, national forests, and private lands (e.g., Collins et al. 2017). Populations are declining on national forest-dominated landscapes, where selective logging and a century of fire suppression have created dense, homogeneous forests with a large-tree deficit (Jones et al. 2018). By contrast, populations appear stable or increasing on national parks, where timber harvest restrictions and the partial restoration of frequent-fire regimes have promoted more heterogeneous forests dominated by large trees (Collins et al. 2017). Finally, spotted owl territory occupancy is unexpectedly high in

landscapes dominated by private lands managed for timber production that contain a mosaic of younger, even-aged forest stands (Hobart et al. 2019). Although patterns of spotted owl population status are well-described, the ecological mechanisms linking forest management and conditions to such patterns remain uncertain (Peery et al. 2017).

We hypothesized that trophic interactions mediate spotted owl population response to habitat differences among national forests, national parks, and private landscapes. Spotted owls consume a diverse array of small mammals and other taxa, but flying squirrels *Glaucomys oregonensis* and woodrats *Neotoma* spp. dominate their diet by biomass in our study region (Verner et al. 1992). Whereas flying squirrels are associated with mature, closed-canopy forests (Waters and Zabel 1995), woodrats utilize a wider range of forest conditions. Dusky-footed *N. fuscipes* and big-eared woodrats *N. macrotis* are relatively abundant in younger forests with ample hardwoods at lower elevations (Innes et al. 2007) but bushy-tailed woodrats *N. cinerea* reside in both young and mature forests – often near rocky features – at higher elevations (Carey et al. 1999). All three woodrat species also occupy riparian forests and utilize cavities in old trees, snags, and downed debris (Innes et al. 2007). Given their habitat associations, it is possible that anthropogenic changes to forest structure (e.g., fire suppression, restoration, and timber extraction) have altered the distribution and abundance of flying squirrels and woodrats in the Sierra Nevada. Moreover, although both are important prey for spotted owls, woodrats are higher-density (up to 40 acre⁻¹ versus ~1 acre⁻¹; Williams et al. 1992) and provide more energy per prey (1205 kJ versus 592 kJ; Weathers et al. 2001), and thus may be more energetically profitable prey when present (i.e., higher-quality). Thus, because prey availability may vary among landscapes and with owl population status in the Sierra Nevada, this system offers a valuable opportunity to investigate whether trophic interactions mediate population response to

anthropogenic habitat change and, in the process, resolve a longstanding uncertainty for a model species in population and landscape ecology.

We integrated stable isotope analyses with individual movement, territory occupancy, and remotely-sensed vegetation data to test three predictions related to our central hypothesis. First, at the local (territory) scale, we predicted that the prevalence of hardwoods, degree of forest heterogeneity, and presence of young forest would promote consumption of woodrats by owls, whereas medium-aged and older forest would promote consumption of flying squirrels. Second, we predicted that consumption of woodrats by owls would be associated with (i) smaller home range sizes and (ii) lower territory extinction rates. Third, at the landscape scale we predicted that spotted owls would consume primarily woodrats on private lands, flying squirrels on national forests, and an intermediate mixture on national parks. Thus, we predicted that consumption of woodrats would roughly positively correspond with landscape-scale population status. By testing these predictions across landscapes with different management strategies and ecological conditions, we offer insights into the role of trophic interactions as mechanisms that shape the response of predator populations to anthropogenic habitat change.

METHODS

Study system

We studied spotted owls across the Sierra Nevada bioregion, USA (Fig. 1) as part of ongoing research (e.g., Atuo et al., 2019; Hobart et al., 2019; Jones et al., 2018). We surveyed for spotted owls on all major landownerships in the region, including national parks (Yosemite and Sequoia-Kings Canyon), national forests (Lassen, Plumas, Tahoe, Eldorado, Stanislaus, and Sierra), and private lands (primarily land owned by Sierra Pacific Industries). Generally, private lands

occurred at lower elevations, national forests at intermediate elevations, and national parks at higher elevations (Table S1). National parks also occurred, on average, at lower latitudes than both national forests and private lands (Table S1).

Field and laboratory methods

We captured 142 adult spotted owls using established methods (Franklin et al. 1996) early in the breeding seasons (April-July) of 2017 and 2018. At the time of capture, we sampled 1-2 growing or recently grown body feathers per owl for isotopic analysis. Because feather is an inert tissue that reflects the diet for the period it was synthesized (Hobson and Clark 1992) and spotted owls molt body feathers during the breeding season (Forsman 1981), our samples reflected the diet for the current breeding season. We affixed GPS transmitters to a subset of 49 owls to quantify home range sizes (see Atuo et al. 2019 for details). We also opportunistically collected regurgitated spotted owl pellets to obtain count-based diet estimates and process prey bones for isotopic analysis. All animal research was approved by the University of Wisconsin institutional animal care and use committee and permitted by the necessary state and federal agencies.

We rinsed feathers 3× with 2:1 chloroform:methanol to remove contaminants, homogenized them with scissors, and dried them at 55°C for ≥72 h. We first soaked prey bones in 0.5N HCl for ≥48 h to remove calcium and associated inorganic carbon. Second, because dietary proteins, but not lipids, are typically routed to feather keratin (Bearhop et al. 2002), and lipid-based carbon differs isotopically from protein-based carbon (Post et al. 2007), we soaked prey bones 3× in 2:1 chloroform:methanol for 24 h to extract lipids. Third, we dried bones at 55°C for ≥72 h and crushed them with scissors. Feather and bone samples were weighed in tin capsules for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ analysis at the University of New Mexico Center for Stable Isotopes on a Thermo Scientific Delta V mass spectrometer connected to a Costech 4010 elemental

analyzer and a high-temperature conversion elemental analyzer. Results were expressed as parts per mil (‰) ratios relative to the international standards Vienna Pee Dee Belemnite (C) and atmospheric nitrogen (N).

Quantifying owl territory characteristics

We modeled owl diet as a function of habitat covariates (Table 1). We included elevation and latitude of owl territory centers because both variables are associated with prey species distributions. We included four forest age class covariates (open, young, medium, and old), as well as Shannon's diversity index (H) of such classes to estimate forest heterogeneity. We also included the mean basal area of hardwoods within owl territories. We calculated forest covariates using gradient-nearest-neighbor (GNN) maps (2012; lemma.forestry.oregonstate.edu) within 1270.5 ha circular buffers around owl territory centers (roosts and nests). Buffer size corresponded to the mean home range area (95% kernel density estimate [KDE]) of GPS-tagged owls calculated using the R package adehabitatHR (Calenge and Fortmann-Roe 2013). We confirmed that forest cover (open, young, medium, and old forest) covariate values within circular buffers of GPS-tagged owls did not differ from values calculated within corresponding KDE polygons (paired t-tests, all $P > 0.05$, Table S2).

Using federal boundary maps, we classified landownership of territories entirely within national parks, national forests, or private lands accordingly. Remaining territories occurred on two ownerships; after calculating the ratio of landownership at such territories, those with a ratio between the first and third quartiles (0.31 and 0.76, respectively) were classified as "mixed-ownership". Territories with a ratio outside the quartiles were classified as the dominant owner. Thus, owl territories were assigned one of five ownership categories: national parks ($n = 35$),

private lands ($n = 25$), national forests ($n = 36$), national park–national forest mixed ownership ($n = 6$), and private–national forest mixed ownership ($n = 40$).

Data analyses

Proportional diet

Based on remains in regurgitated pellets, flying squirrels, woodrats, and pocket gophers *Thomomys* spp. were the only prey that each constituted >5% of biomass-corrected owl diet, and collectively constituted ~94% of biomass-corrected owl diet (Table S3). These prey were the only groups included in isotopic analyses because including infrequently consumed resources can bias proportional diet estimates (Phillips et al. 2014). We implemented K-nearest-neighbor randomization tests (Rosing et al. 1998) to establish that prey isotopic signatures did not vary regionally (all $P > 0.05$). Additional KNN tests indicated that woodrats ($n = 35$) and pocket gophers ($n = 30$) were isotopically indistinguishable ($p = 0.50$) but were distinct from flying squirrels ($n = 35$) individually and when grouped ($p < 0.001$), resulting in two isotopically distinct prey groups: (i) woodrats and pocket gophers and (ii) flying squirrels. We note, however, that between woodrats and pocket gophers, owl consumption of the former is more spatially variable and, at times, accounts for a majority of owl diet (e.g., Munton et al. (2002) found that whereas pocket gophers consistently accounted for 10-15% of biomass-corrected owl diet, woodrats represented >80% in some landscapes and <10% in others). Thus, we had *a priori* evidence that observed variability in the woodrat–pocket gopher prey group was largely due to woodrats.

We employed MixSIAR Bayesian mixing models (Stock et al. 2018) to quantify proportional diet. We corrected for trophic discrimination ($\delta^{13}\text{C} \pm \text{sd}$: $1.88\text{‰} \pm 0.04$; $\delta^{15}\text{N} \pm \text{sd}$: $4.12\text{‰} \pm 0.26$) based on snowy owl *Bubo scandiacus* captive-feeding trials (Robillard et al. 2017).

After trophic correction of prey isotopic signatures, nearly all owl isotopic signatures fell within the mixing space, suggesting that we adequately sampled prey and applied appropriate trophic discrimination factors (Fig. S1A). For each model, we specified generalist (“uninformative”) priors and ran three Markov chains (length = 300,000; burn-in = 200,000; thinning rate = 100). We specified process $\times$ residual error structure for all models except those containing factors with 1 level (the individual model, see below), for which only process error was estimated (Stock et al. 2018). We considered Gelman-Rubin diagnostic ($\hat{R}$) values <1.05 to indicate model convergence.

To assess habitat–diet relationships, we included habitat covariates in a set MixSIAR models (one covariate per model; Table 1; see Stock et al. 2018 for model-fitting details). We used leave-one-out (LOO) cross-validation to identify which covariate(s) better-predicted proportional diet than a null model.

We also included individual and territory as fixed factors in MixSIAR models and calculated medians of posterior distributions for subsequent analyses. Although this approach ignored uncertainty associated with each posterior distribution, the high Pearson correlations between median values and both upper ($r_{\text{ind}} = 0.76$, $r_{\text{terr}} = 0.85$) and lower ($r_{\text{ind}} = 0.92$, $r_{\text{terr}} = 0.94$) credible interval bounds indicated that resulting estimates of diet were largely unbiased and subsequent relationships would hold at the bounds of credible intervals.

Finally, we included territory ownership as a fixed factor in a MixSIAR model and tested for dietary differences using two-sided pairwise measures of overlap between posterior distributions of mixing model solutions (see Hopkins et al. 2014 and Manlick et al., 2019 for details). Such tests are analogous to t-tests; significance was evaluated at $\alpha = 0.05$.

Diet – space use associations

We used least-squares regression to model home range size (95% KDE polygon area [ha]) as a function of individual diet (proportion of woodrats and pocket gophers). Before interpreting model output, we ensured that assumptions of linear regression were met (i.e., normal residuals, constant variance, no influential points [all Cook's distances < 1.0]).

Occupancy models

We used a simple multi-season occupancy model (MacKenzie et al. 2003) to assess whether diet – and proxies for diet (prey habitat, elevation) – could explain territory occupancy dynamics.

Using the best-available spotted owl detection histories across a range of landownerships and ecological conditions ($n = 73$ territories with occurrence data for various intervals between 1993 and 2017; see Appendix 2 for details), we first determined that detection probability (p) varied among surveys within years ($w = 0.99$) but not among years ($w \leq 0.001$). Then, holding initial occupancy (ψ_1) constant and colonization (γ) in a year-varying structure, we modeled territory extinction probability (ϵ) as a function of (i) hardwoods, (ii) elevation, and (iii) dietary proportion of woodrats and pocket gophers (all covariates were z-standardized). We used AIC to evaluate support for models relative to each other and to a null model.

RESULTS

We found strong evidence that spotted owl diet was related to local habitat conditions: six covariates outperformed a null model, the best of which was the mean basal area of hardwoods in an owl territory (Fig. 2, Table 1). This variable (hardwoods) was positively associated with the estimated dietary proportion of woodrats and pocket gophers (Fig. 2A) and tended to be more abundant within territories on private lands than national forests and parks (Table S1). Elevation,

latitude, medium forest, young forest, and heterogeneity of forest types also outperformed the null model (Table 1, Figure 2).

At the local scale, spotted owl home range size significantly decreased as individual consumption of woodrats and pocket gophers increased ($\beta_{\text{WR-PG}} = -3185.4$, 95% CI = -4855.30 to -1515.48 ; Fig. 3A). Territory extinction probability (ϵ) was also significantly lower when owl diet contained a greater proportion of woodrats and pocket gophers ($\beta = -0.47$, 95% CI = -0.76 to -0.18 ; Fig. 3B). Moreover, hardwoods ($\Delta\text{AIC} = 7.25$) and elevation ($\Delta\text{AIC} = 9.19$) poorly explained extinction probability relative to proportional diet ($w = 0.94$; Table S4). Home range size and extinction probability results based on proportional diet were corroborated by significant positive relationships between both response variables and raw isotopic values ($\delta^{13}\text{C}$, i.e., consumption of flying squirrels; Fig. S2).

At the landscape scale, spotted owls occupied divergent trophic niches among landownerships. Owls on national parks and private lands consumed significantly more woodrats and pocket gophers than did owls on national forests (Fig. 4). Moreover, comparison of diet at geographically paired national forests and national parks (Sierra NF and Sequoia-Kings Canyon NP) revealed strong trophic differences, where owls on the latter consumed significantly more woodrats and pocket gophers ($p < 0.001$; Fig. S3). Diet of owls with mixed-ownership territories generally fell intermediate to primary ownership groups (Fig. S4B).

DISCUSSION

Our results suggest that trophic interactions contribute to spotted owl population differences among landscapes with contrasting land management and habitat conditions. Specifically, the consumption of presumably high-quality prey – which varied with habitat conditions – appeared

to benefit spotted owls at both local and landscape scales. Although prey consumption has previously been linked to variation in spotted owl life-history traits (e.g., Zabel et al. 1995, Franklin et al. 2000), our findings are the first to show that it has consequences for territory occupancy dynamics and appears associated with landscape-scale population metrics such as density and trends in abundance. Our study also corroborates mounting evidence that (i) Eltonian niches are more plastic than previously recognized (Terry et al. 2017, Manlick et al. 2019) and (ii) trophic interactions can mediate species response to anthropogenic habitat changes (Narango et al. 2018), thus supporting the concept that consideration of trophic interactions – in addition to habitat conditions – is important to the conservation of predator populations (Stier et al. 2016).

Our diet analyses were based on stable isotopes, which offer space- and time-integrated estimates of proportional biomass assimilation but depend on at least two key assumptions (Phillips et al. 2014). First, because consumers may utilize resources not included in mixing models, it is possible that our estimates of proportional diet are confounded with the consumption of other prey (Phillips et al. 2014). The direction and magnitude of any such biases depends on the functional roles, isotopic signatures, and dietary importance of prey not included in mixing models. In our study system, predation of primary consumers (e.g., chipmunks) by owls may result in the overestimation of woodrats and pocket gophers, predation of secondary consumers or mycophagous prey (e.g., voles) may result in the overestimation of flying squirrels, and predation of omnivorous prey with isotopic signatures intermediate to our two prey groups (e.g., *Peromyscus* spp.) may not introduce any biases in diet estimations. However, independent diet information (from regurgitated pellets) provided a measure of confidence that we included all major spotted owl prey groups in our isotopic analyses. Indeed, woodrats, pocket gophers, and flying squirrels constitute ~94% of owl diet by biomass (Table S3). Still, owls consume

small amounts of other prey, so our dietary estimates of woodrats, pocket gophers, and flying squirrels must be considered relative. Nevertheless, we consider comparative differences and directional relationships to be meaningful. Second, processes other than food consumption may affect isotopic assimilation (e.g., body condition, prey digestibility, isotopic routing; Bearhop et al., 2002). However, our sample sizes were large and spanned a broad gradient of ecological conditions such that among-individual variability in such factors was unlikely to introduce a systematic bias in dietary estimates. Thus, stable isotopes appeared well-suited to quantify trophic interactions in our study system.

Isotopic mixing models provided strong evidence for relationships between habitat and prey consumption in spotted owls. In agreement with our predictions and earlier pellet-based analyses (Munton et al. 2002), owls consumed more flying squirrels in areas with prevalent medium-aged forest, at higher elevations, and at higher latitudes. Conversely, owls consumed more woodrats and pocket gophers at territories containing more hardwoods and young forest, higher forest heterogeneity, and at lower elevations – habitat features particularly important to the distribution of dusky-footed and big-eared woodrats. Thus, prey utilization varied predictably with habitat features important to flying squirrels and woodrats, but not pocket gophers (Waters and Zabel 1995, Innes et al. 2007). This suggests that, in general, woodrats contributed more to spotted owl diets than pocket gophers (Munton et al., 2002; but see below). These findings also suggested that owls select woodrats and flying squirrels over other prey, but also that the relative consumption of these species varies, at least in part, according to availability. We recognize, however, that a lack of prey availability data precluded the distinction between selective versus proportional use of resources (Macarthur and Pianka 1966). Regardless, our findings supported

the notion that predators shift their diet in response to local habitat conditions which, in turn, may drive spatial variability in predator behavior and population status (Moss et al. 2016b).

At the individual-scale, consumption of high-quality resources leads to the utilization of smaller home ranges, which reduces energetic expenditures and predation risk (McNab, 1963). Here, we found that for the spotted owl, a central place forager, individuals that consumed more woodrats and pocket gophers had smaller home ranges (Fig. 3A). Past studies reported similar results (Zabel et al. 1995), suggesting that consumption of woodrats and pocket gophers – and particularly the former given they are large-bodied and locally high-density – may optimize foraging-related energetic expenditures. Although a formal assessment of optimal foraging in spotted owls is hampered by a lack of information on, for example, prey handling times (Macarthur & Pianka, 1966), variability in home range sizes may nonetheless be associated with energetic consequences for individual owls.

We found a novel relationship between spotted owl occupancy dynamics and prey use: territory extinction probability was lower when owls consumed more woodrats and pocket gophers, indicating that owls were less likely to die at or abandon territories where such prey was readily consumed, presumably owing to energetic benefits. Of note, the extinction–diet relationship was strongly supported despite including diet as a static, site-level covariate in occupancy models, thus assuming that resource utilization did not vary temporally. Although this assumption was likely violated to some degree, we suggest that diet is more spatially than temporally variable because (i) we found that diet varies strongly as a function of habitat conditions, which themselves have remained reasonably stable over the course of our study (Jones et al. 2018) and (ii) pellet-based data suggest that dietary proportions were relatively stable over a 25-year window in the Eldorado National Forest (B.K. Hobart, *unpublished data*).

Future research that includes trophic information as a dynamic covariate (i.e., year-varying) may provide new insights into the importance of temporal variability in trophic interactions for territory occupancy of spotted owls. Regardless, because extinction probabilities drive site occupancy for long-lived species with high site fidelity such as the spotted owl, this result suggests that future shifts in prey species distributions (e.g., with climate change; Moritz et al., 2008) may cause concomitant changes in spotted owl population abundance and occupancy dynamics (Jones et al. 2016). Our results and findings by others (e.g., Chamberlain et al. 2005, Garces-Restrepo et al. 2019) indicate that trophic interactions can be an important determinant of spatial variability in population status. Thus, failure to account for such interactions in applied ecological research may lead to knowledge gaps and, at worst, ineffective or detrimental conservation measures (Stier et al. 2016).

Long-term research of spotted owls has elucidated numerous associations between occupancy dynamics and habitat conditions but few of the mechanisms that underlie those observed patterns (reviewed in Roberts 2017). In particular, the prevalence of old forest in national parks and young forest with hardwoods in private-dominated areas explained favorable population metrics in such landscapes relative to national forests (Jones et al. 2018, Hobart et al. 2019). However, our finding that owls consumed significantly more woodrats and pocket gophers in national parks and private lands than in national forests provides preliminary evidence that trophic interactions between spotted owls and their prey may be partly responsible for differences in population abundance and occupancy dynamics among these three landscapes.

Although the historical loss of nesting and roosting habitat is one factor limiting spotted owl populations on national forests (Jones et al. 2018), forest management leading to an overreliance on relatively low-quality flying squirrels may also contribute to and exacerbate

downward population trends. It is possible that forest densification and homogenization resulting from fire suppression have increased the abundance of suitable habitat for flying squirrels but not woodrats and pocket gophers (Collins et al. 2017). Bottom-up shifts in prey communities may have then altered spotted owl trophic interactions, with consequences for home range size, occupancy dynamics, and population trends. We acknowledge the alternative explanation that such downward trends could also be due to declines in flying squirrel abundance from historical levels. However, owl consumption of flying squirrels increased with medium forest – which has likely become more common on national forests owing to large-tree logging and fire suppression – suggesting that reductions in flying squirrel availability may not limit owl populations in such landscapes. A second alternative hypothesis is that rodenticides originating at illegal marijuana growing operations – which could be more common on national forests than other ownerships – is poisoning owls in such landscapes, leading to lower survival, reproduction, and territory occupancy (Gabriel et al. 2018). However, flying squirrels, which rely heavily on lichens and hypogeous fungi (Meyer et al. 2005), likely experience lower exposure to rodenticides than woodrats and pocket gophers. Thus, it is unlikely that contaminant exposure explains the relatively estimated high extinction rates at territories where spotted owls consume high proportions of flying squirrels.

In contrast to national forests, a greater reliance on woodrats and pocket gophers by spotted owls in national parks and private lands may contribute to relatively high owl abundance and occupancy rates in such landscapes. On private lands, even-aged forest management may promote patches of young forest woodrat habitat (Sakai and Noon 1993), particularly when landowners manage for the retention and recruitment of hardwood species (e.g., California black oak) and shrub cover (Innes et al. 2007, Gray et al. 2019). Although private lands have long been

thought to provide only modest suitable habitat for spotted owls owing to active logging operations (Bias and Gutiérrez 1992), such land management may benefit owls by providing key prey resources if younger forests with shrubs and hardwoods are juxtaposed with ample nesting and roosting habitat (older forest).

Spotted owls in national parks consumed a high proportion of woodrats and pocket gophers despite a relative paucity of habitat features (e.g., young forest and hardwoods at low elevations) that our stable isotope analyses suggested promoted consumption of these two species (Table S1). By using coarse remote-sensed landcover data, we may not have captured fine-scale habitat characteristics important to pocket gophers (e.g., small meadows) and woodrats (e.g., patchy understory brush) in national parks. Such conditions are likely promoted by the prescription of frequent, low-intensity fire regimes in the national parks studied here (Collins et al. 2017). Moreover, because bushy-tailed woodrats den in rocky areas like talus slopes (which are relatively common in the national parks studied here; S.L. Roberts *personal communication*) and in cavities of large trees, it is possible that naturally-occurring geological features and the protection of defect trees in national parks acted to increase the availability of woodrats to owls. Thus, although some uncertainties remain, our results provided a plausible mechanism to explain landscape-scale variability in spotted owl population measures and suggest that incorporating information about trophic interactions is an important prerequisite to understanding how predators respond to habitat differences among landscapes with contrasting land use histories and strategies.

Our results collectively suggest that restoration and management activities that promote key prey species may also benefit predator conservation, even if prey habitat does not necessarily reflect predator habitat (e.g., nesting areas). For example, forest management in the Sierra

Nevada that produces woodrat and pocket gopher habitat may also benefit spotted owls. Specifically, promoting patches of brushy woodrat habitat and grassy pocket gopher habitat adjacent to closed-canopy forests could enhance foraging opportunities for spotted owls. Our results also point to linkages among forest management, restoration, and species conservation: the regeneration of hardwoods – which has slowed owing to fire suppression – following natural and anthropogenic disturbance may simultaneously benefit woodrats, spotted owls, and forest restoration. Moreover, all three woodrat species nest and den in tree cavities, underscoring the potential benefits of forest management and restoration that retain and promote snags and trees with cavities – key structural features that have declined significantly from historical levels owing to the selective harvesting of large trees (Collins et al. 2017). Thus, as is increasingly being recognized for a range of taxa in diverse ecosystems (Samhouri et al. 2017), our research on trophic interactions suggests that compatibility may exist between ecosystem restoration in the Sierra Nevada and the conservation of the spotted owl.

More broadly, our work highlights the importance of biotic interactions as drivers of species' responses to land use and management. Consider, for example, the dramatic and ongoing decline of woodland caribou *Rangifer tarandus caribou* in North America, driven by both bottom-up (loss of lichen food resources owing to logging; Bergerud 1974) and top-down (expansion of predators following the construction of industrial linear features; Latham et al. 2011) trophic interactions. Thus, our research and that of others suggests that failure to incorporate information about trophic interactions into species management may lead to undesirable outcomes and conservation conflicts (Stier et al. 2016). Indeed, interactions among members of ecological communities (e.g., predation) shape the role and stability of populations in novel ecosystems. Considering biotic interactions is thus likely to be important to emerging

conservation issues such as reintroduction (Carlson et al. 2014) and rewildling efforts (Alston et al. 2019), climate-driven spatial (Kudrna et al. 2008) and temporal (Jara et al. 2019) shifts, and species invasions (Larson et al. 2010). Because the consequences of novel or decoupled trophic interactions extend beyond populations to both communities and ecosystems (Estes et al. 2011), incorporating the Eltonian niche is broadly valuable to applied ecological research.

Our research provides both impetus and direction to quantify linkages between anthropogenic change, trophic interactions, and population processes in other ecological systems. Despite the historical difficulty of measuring trophic interactions (Rosado et al. 2016), our stable isotope approach offers a potentially tractable avenue to quantify such relationships more broadly for three reasons. First, isotopic analyses require small quantities of biomaterials that can generally be collected with relative ease as part of ongoing ecological studies, from museum collections, or from harvested individuals. Second, recent developments have provided flexible, robust statistical tools to analyze isotopic data (e.g., MixSIAR, used here) and well-documented best practices for isotopic research (Ben-David and Flaherty 2012, Layman et al. 2012, Phillips et al. 2014). Third, isotopic information can be combined with additional, potentially preexisting data (e.g., behavioral, occupancy, fitness, or demographic) to improve and augment understanding of how biotic interactions affect species. Our two-step approach demonstrated that the benefits of modern isotopic analyses can be leveraged to (1) identify how trophic interactions vary with habitat conditions and (2) identify the consequences of changes in trophic interactions for a focal species. However, this approach is not limited to questions about linkages among habitat, diet, and population processes, but could be used to study how trophic interactions mediate population responses to invasions, extinctions, light and noise pollution, disturbance, and climate change. Although such relationships are seldom tested explicitly, doing so could

412 help elucidate previously unrecognized and cryptic mechanisms by which species respond to
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419

420 DATA ACCESSIBILITY

421 The data associated with this paper have not been archived due to the sensitive legal and political
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424

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611 TABLES

Table 1. Definition and ranking of covariates included in isotopic mixing models to quantify spotted owl habitat–diet relationships. “QMD” abbreviates quadratic mean diameter. “LOO” abbreviates leave-one-out cross-validation results, where lower values indicate higher predictive capability.

Covariate	Definition	LOO
Hardwoods	Mean basal area of live hardwoods in a buffer	460.8
Elevation	Elevation (m) of territory center	472.6
Latitude	Latitude (°) of territory center	487.7
Medium forest ^A	Forest with QMD 30-61cm and canopy cover>40%	491.1
Forest heterogeneity ^B	Shannon’s index calculated for the four cover types: $H = \sum_{i=1}^S (p_i) \times \ln (p_i)$	493.4
Young forest ^A	Forest with QMD<30cm and canopy cover>40%	495.2
Null	No covariate included	496.4
Old forest ^A	Forest with QMD >61cm and canopy cover>40%	498.3
Open area ^A	Land cover with canopy cover <40%	498.8

^A Unit is proportion of pixels in territory buffer
^B Unitless index

FIGURES

Figures 1, 2, and 4 should be printed in color

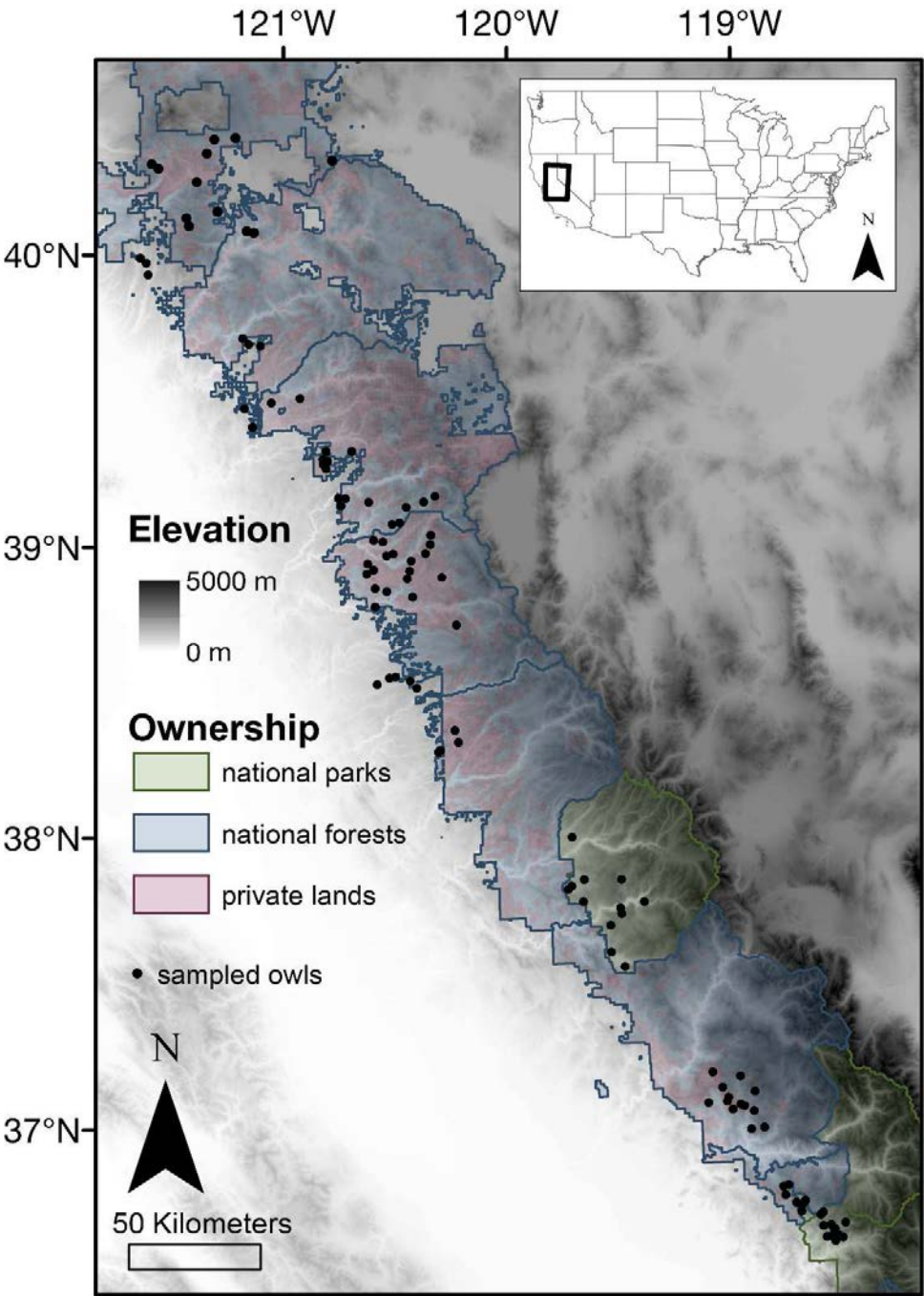
Figure 1. Map of the Sierra Nevada, USA depicting locations where spotted owl feathers were sampled for isotopic analyses. Thick lines denote federal administrative boundaries and colored shading denotes ownership within such boundaries. Territories outside federal boundaries occurred on private lands.

Figure 2. Relationships between spotted owl habitat and proportional diet estimated by isotope mixing models. Only covariates that performed better than a null model based on leave-one-out cross-validation are included here. Forest class covariate units are proportions of owl territories.

Figure 3. Relationships between the proportion of spotted owl diet comprised of woodrats and pocket gophers and (A) home range size and (B) territory extinction probability. Thick lines indicate best fit, thin lines represent 95% CI bounds, and points indicate individual owls.

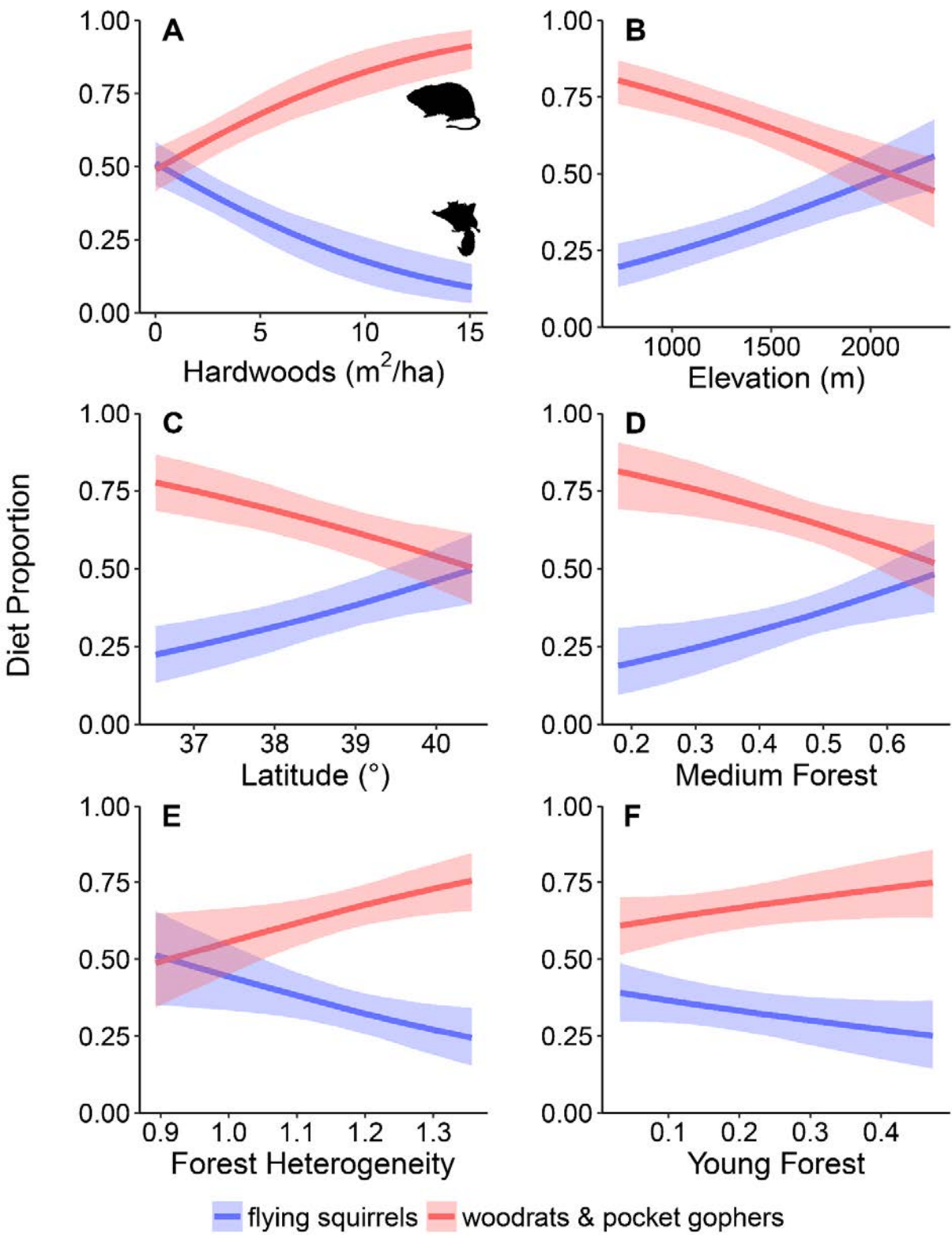
Figure 4. Frequency distributions of proportional diet for spotted owls inhabiting the primary landownerships studied here. Letters above distributions indicate significant differences according to a two-sided test of overlap ($\alpha = 0.05$).

631 Figure 1.



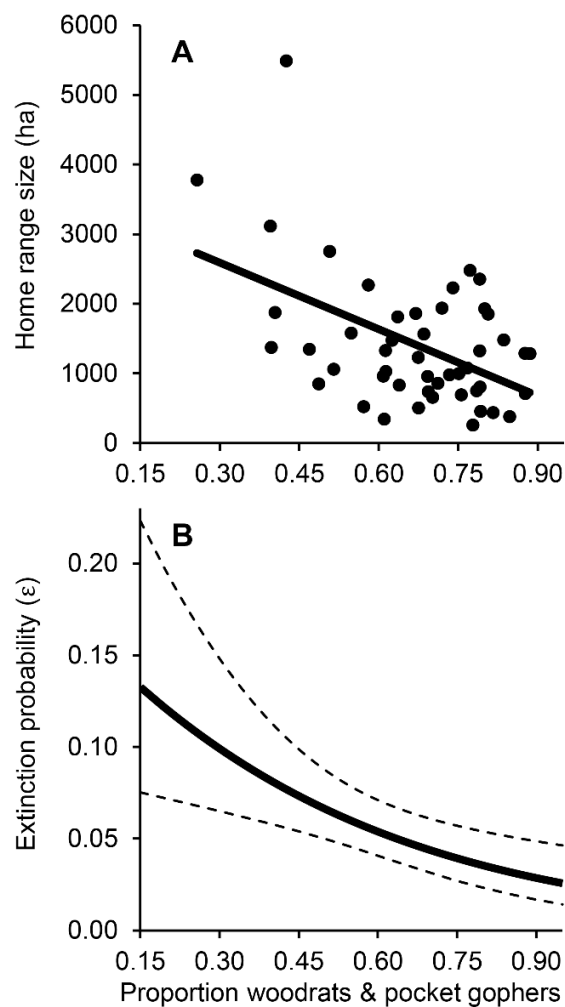
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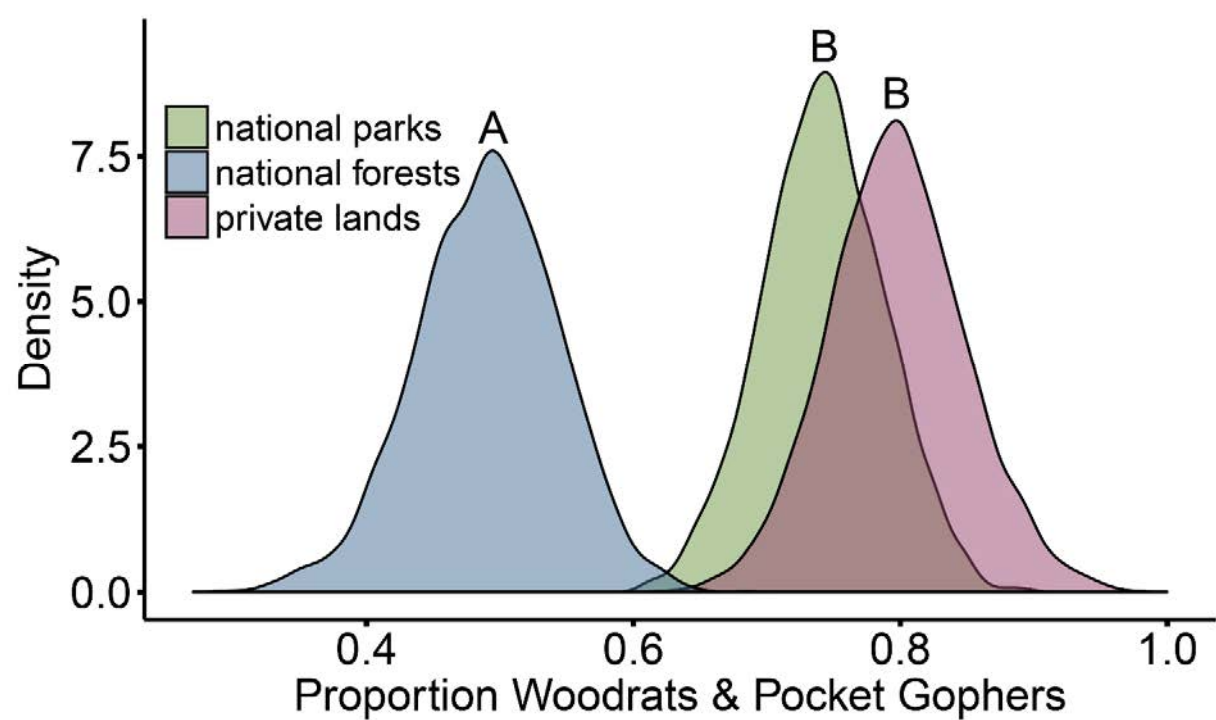
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Associations between Forest Fire and Mexican Spotted Owls

Jeffrey S. Jenness, Paul Beier, and Joseph L. Ganey

ABSTRACT. In 1993, the US Fish and Wildlife Service listed the Mexican spotted owl (*Strix occidentalis lucida*) as threatened, in part because of the rising threat to its habitat from stand-replacing wildfires. In 1997, we surveyed 33 owl sites that, in the previous four years, had burned at various levels ranging from light controlled burns to stand-replacing fires. We compared owl occupancy and reproduction in these burned sites to 31 unburned owl sites with similar habitat and topography. Although unburned sites showed higher proportions of both occupancy and reproduction, the negative relationship observed between recent fire occurrence and owl occupancy rank was statistically weak (Test for Marginal Homogeneity, $P = 0.110$). Owls tended not to be present where pure pine stands (*Pinus* spp.) comprised a large proportion (38–85%) of burned sites, but no other factors relating to habitat or fire severity had a significant, biologically interpretable influence on occupancy rank. We suspect that relatively low-intensity ground fires, including most prescribed fires, probably have little or no short-term impact on Mexican spotted owl presence or reproduction, but we have no data on long-term effects of fire. We recommend proactive fuels-management treatments in areas not currently occupied by owls as a means of reducing fire risk in areas occupied by owls. Within areas occupied by owls, judicious treatments may be appropriate after case-by-case evaluations of potential benefits and risks within those sites. FOR. SCI. 50(6): 765–772.

Key Words: Prescribed burn, occupancy, reproduction, stand-replacement, stand-maintenance.

WILDFIRE HISTORICALLY HAS BEEN a major disturbance agent important in structuring southwestern forests (Swetnam 1990, Covington and Moore 1994a). Fire suppression, timber harvesting, and grazing have altered southwestern forests greatly over the past century, however (Marshall 1963, Covington and Moore 1994a, 1994b, Kolb et al. 1994). These activities have markedly increased litter and combustible debris on

the ground, and density of understory shrubs and small trees (Leopold 1924, Madany and West 1983, Savage and Swetnam 1990). In turn, these conditions increase the potential for larger and hotter fires (Moody et al. 1992, Covington et al. 1994). Thus, management actions have altered the fire regime in some southwestern forest types, such as ponderosa pine (*Pinus ponderosa*) and mixed-conifer forests, from one characterized by frequent, low-intensity

Jeffrey S. Jenness, USDA Forest Service, Rocky Mountain Research Station, 2500 S. Pine Knoll Drive, Flagstaff, AZ 86001—Phone: (928) 526-4139; Fax: (928) 556-2130; jeffj@jennessent.com. Paul Beier, School of Forestry and Merriam-Powell Center for Environmental Research, Northern Arizona University, Flagstaff, AZ 86011—Phone: (928) 523-9341; Paul.Beier@nau.edu. Joseph L. Ganey, USDA Forest Service, Rocky Mountain Research Station, 2500 S. Pine Knoll Drive, Flagstaff, AZ 86001—Phone: (928) 556-2156; jganey@fs.fed.us.

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fires, to one characterized more by infrequent, high-intensity fires.

The Mexican spotted owl (*Strix occidentalis lucida*) inhabits mixed-conifer and pine-oak (*Quercus* spp.) forests and rocky canyonlands in the southwestern United States and Mexico (Gutiérrez et al. 1995, USDI Fish and Wildlife Service 1995). This owl thus has a long evolutionary history in forests structured by frequent, low-intensity fires. The Mexican spotted owl was listed as a threatened species in 1993, based on historical and ongoing habitat alteration resulting from timber-management practices and the threat of additional habitat loss from stand-replacing wildfires (USDI Fish and Wildlife Service 1993). Large-scale stand-replacing fires occurring throughout the owl's range could harm the owl by reducing or eliminating roosting, nesting, and foraging habitat (Sheppard and Farnsworth 1997). The indirect effects of high-intensity wildfire on Mexican spotted owls are not known, unfortunately, and descriptive data are lacking on fire behavior at sites used by owls and how owls respond to fire-induced changes to their habitat (but see Sheppard and Farnsworth 1997).

Fire may affect spotted owls either directly or indirectly. Mexican spotted owls typically nest and roost in structurally-complex, diverse forests with a variety of age and size classes, a component of large trees, often with many snags and down logs and relatively high basal areas and canopy closures (Ganey and Dick 1995, Ganey et al. 1999). Fire directly affects these habitat components either by destroying them, as is typical in a stand-replacing fire, or enhancing them by creating snags, thinning densely packed stands, and reducing competition for water and nutrients. Fire may indirectly affect these habitat components by reducing fuel loads and thereby reducing the chance for stand-replacing fires.

Spotted owls may select habitats partially based on prey availability (Verner et al. 1992, Ward and Block 1995), so fire can affect owls indirectly by altering habitat conditions for their prey. Ward and Block (1995) summarized data suggesting that reproductive success of Mexican spotted owls was influenced by total prey biomass rather than the relative abundance of any particular species.

Some Mexican spotted-owl prey species show a decline or mixed response after fire, but many species, especially deer mice (*Peromyscus maniculatus*), increase in abundance after fire (Tevis 1956, Buech et al. 1977, Wirtz et al. 1988). Early successional specialists (such as the deer mouse) and species that require open habitats with well-developed herbaceous understories (such as pocket gophers [*Thomomys* spp.] or microtine voles [*Microtus* spp.]) benefit from intense stand-replacing fires, whereas species that require dense canopies or ground cover decline (McGee 1982, Ward and Block 1995). Seed-eating species would find a sudden increase in their food supply when annual grasses come in.

The effects of fire on prey biomass are varied, but generally appear to be short-lived (Bock and Bock 1983, Martell 1984, Kirkland et al. 1996). Deer mouse populations appear to universally increase after fire (Wirtz 1982,

Kaufman et al. 1988, Schwilk and Keeley 1998). Total prey biomass after fire appears to increase in some areas and decrease in others. Thus, overall effects of fire on prey biomass also are equivocal. The reduction in ground cover caused by fire could benefit the owl by leaving the prey more exposed, however, thus increasing prey availability.

To assess potential impacts of fire on Mexican spotted owls, we compared the presence and reproductive success of owls between recently burned sites and similar unburned sites (we use "sites" to refer to areas with a history of recent occupancy by owls, loosely analogous to owl territories). We also collected data on severity and extent of burn, topographic characteristics, and dominant forest cover types in burned sites to compare the importance of fire to other possible predictor variables. Our research questions were: (1) Does fire in an owl site influence spotted owl occupancy and reproduction 1–4 years after the fire, compared to unburned sites; and (2) Given a fire within an owl site, does severity and extent of fire, dominant cover type, or topography within the burned site influence spotted owl occupancy and reproduction? We also briefly describe fire extent (percent of forest cover types burned) for recent fires in owl sites.

Methods

Study Area and Site Selection

Using information gathered from USDA Forest Service (USFS) offices, we selected owl sites in Arizona and New Mexico that burned during 1993–1996. These included sites burned by prescribed and prescribed-natural fire (naturally occurring fires that burn in preplanned locations, which are allowed to burn while they meet management objectives), and wildfire. For each burned site, we selected a paired unburned site (i.e., no evidence of recent burn) within 12 km that had similar topography and forest cover types. We selected paired sites based on recommendations from local USFS and other research biologists, drawing on their experience and knowledge of the area. We initially selected 32 pairs of burned and unburned sites. Ground surveys revealed no evidence of recent fire in one of the "burned" sites, however, and extensive burned areas in two "unburned" sites. Thus, our sample consisted of 33 burned sites and 31 unburned sites, including 29 pairs of burned/unburned sites, distributed among nine geographic areas and four national forests (Fig. 1).

Prior knowledge of occupancy patterns on these sites varied greatly in quality and quantity, but all sites had a record of, at minimum, either a pair of owls in a single year or a single owl in at least two years, between 1990 and 1996. USFS survey histories were available for 53 of the 64 sites. Historic occupancy rates for these sites are calculated as the number of years of occupancy recorded divided by the number of years the site was observed. On average, burned sites ($n = 29$) were surveyed 5.1 ± 2.2 (SD) years, with an occupancy rate of 0.88 ± 0.21 . Unburned sites ($n = 24$) were surveyed 5.3 ± 3.3 years with an average occupancy rate of 0.96 ± 0.08 . Of the remaining sites, eight were surveyed numerous years as part of a study on

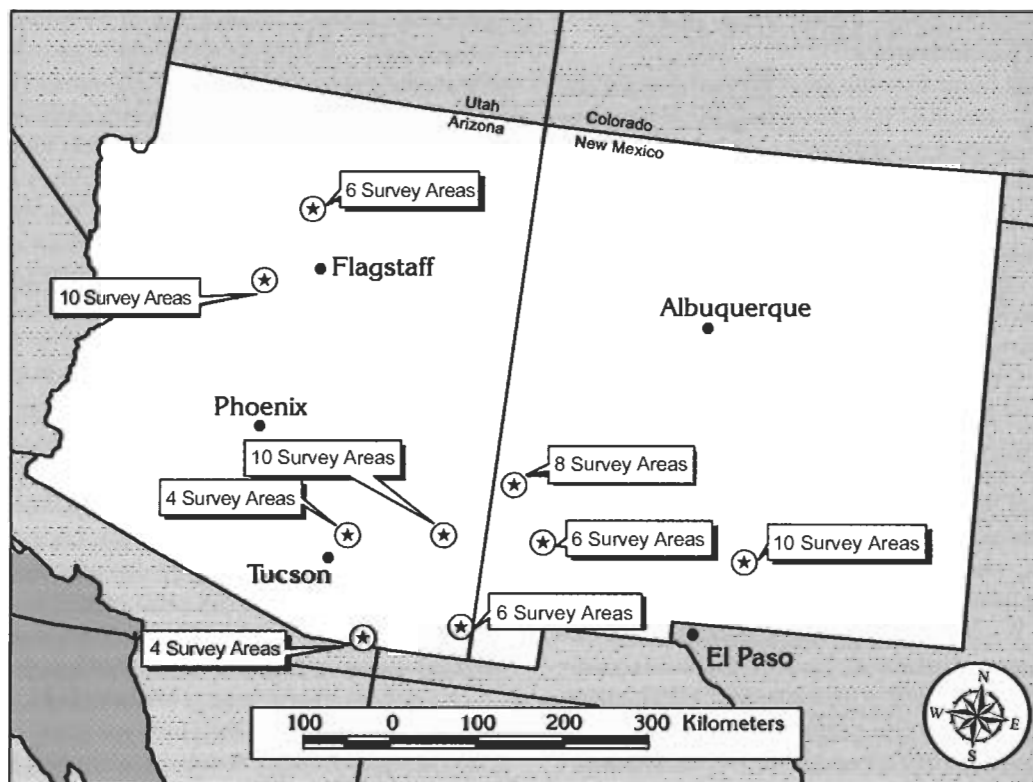


Figure 1. Distribution of Mexican spotted owl survey areas in Arizona and New Mexico, 1997. Forty survey areas were located in Arizona (16 in the Coconino National Forest and 24 in the Coronado National Forest [Catalina, Pinaleno, Chiricahua, and Huachuca mountain ranges]), and 24 were in New Mexico (14 in the Gila National Forest and 10 in the Lincoln National Forest). All locations have an equal number of burned and unburned survey areas.

demography of Mexican spotted owls (Seamans et al. 1999), but actual survey histories were not available. For the remaining three sites, the records did not show survey history but indicated only owl locations and dates.

We conducted owl surveys within each site using three delineations of the site boundary. These were: (1) activity centers delineated by USFS biologists, based on historical use patterns and professional judgment; (2) a 400-m radius circle centered on the nest site or cluster of owl detections for each site; and (3) a 1-km radius circle centered on the nest site or cluster of owl detections for each site. The 1-km radius circle (314.2 ha) was chosen because it was a convenient number that approximated the current guidelines for size and extent of Mexican spotted owl Protected Activity Centers (243 ha with irregular boundary; USDI Fish and Wildlife Service 1995). Because results differed little among the three types of boundary delineation and because the 1-km circles had a more uniform size and shape than delineated activity centers and contained more grid points (see below) than the 400-m circles, we will restrict our discussion here to results from the 1-km circles and hereafter refer to them as "survey areas." Results of analyses involving the other two survey-area delineations are available in Jenness (2000).

Owl Surveys

We conducted nocturnal calling surveys from 1 Mar. to 31 Aug. 1997, following established protocols (Forsman

1983, USDA Forest Service 1988). All surveys occurred between 30 min after sunset and 30 min before sunrise. Calling was discontinued in windy and stormy conditions. We called for owls from either fixed points or while walking along continuous transects, located so that calls were audible over the entire survey area. Each area was surveyed four times unless young spotted owls were observed outside the nest, confirming successful reproduction, before the fourth survey. If we heard a spotted owl at night, we returned to the area within 48 h to conduct a daytime follow-up survey to search for evidence of nesting. We searched for nests visually and, if unsuccessful, offered mice to the owls to attempt to locate the nest. In all cases, the same individuals surveyed both burned areas and their unburned counterparts. We assigned each survey area to one of four Owl Occupancy Ranks on completion of surveys. These were: (1) no owls detected; (2) one owl detected, but no conclusive evidence of pair occupancy; (3) a pair of owls detected, but no evidence of successful reproduction; and (4) young spotted owls observed outside the nest. This four-level ordinal categorization provides a reasonable basis for comparing occupancy or successful reproduction within established owl territories because each increasing level reflects increasing fitness. Quantitative measures of fecundity and survival over several years would better describe potential impacts on spotted owls (see Burnham et al. 1996, Gutiérrez et al. 1996, Raphael et al. 1996), but we did not have such data.

Determining Fire Severity, Cover Type, and Topographic Characteristics

We sampled all burned survey areas for fire severity and dominant prefire vegetation type by systematically surveying a grid (186-m spacing, with an average of 91 ± 2.9 points per survey area) randomly overlaid on each survey area map. Using each point as the center of a 10-m radius circle, we assigned the plot to one of four fire severity classes and one of four prefire vegetative cover types.

We used criteria described by Wenger (1984) to distinguish between stand-replacing and stand-maintaining fires. Stand-replacing ("catastrophic") fires kill most vegetation within the fire boundary. Depending on the fire intensity and the vegetation density, stand-replacing fires may leave large amounts of dead vegetative material that increases the risk and intensity of future fires. Stand-maintaining fires generally burn close to the ground, killing the aboveground parts of grasses, shrubs, forbs, small trees, and burning accumulated ground fuels, without killing larger trees (Wenger 1984). We subdivided stand-maintaining fires into canopy-level and surface-level fires. Our fire severity classes were: (1) no evidence of fire within plot (unburned); (2) no evidence of canopy fire within the plot, but evidence of ground fire (ground fire); (3) evidence of patchy canopy fire within the plot (canopy fire); and (4) all canopy vegetation within the plot killed by fire (stand-replacement fire).

We classified each site into one of four vegetation cover types (mixed-conifer, pine, pine/oak, other) based on the primary species composition of overstory and understory vegetation. Mixed-conifer sites were primarily Douglas-fir (*Pseudotsuga menziesii*), spruce (*Picea* spp.), or true fir (*Abies* spp.). Pine sites were characterized by forests of long-needled pines (*Pinus* spp.). Pine/oak sites included mixed species stands of pine and oak (*Quercus* spp., primarily *Q. gambelii*).

We also used 7.5' Digital Elevation Models (DEMs; Arizona State Land Department 1997, USDA Forest Service Geomtronics Center 1997) to derive slope and aspect data and a crude index of topographic roughness within survey areas. We estimated topographic roughness by generating 20-m contour lines over the survey area, clipping them to the survey area boundary, summing the total length of the clipped contour lines, and dividing by the survey area to yield a density of 20-m contour lines in meters per hectare.

Statistical Analysis

We analyzed our data in two steps. First, we compared occupancy rank between paired burned and unburned sites. Second, for burned sites only, we evaluated potential relationships between site characteristics and occupancy rank.

We used a Test of Marginal Homogeneity (Mehta and Patel 2001) to compare occupancy rank among the 29 pairs of burned and unburned survey areas. We used a two-tailed test because fire could potentially degrade or improve owl habitat.

We used the Multiple Response Permutation Procedure (MRPP [Mielke and Berry 1995]) as implemented in pro-

gram BLOSSOM (Slauson et al. 1994) to examine the associations between occupancy ranking at burned sites and the severity and extent of fire, dominant cover type, and topographic characteristics in those sites. MRPP uses permutations of the actual data to calculate the probability that the observed grouping of observations could be due to chance, and thus can be used even when underlying distributions are non-normal. After a significant omnibus MRPP, we used univariate MRPP tests to identify specific variables associated with occupancy rank.

Results

Description of Fire Extent in Owl Survey Areas

On average, fires affected 55% of the area in burned sites (range 1–99%). This included 25% burned only by understory fire (range 1–73%) and 30% of the survey area burned by canopy-level fire (range 0–91%). On average, 14% of a survey area burned only partially into the canopy (range 0–44%), and 16% of the area burned at stand-replacing level (range 0–55%). Within the combined area of all our burned survey areas, fires burned 56% of the mixed-conifer type (24% at ground level, 17% in canopy, and 16% stand-replacement), 66% of the pine type (26% at ground level, 18% in canopy, and 22% stand-replacement) and 54% of the pine/oak type (34% at ground level, 8% in canopy, and 13% stand-replacement). Thirty-three percent of the burned portions were in mixed-conifer, 44% were in pine, and 14% were in pine/oak.

Associations Between Fire Presence and Owl Occupancy Rank

Unburned survey areas tended to have more pairs and more reproductive pairs than did burned survey areas (Fig. 2). Compared to the 33 burned sites, the 31 unburned sites had a higher proportion of occupied sites (84% versus 70%) and reproduction (16% versus 9%) in 1997. Of the 29 paired sites, 6 cases had a higher occupancy rank in the burned survey areas, 9 pairs resulted in ties, and 14 cases had a

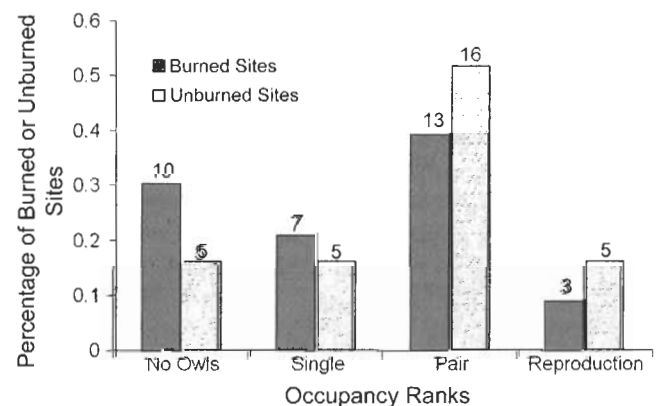


Figure 2. Relative proportions of burned and unburned Mexican spotted owl survey areas that had either no owls, a single bird, a pair, or confirmed reproduction. The numbers above the bars represent the actual numbers of survey areas at each response level, whereas the Y-axis represents the proportion of either burned or unburned survey areas at each response level.

higher occupancy rank in the unburned survey areas. These differences were not statistically strong ($P = 0.110$).

There was no marked difference in occupancy rank in relation to time since fire. Of the survey areas that burned in 1996 (one year before our surveys), six of eight were occupied, compared to 17 of 25 survey areas that burned 2–4 years before our surveys.

Owls were present and reproducing at several sites that experienced severe fires. Fires burned >50% of each of the three burned survey areas with successful nests in 1997 (including stand-replacement-level percentages of 8, 31, and 32%), and the most severely burned survey area had a single owl in 1997. Thirty of the survey areas burned only once in the 4 years before our surveys, but three burned multiple times. At the latter sites, we found single owls at two sites and a nonreproducing pair at the other site.

Associations Between Fire Severity/Habitat Variables and Owl Occupancy Rank

The omnibus MRPP test indicated that occupancy rank was significantly influenced by some variable or combination of variables ($P = 0.040$). Subsequent univariate tests identified three variables as showing the most significant differences among the occupancy ranks: percent pine ($P = 0.003$), percent mixed conifer ($P = 0.038$), and percent of survey area unburned ($P = 0.075$) (Table 1, Fig. 3). Owl sites where we detected no owls in 1997 contained more pine than sites where owls were present, and successful reproduction was associated with a higher proportion of mixed conifer (Fig. 3). The differences in percent of area burned relative to occupancy rank did not follow a biologically interpretable pattern (Fig. 3).

Discussion

Our results were equivocal regarding the potential impact of fire on Mexican spotted owls. Although statistical significance was weak, our sample size was small, resulting in low power to detect a significant association between occupancy rank and fire. Further, we lack information on

Table 1. For 33 burned sites, the probability that each fire severity and habitat variable did not differ among the four levels of occupancy rank (no owls, single owl, pair, reproduction) as determined by MRPP.

Variable	P-value
Average slope in degrees	0.524
% North-facing slope	0.224
% East-facing slope	0.716
% South-facing slope	0.103
% West-facing slope	0.923
% Unburned	0.075
% Ground fire	0.712
% Canopy fire	0.178
% Stand-replacement fire	0.263
% Pine	0.003
% Pine/Oak	0.226
% Mixed-conifer	0.038
Topographic roughness	0.597

The omnibus MRPP test using all predictor variables suggested that at least one variable differed among owl occupancy types ($P = 0.04$).

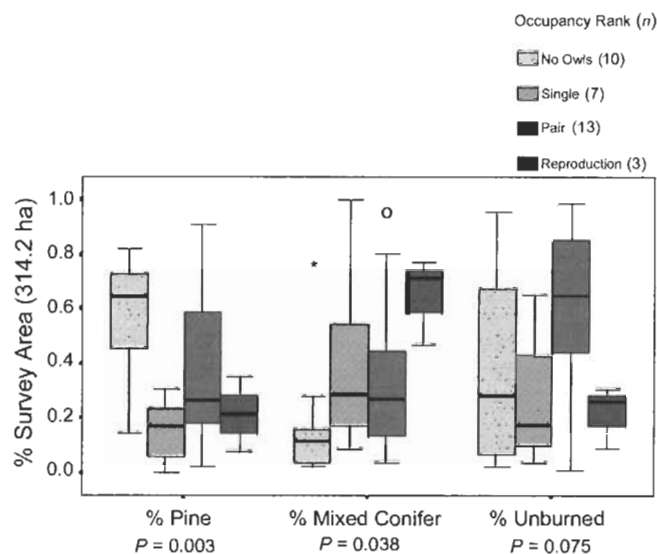


Figure 3. Percent pine, mixed-conifer, and unburned predictor variables in 33 burned areas (314.2 ha each). Horizontal bars within boxes represent the median, the tops and bottoms of the boxes represent the 75th and 25th quantiles, and the whiskers represent the range excluding outliers and extremes. Outliers (values >1.5 box lengths from box) are displayed with the symbol "o" and extremes (values >3 box lengths from the box) are displayed with the symbol "*".

spatial and temporal variability in owl occupancy rates, and our burned areas encompassed a wide range in both burn extent and severity. These factors further complicate interpretation of our data. However, point estimates of effect size (e.g., probability of occupancy 14% higher and probability of successful reproduction 7% higher in unburned sites) were suggestive of a biologically significant impact. Consequently, we caution against interpreting our results as indicative that fires do not affect spotted owls.

Our MRPP tests suggested that the percentage of pure pine in a survey area was most strongly associated with occupancy rank. Because fires burned greater proportions of the pine type in our survey areas, there may have been an interaction between fire effects and cover type.

Previous evidence also is equivocal with respect to the effects of fire on Mexican spotted owls. Willey (1998) radiotracked three pairs of Mexican spotted owls before and after relatively low-intensity prescribed burns in Saguaro National Park, southern Arizona, finding that, at least in the short term, the owls tended to stay in the same general area after the fires. Bond et al. (2002) documented survival, site and mate fidelity, and reproductive success after large fires for 21 owls in 11 territories in California, Arizona, and New Mexico, finding high survival, site and mate fidelity, and reproductive success. Several Mexican spotted owls in the Gila National Forest continued to occupy territories after prescribed natural fires that minimally altered stand structure (USDA Forest Service 1995), and there are numerous anecdotal observations of Mexican spotted owls occupying areas after wildfires and prescribed burns (Paul Boucher, Gila National Forest, 1997; Peter Stacey, Univ. New Mexico, July 8, 2001).

Other anecdotal evidence demonstrates possible negative response to fire, such as Elliot's (1985) observation that at least one California spotted owl (*S. o. occidentalis*) territory apparently was abandoned for several years after a highly destructive fire in 1977. Gaines et al. (1997) described impacts of 1994 wildfires on six northern spotted owl (*S. o. caurina*) activity centers in eastern Washington, noting a small decrease in the number of reproductive pairs on these sites, and an increase in the number of unoccupied sites the year after the fires. Bevis et al. (1997) discussed two pairs of radio-tagged northern spotted owls in south-central Washington that stayed near their territories after a 1994 wildfire but shifted their primary activity to lightly burned or unburned areas. One female owl in that study was found dead in an emaciated condition 2.5 months after the fire, leading to speculation that the fire may have reduced prey availability, and her mate disappeared over the winter. Two new owls occupied the territory one year after the fire, suggesting that, by then, the territory could support owls despite the fire.

The potential for widespread stand-replacing fire, identified as a leading factor endangering the Mexican spotted owl by USDI Fish and Wildlife Service (1993, 1995), has not abated during the last decade. For example, Sheppard and Farnsworth (1997) estimated that at least 10 Mexican spotted owl territories were affected by fire in Arizona and New Mexico during the 1994 fire season alone. They further estimated that >20,234 ha of owl habitat experienced stand-replacing wildfire from 1989–1994. Severe wildfires have occurred in virtually every year since 1994, with peaks in 1996 and 2002. Thus, stand-replacing wildfire remains a significant threat to owls and their habitat in both the short and long-term. We recognize that most wildfires burn in a patchy nature and leave pockets of useable habitat for owls. We further recognize that some owls locate and use these patches and thus are relatively resilient to wildfire, at least in the short term. Nevertheless, we continue to view the potential cumulative loss of habitat to wildfire as a major threat to the owl, especially given lack of data on long-term responses of owls to fire.

Our concern over loss of owl habitat to wildfire is exacerbated by several factors. One is the current structure of southwestern forests. Although owl habitat as we know it today is inherently fire prone, with high tree densities, canopy cover, and fuel loadings (Ganey and Dick 1995), we suspect that those conditions were not continuous on the landscape under natural fire regimes (Marshall 1963, Covington et al. 1994). Such conditions now are relatively continuous on the landscape, raising the specter of more, larger, and more intense wildfires. This creates greater potential for widespread loss of owl habitat.

Further, much of the currently occupied owl habitat occurs in canyons featuring cool microsites and rock outcrops. These areas may have functioned as fire refugia (*sensu* Camp et al. 1997) in historic times, escaping some of the frequent fires and allowing longer fire-free periods for stand development. With increasing intensity of wildfires (Moody et al. 1992) and greater continuity of heavy fuels,

the potential for fire to spread into these refugia would appear to be higher as well. This problem is further exacerbated by the fact that the southwest is currently experiencing a severe drought of unknown duration, further increasing the potential for large and intense wildfires (Swetnam 1990, Swetnam and Betancourt 1990).

Finally, the seasonality of fire in the southwest has changed. Most naturally occurring fires in Arizona and New Mexico occur during the monsoon season between July and September as a result of lightning strikes during thunderstorms (Sackett et al. 1994, Fulé et al. 1997, Brown et al. 2001). This is a rainy season in the southwest when fuel moistures are often high and precipitation is likely to fall concurrent with or soon after the lightning strikes, both factors which can moderate fire behavior and extent.

In contrast, many large wildfires in recent years have been human-caused, and have occurred in May and June (historical data on timing, size, and cause of large fires, www.fs.fed.us/r3/fire/swainfo/swainfo.htm, Sept., 2003). This is a dry period in the southwest, falling between periods of winter precipitation and summer thunderstorms. This season is characterized by low fuel moistures, high winds, and little chance of precipitation to moderate fire behavior. These conditions, coupled with high and relatively continuous fuel loadings as a result of fire suppression, favor extreme fire behavior and large fires.

We also suspect that fire may affect owls differently based on whether it burns in core/nest areas where it may cause changes in the microclimate and cover necessary for raising young, or foraging areas where it may affect prey availability and diversity. We were unable to analyze this possibility because of a lack of sufficient historical nesting locations in our dataset, but we feel it could have important management implications and should be considered in future research or management actions.

Management Implications

The recovery plan for the Mexican spotted owl (USDI Fish and Wildlife Service 1995) recommended proactive fuels management to reduce continuity of fuels on the landscape. We support that recommendation. The plan further recommended that initial fuels-reduction efforts focus on areas not currently occupied by owls (Protected Activity Centers or PACs) because of uncertainty over the effects of those treatments on owls. We also believe this recommendation is appropriate. We agree with the plan's conclusion that treatment of areas outside of PACs can provide considerable protection to those PACs by allowing managers to reduce continuity of fuels on the landscape, thus reducing the potential for fires to start elsewhere and spread into PACs. Because owl PACs comprise only approximately 2.1% of National Forest lands in Arizona and New Mexico (USDA Forest Service, unpublished data), we further believe that this approach leaves open to management more area than land management agencies can reasonably treat in the near future, and thus should not prevent managers from addressing fuels-management issues in most areas. We recognize, however, that unique situations may exist requiring

treatments to proceed in PACs. One example is cases where owls occur in the wildland–urban interface, and treatment of those areas is necessary to reduce fire risk to rural and urban areas of human settlement. Other examples undoubtedly exist. We recommend that managers evaluate these situations on a case-by-case basis. Ideally, where fuels reduction treatments proceed in PACs, associated effects on Mexican spotted owls and key ecological linkages (e.g., prey and important habitat variables) should be determined by incorporating those treatments in a management experiment using a credible scientific design, examining long-term survival and fecundity, and including a rigorous multi-year monitoring program. However, such an effort may prove prohibitively expensive. Therefore, as an alternative, we suggest that response of owls be monitored using systematic and standardized research designs that will allow results from various areas to be included in a meta-analysis evaluating effects of fuels treatments on owls, their habitat, and important prey species.

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A dissertation submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy
(Wildlife Ecology)

at the

UNIVERSITY OF WISCONSIN – MADISON

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The dissertation is approved by the following members of the Final Oral Committee:

M. Zachariah Peery, Professor, Forest and Wildlife Ecology (Chair)

Volker C. Radeloff, Professor, Forest and Wildlife Ecology

Benjamin Zuckerberg, Associate Professor, Forest and Wildlife Ecology

Monica G. Turner, Professor, Integrative Biology

R. J. Gutiérrez, Professor Emeritus, Fisheries, Wildlife and Conservation Biology,
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Dedication

To my children, Miri and Hugo.

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Dissertation abstract

Fire suppression and climate change have produced disturbance regimes in the Sierra Nevada, California, USA that are increasingly characterized by large, severe fires. Landscape-scale fuel reduction and forest restoration treatments (e.g., thinning and prescribed fire) have the potential to restore more “natural” disturbance regimes to dry forest ecosystems and increase forest ecosystem resilience under climate change. However, treatments that alter forest structure could exacerbate ongoing declines in populations of spotted owls (*Strix occidentalis*) as well as other old-forest species that inhabit dense, fire-suppressed forests. Potential short-term negative effects of treatments might be outweighed by longer-term benefits if treatments are able to mitigate disturbance-induced habitat loss. However, there are key uncertainties concerning the absolute and relative effects of treatment and severe fire on spotted owl populations.

This dissertation seeks to reduce these key uncertainties to facilitate science-based management of dry forest ecosystems and spotted owl populations in the Sierra Nevada. Chapter 1 documents the empirical effect of a large, severe fire (the 2014 King Fire) on a population of spotted owls in the central Sierra Nevada via a natural before-after control-impact experiment. Chapter 2 draws on monitoring data from four long-term spotted owl study areas spanning the latitudinal range of the Sierra Nevada to quantify empirical associations of forest structure (e.g., tree size and canopy cover) on local territory extinction dynamics. The empirical relationships between severe fire, forest structure, and spotted owl occupancy dynamics derived in Chapters 1 and 2 come together in Chapter 3, which projects spotted owl occupancy dynamics as a function of simulated fuel treatment and severe fire occurrence under climate change.

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Chapter 1 - Megafires: an emerging threat to old-forest species

Gavin M. Jones¹, R. J. Gutiérrez², Douglas J. Tempel¹, Sheila A. Whitmore¹,
William J. Berigan¹, M. Zachariah Peery¹

¹*Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA;* ²*Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, 1980 Folwell Avenue, St. Paul, MN 55108, USA*

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Abstract

Increasingly frequent “megafires” in North America’s dry forests have prompted proposals to restore historical fire regimes and ecosystem resilience. Restoration efforts that reduce tree densities (e.g., via logging) could have collateral impacts on declining old-forest species, but whether these risks outweigh the potential effects of large, severe fires remains uncertain. We demonstrate the effects of a 2014 California megafire on an iconic old-forest species, the spotted owl (*Strix occidentalis*). The probability of owl site extirpation was seven times higher after the fire (0.88) than before the fire (0.12) at severely burned sites, contributing to the greatest annual population decline observed during our 23-year study. The fire also rendered large areas of forest unsuitable for owl foraging one year post-fire. Our study suggests that megafires pose a threat to old-forest species, and we conclude that restoring historical fire regimes could benefit both old-forest species and the dry forest ecosystems they inhabit in this era of climate change.

Introduction

The frequency and severity of “megafires” (i.e., large wildfires > 10,000 ha in extent [Stephens *et al.* 2014b]) in the dry forests of North America has increased following a century of fire suppression and climate warming (Westerling *et al.* 2006, Miller *et al.* 2009b), incurring considerable societal and economic costs by destroying homes, human infrastructure, timber resources, and elevating taxpayer support for fire-fighting (Stephens *et al.* 2013, 2014c). In the western United States, major reforms in forest fire management have been proposed to restore low- and moderate-severity fire regimes through forest tree thinning (North *et al.* 2015b). However, the vision of restoring “pre-European” fire regimes, as well as forest structure and composition, is constrained by concern over fuels-reduction treatments that simplify the structurally and floristically diverse forests inhabited by old-forest species (Pilliod *et al.* 2006). Potential short-term consequences of fuels-reduction and restoration treatments may be outweighed by long-term benefits of forest restoration if large, high-severity fires negatively impact old-forest species (Sweitzer *et al.* 2015, Tempel *et al.* 2015a). However, recent work suggests that severe fires may have neutral or beneficial effects on biodiversity including old-forest species (Hutto 2008, Swanson *et al.* 2011, DellaSala and Hanson 2015, Lee and Bond 2015), which seemingly exacerbates the perceived divide between forest restoration and species conservation objectives. Nevertheless, the ecological effects of high-severity fire likely depend, in part, on the size, distribution, and configuration of burned patches (Fontaine and Kennedy 2012), and the impacts of large, severe fires remain a source of considerable uncertainty.

Here, we demonstrate the definitive negative short-term impacts of a California megafire on a model old-forest species, the spotted owl (*Strix occidentalis*; Figure 1), by taking advantage of a natural Before-After-Control-Impact experimental design on our long-term (23-year)

demographic study area. The human-ignited “King Fire” burned 39,545 ha and was one of the largest and most severe forest fires recorded in California history (Figure 2), with high-severity fire (75-100% canopy mortality) occurring on 19,854 ha (50% of the area burned), with one continuous 13,683 ha high-severity burned patch. The King Fire affected 15,594 ha (44%) of our 35,500 ha study area and overlapped 30 of 45 spotted owl sites we continuously monitored since 1993 (Tempel et al. 2014b). Of the 15,594 ha that burned within our study area, 64% burned at high-severity (Supplementary Table 1). The extreme nature of the fire, more than two decades of pre-fire site occupancy data, and location information on banded and GPS-tagged owls allowed us to draw strong inference regarding the effect of severe fire on a species considered to be a barometer of old-forest wildlife community health (Simberloff 1998). Our results suggest that (i) reducing the frequency of large, severe fires could benefit spotted owls and, by extension, other less vagile old-forest species for which we have little information on their response to megafires, and (ii) forest restoration and old-forest species conservation objectives may be more compatible than previously believed.

Methods

Study area and spotted owl surveys

We conducted our study on the contiguous 35,500-ha Eldorado Density Study Area (EDSA) on the Eldorado National Forest in the central Sierra Nevada, California. The EDSA has been the site of a long-term mark-recapture demographic study of California spotted owls (Tempel and Gutiérrez 2013), and forms the primary part of a larger study area containing a greater number of owl sites (Tempel et al. 2014a). We only used data from owl sites within the EDSA because some sites outside of the EDSA experienced a complex history of fire and post-fire management that could have confounded the natural BACI design within the EDSA. Moreover, sites outside

of the EDSA were added at various times during the study, potentially complicating our evaluation of the effect of the King Fire on long-term spotted owl population trends.

Approximately 60% of the EDSA was public lands managed by the USFS and 40% was private land managed by timber companies. The primary vegetation type on the EDSA was mixed-conifer forest dominated by Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), and California black oak (*Quercus kelloggii*). Forests on the EDSA have a complex history of management, logging, and fire suppression dating back at least 100 years. Early timber harvesting generally involved the selective removal of large, commercially valuable trees, with a more recent emphasis on clear-cutting on private lands and “diameter-limited thinning from below” on public lands. Prior to fire suppression, the ingrowth of shade-tolerant trees, and the removal of large trees, historic fire regimes consisted mainly of frequent low- to moderate-severity fire occurring in 5-15 year intervals (Stephens and Collins 2004). Elevation on the EDSA ranged from 360 to 2400m, and the climate was characterized by cool, wet winters and warm, dry summers.

We surveyed the entire area each year for territorial spotted owls during the breeding season (1 April to 31 August) without regard to land cover, topography, access, or land ownership, and we used survey data from 1993–2015. Spotted owls (usually mated pairs, but sometimes single birds) occupy and defend sites (i.e. “territories”), the locations of which remain reasonably stable across years. We considered a site to be occupied in a given year when at least one owl was detected. Additional survey details can be found elsewhere (Tempel and Gutiérrez 2013, Tempel et al. 2014b).

Before-After Control-Impact analysis

We evaluated the potential impact of high-severity fire on spotted owls using a Before-After Control-Impact (BACI) design with multi-season site occupancy data (MacKenzie et al. 2003, Popescu et al. 2012). We carried out parallel continuous and categorical BACI analyses, where the proportion of a spotted owl site (a circle with radius equal to one-half the mean nearest-neighbor distance across years = $\sim 1,100\text{m}$; Tempel *et al.* 2014a) affected by high-severity fire was the impact covariate (i.e., “treatment”). We defined “high-severity” as forests that experienced 75-100% canopy mortality (Lee and Bond 2015), corresponding to a relative differenced Normalized Burn Ratio (RdNBR) threshold of >572 (Miller et al. 2009a). The continuous BACI analysis contained two groups: sites that were unburned ($n = 15$) and sites that overlapped with the King Fire and thus experienced some degree of burn ($n = 30$). The categorical BACI analysis contained three groups: sites that were unburned ($n = 15$), sites that experienced $<50\%$ high-severity fire ($n = 16$), and sites that experienced $> 50\%$ high-severity fire ($n = 14$). For both continuous and categorical BACI analyses, we followed a hierarchical modeling procedure by first modelling within-season detection probability as a function of covariates (Supplementary Table 2). We then modeled the potential effects of high-severity fire on colonization (γ) and extinction (ϵ) rates separately using AIC to select between competing models (Supplementary Table 3), while allowing the non-focal parameter to vary by year (Tempel et al. 2014a).

Previous attempts to test for the effects of wildfire on spotted owls have been hindered by the potential confounding effect of post-fire salvage logging (Lee et al. 2012, Clark et al. 2013). However, in our study, all surveys used to estimate occupancy metrics were completed prior to the implementation of proposed post-fire salvage logging on public lands (USFS 2015), which comprised a median of 89% of the area that occurred within burned owl sites (versus $\sim 11\%$ on

private lands). We also evaluated the potential effects of post-fire salvage logging on private lands in the continuous site occupancy analysis. Specifically, when fire effects were supported, we introduced a covariate representing the proportion of spotted owl sites that experienced salvage logging. The continuous variables, high-severity fire and salvage logging, were not strongly associated at fire-affected sites ($R^2 = 0.10$).

Population trend analysis

We fit a fully time-varying dynamic occupancy model to our 23-year detection/non-detection data to obtain unconstrained annual estimates of occupancy (ψ_t) and rate of change in occupancy (λ_t) for the study area (MacKenzie et al. 2003). Our statistical model directly estimated initial occupancy (ψ_1), annual estimates of extinction (ε_t), and annual estimates of colonization (γ_t), so we used the recursive equation

$$\psi_t = \psi_{t-1}(1 - \varepsilon_{t-1}) + (1 - \psi_{t-1})\gamma_{t-1}$$

to estimate occupancy (ψ_t) for each year of the study period. Then, using the estimates of ψ_t , we calculated the rate of change in occupancy (λ_t) for each year using the equation:

$$\lambda_t = \frac{\psi_{t+1}}{\psi_t}$$

This analysis allowed us to consider occupancy and rate of change in occupancy following the King Fire within the context of a long-term decline in our study population (Tempel and Gutiérrez 2013). We fit several linear models to annual estimates of occupancy ψ_t and used AIC to evaluate relative support for different time trends (linear, log-linear, quadratic) and a segmented (i.e., “break-point”) model over the pre-fire years 1993-2014 (Supplementary Table 4). We used the segmented model to evaluate support for an initial decline followed by a period of apparent population stability prior to the King Fire.

Habitat use and selection analysis

We collected post-fire foraging locations from nine spotted owls during the 2015 breeding season using backpacks having a Lotek Pinpoint 100 mini-GPS archival tag and a VHF radio transmitter. GPS tags recorded 1-2 locations at random times between dusk and dawn each night May–August to characterize breeding season nocturnal habitat use. We collected 1085 locations but discarded ~11 locations/owl with suboptimal measures of precision (dilution of precision; $DOP \geq 5$). Using burn severity maps produced by the United States Forest Service, we performed a compositional analysis of habitat use (Aebischer et al. 1993) and derived Manly's selection ratios (w_i ; Manly *et al.* 2002) for third-order habitat selection to assess selection or avoidance of forests in different burn classes (unburned, low-severity, high-severity).

We defined available habitat area for each owl using a circle with the center equal to the geometric mean of 2015 nest tree, roosts, and daytime capture locations (i.e., “activity center”) and a radius equal to the 95th percentile of linear foraging distances from the activity center (similar to Bond *et al.* 2009). We used the 95th (not 100th) percentile so that distant areas rarely visited by owls in foraging bouts (Bond et al. 2009) were not counted as “available” habitat. As a result, the analysis consisted of GPS locations that occurred within distance ranges used at relatively high frequencies (Supplementary Figure 2). We used a circle instead of a minimum convex polygon (MCP) to define available habitat because MCPs often failed to include the large, high-severity patch as “available” although it was generally within the foraging radius of owls (Supplementary Figure 3). We performed habitat selection analyses using the R package ‘adehabitatHS’ (Calenge 2006).

Results and Discussion

The BACI analysis indicated that high-severity fire had a strong negative impact on spotted owls. The probability of site extinction (ϵ) increased from 0.01 to 0.98 as the proportion of high-severity fire at a spotted owl site increased from 0 to 1 (Figure 3a). Moreover, extinction rates at severely burned sites (>50% of site area burned at high severity) increased sevenfold following the King Fire ($\hat{\epsilon}_{1993-2014} = 0.12$, 95% confidence interval [CI] = 0.08–0.18; $\hat{\epsilon}_{2015} = 0.88$, CI = 0.49–0.98), whereas post-fire extinction rates were estimated to be zero at less severely burned and unburned sites (Figure 3b). Sites that burned <50% at high-severity were more likely to be colonized after the fire ($\hat{\gamma}_{<50\% \text{ High-severity}} = 0.30$, 95% CI = 0.07–0.72) than unburned sites and sites that burned >50% at high-severity ($\hat{\gamma}_{\text{Unburned}}$ and $\hat{\gamma}_{>50\% \text{ High-severity}} = 0$; Figure 3c).

Colonization of sites after the fire was largely the result of individuals moving to less burned sites after abandoning their original sites that burned at >50% high-severity (Supplementary Figure 4). Predicted occupancy rates ($\hat{\psi}$) at sites that burned >50% at high-severity declined by almost nine-fold from their pre-fire value ($\hat{\psi}_{2014} = 0.72$, 95% CI = 0.62–0.82; $\hat{\psi}_{2015} = 0.08$, 95% CI = 0.00–0.24), based on a model that combined top colonization and extinction covariate structures in the categorical analysis (Figure 3d).

Post-fire salvage logging on private lands constituted a median of only 2% of the area within owl sites based on spatially explicit data obtained from privately-owned natural resource companies managing timberlands on our study area (Sierra Pacific Industries and Mason, Bruce & Girard, Inc.). The extent of high-severity fire was large relative to the extent of salvage logging within owl territories (Supplementary Figure 1), strengthening potential inferences because this ratio reduced the confounding effects of high-severity fire and post-fire salvage logging on spotted owls. In addition, the term for salvage logging appeared as an uninformative

parameter in the modeling procedure (Arnold 2010), also suggesting that post-fire salvage logging operations did not confound associations between occupancy metrics and high-severity fire (Supplementary Table 3, Supplementary Figures 1 and 5).

The King Fire exacerbated a longer-term decline in spotted owl occupancy within our study area. The proportion of occupied spotted owl sites declined by 43% over a 22-year period leading up to the 2014 King Fire ($\hat{\psi}_{1993} = 1.0$, SE = 0.0; $\hat{\psi}_{2014} = 0.57$, 95% CI = 0.41–0.73) (Figure 3e). After the King Fire, occupancy dropped from 0.57 to 0.44 ($\hat{\psi}_{2014} = 0.57$, 95% CI = 0.41–0.73; $\hat{\psi}_{2015} = 0.44$, 95% CI = 0.29–0.60) following ~7 years of relatively stable occupancy (Figure 3e). The 22% decline in site occupancy after the fire ($\hat{\lambda}_{2015} = 0.78$, 95% CI = 0.53–1.03) was the greatest single-year decline recorded over our 23-year study period (Figure 3f).

Analyses of spotted owl foraging locations along the perimeter of the King Fire (no owls were present in the interior of the large patch that burned at high-severity; Figure 4a-d) indicated that spotted owls foraged non-randomly (Wilks's lambda $\Lambda = 0.40$, $P = 0.017$) by avoiding foraging in areas that burned at high-severity ($\hat{w}_{\text{High-severity}} = 0.31$, 95% CI = 0.10–0.51) (Figure 4e-f). Forests that burned at low severity and unburned forests were used in proportion to their availability on the landscape ($\hat{w}_{\text{Low-severity}} = 1.21$, 95% CI = 0.82–1.60; $\hat{w}_{\text{Unburned}} = 1.12$, 95% CI = 0.87–1.38) (Figure 4e-f).

The observation that lower-severity fire is benign, and perhaps even moderately beneficial, to spotted owls is consistent with previous studies (Roberts et al. 2011, Lee et al. 2012) and is not surprising given that, within dry mixed-conifer forests, the spotted owl and other old-forest species evolved in association with such fire regimes (Noss et al. 2006, North et al. 2009). However, we provide the first definitive evidence that a large, high-severity fire (i.e., a megafire) had strong negative population impacts on an old-forest species and that areas burned

at high severity were avoided by individuals. These findings contrast with a recent study of a population of spotted owls which reported high site occupancy after another megafire (the “Rim Fire”) (Lee and Bond 2015). The Rim and King Fires could have impacted owls differently because of differences in the patterns of patches that burned at high-severity and the resulting distribution of remnant habitat. The largest high-severity patch in the Rim Fire (21,426 ha) was 1.5× larger than that of the largest high-severity patch in the King Fire (13,683 ha), but made up a smaller percentage of the total area burned (21% vs. 36% for the Rim and King fires, respectively) and, despite its larger area, had an edge-to-area ratio 1.5× greater than that of the King Fire. The relatively high spatial complexity and heterogeneity in high-severity burn patterns in the Rim Fire may have resulted in a wider range of vegetation conditions and more remnant live trees suitable for owls (Lee and Bond 2015) compared to the King Fire, where the largest patch of high-severity fire was more homogeneously severe and overlapped a greater density of owl sites (Figure 2; see Supplementary Figure 6). Alternatively, because owls were not individually marked in the Rim Fire study, some detections at “occupied” sites may have involved individuals from neighboring territories or non-territorial “floaters” (Lee and Bond 2015), both of which may have contributed to inflated estimates of territory occupancy. Regardless, our study demonstrates that megafires can have strong negative effects on spotted owls, particularly when severely burned areas occur as large homogenous patches that leave little or no interspersed remnant habitat.

While we only used one year of post-fire data, the substantial decline in occupancy at severely burned sites is unlikely to reflect a temporary loss of individuals that will soon be replaced by colonization, but rather reflects a direct loss of suitable habitat that will likely not be replaced for many decades. Moreover, we found the scorched remains of one adult spotted owl

from a severely burned site (Supplementary Figure 7), indicating that, in some instances, this highly vagile species was unable to avoid this rapidly moving fire. It is not unreasonable to suspect that less vagile old-forest specialists will be equally—and perhaps more—impacted by megafires like the King Fire. Collectively, these findings suggest that megafires constitute an additional mechanism by which climate change will threaten old-forest species, along with previously recognized climate-associated stressors such habitat shifts, physiological impacts, and changes in community interactions (Dawson et al. 2011).

Conclusions

Our study demonstrated that increasingly frequent megafires pose a threat to spotted owls and likely other old-forest species and, as a result, suggests that forest ecosystem restoration and old-forest species conservation may be more compatible than previously believed. Restoration practices that can demonstrably reduce the frequency of large, high-severity fires and reintroduce low- to moderate-severity fire as the dominant disturbance regime will likely benefit both dry-forest ecosystems and old-forest species such as spotted owls. However, forest restoration efforts that remove key habitat elements and areas of currently suitable habitat could exacerbate the risk of extirpation in the short-term before the long-term benefits of restored fire regimes are realized, particularly in light of the present deficit in large and old trees in natural landscapes (Tempel et al. 2015a). Rather, implementing fuels and restoration treatments outside of key habitats (e.g., nesting and denning areas) is more likely to minimize short-term impacts and ensure that old-forest species persist until forest resiliency objectives are achieved (Stephens et al. 2014a). The calculus behind these trade-offs, however, is complex and depends on several considerations that merit additional research such as the magnitude of short-term impacts that treatments impose on old-forest species, the relative increase in the frequency of severe fire as a function of climate

change, and the efficacy of forest restoration for reducing both severe fires and tree mortality from drought and insects (Asner et al. 2015a). Managers and policy-makers will be faced with challenging decisions regarding the pace and scale of forest restoration efforts in light of scientific uncertainty and conflict among stakeholders (Redpath et al. 2013). We suggest, however, that old-forest species should not be viewed as an impediment to forest restoration objectives; rather, ensuring the persistence of old-forest species such as spotted owls, northern goshawks (*Accipiter gentilis*), pileated woodpeckers (*Dryocopus pileatus*), Pacific fisher (*Pekania pennanti*), American marten (*Martes americana*), and other species can serve as a barometer for the successful restoration of the ecosystems they inhabit.

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Figure legends

Figure 1. A female California spotted owl (*Strix occidentalis occidentalis*) within the Eldorado Density Study Area in the central Sierra Nevada, California.

Figure 2. The geography and historical context of the 2014 King megafire. (a) The distribution of occupied and unoccupied spotted owl sites in 2015 within our 23-year demographic study area, which was located ~20 km west of Lake Tahoe, California. Elevation is represented by brown shading (darker brown = low elevation, lighter brown = high elevation) and ranges from approximately 150 to 3000 m. (b–d) A comparison of the King Fire to all California fires since 1984 in terms of area of high-severity burn (b), total fire size (c), and proportion burned at high-severity (d); the solid black lines represent the 50th percentile, the dashed black lines represent the 95th percentile, and the dashed red lines represent the 2014 King Fire.

Figure 3. Before–after control–impact and population analyses. (a) The continuous relationship between the proportion of an owl site that burned at high-severity and the probability of site extinction. (b–d) Colonization (b), extinction (c), and occupancy (d) probabilities for owl sites that experienced different degrees of high-severity burn both pre- and post-fire. (e) Annual estimates of occupancy (ψ) over the study period, where the black line represents a segmented regression function fitted to the mean occupancy for years 1993–2014 (Supplemental Figure 4) demonstrating the periods of decline and subsequent stability before the 2014 King Fire (solid red circle). (f) Annual estimates of rate of change in occupancy (λ) over the study period, where the dashed black line at $y = 1$ indicates a stable rate of change, and the solid red circle indicates

the rate of change after the 2014 King Fire. The black curved lines in (a) and all error bars in (b–f) represent ± 1 SE of the mean.

Figure 4. Distribution of spotted owl foraging locations following a megafire developed from 985 GPS locations from nine owls (individuals represented by different colors) during the 2015 breeding season in relation to the 2014 King Fire (d). Inset examples (a–c) of foraging locations for three owls (small solid-colored circles) and the area defined as available habitat (large open black circles) compared to a minimum convex polygon (black dashed polygon) demonstrate the owls' apparent avoidance of the high-severity burned area. Burn severity for the King Fire is displayed in 25% classes as in Figure 2a. (e) Manly's selection ratios ($\hat{w}$) $\pm 1.96 \times \text{SE}$, where a selection ratio $\hat{w} > 1$ indicates habitat preference, $\hat{w} < 1$ indicates habitat avoidance, and $\hat{w} = 1$ indicates neither preference nor avoidance. (f) Mean ($\pm$ SE) availability and use among nine owls for unburned forests, forests that experienced 0–75% canopy mortality (low-severity), and forests that experienced 75–100% canopy mortality (high-severity).



Figure 1.

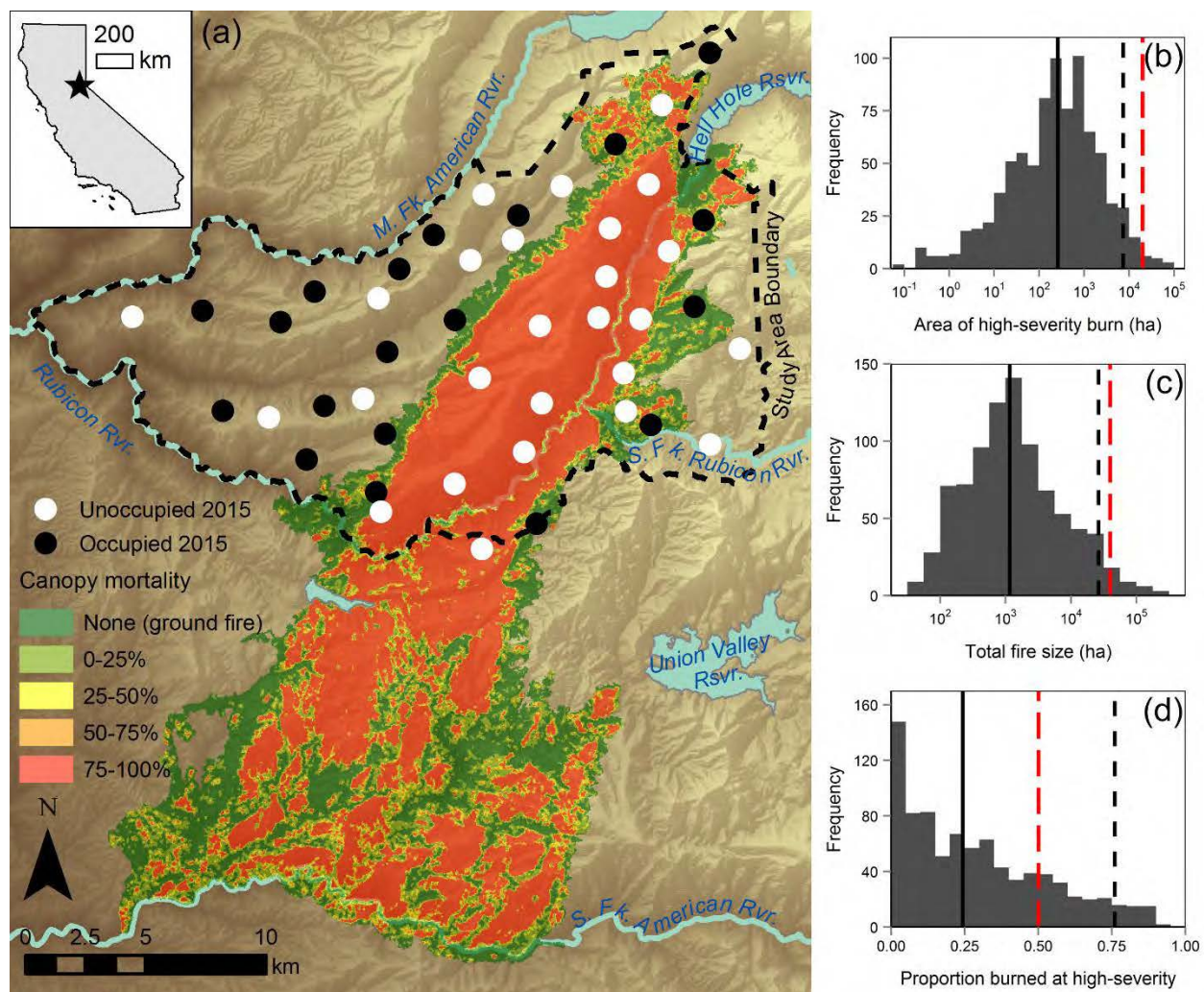


Figure 2.

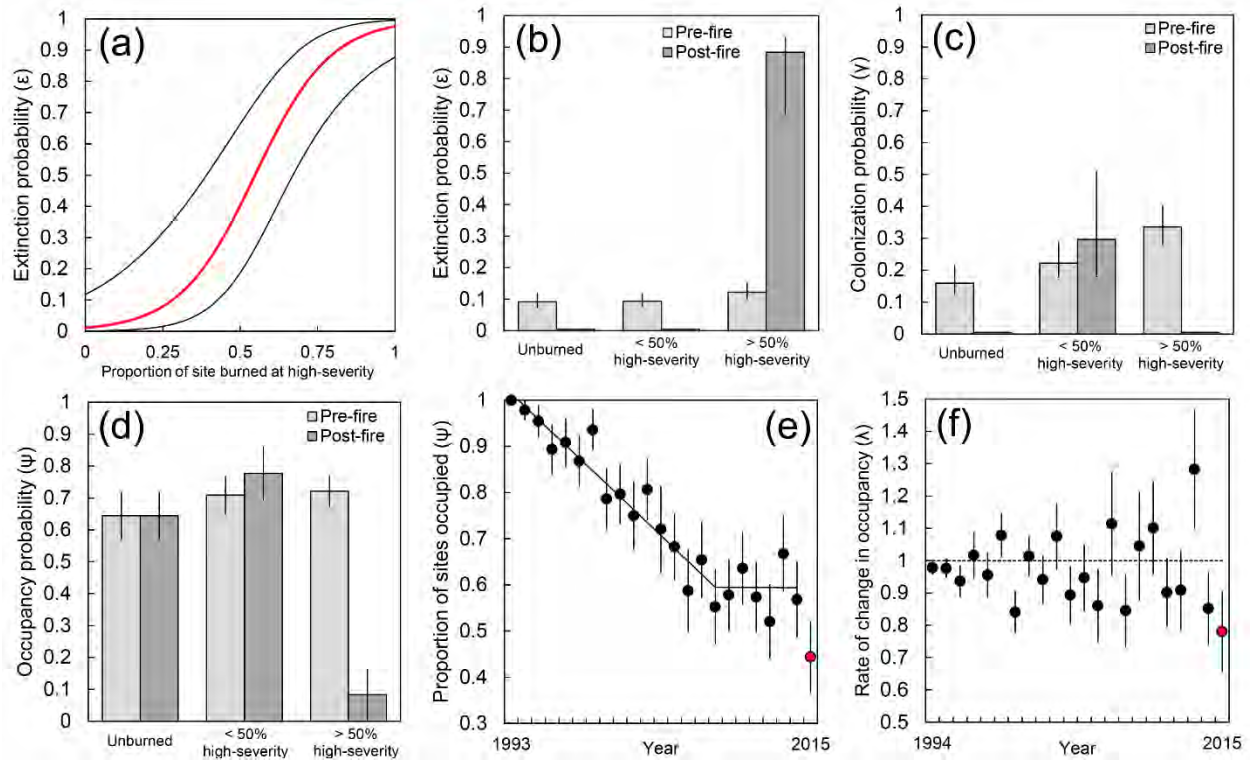


Figure 3.

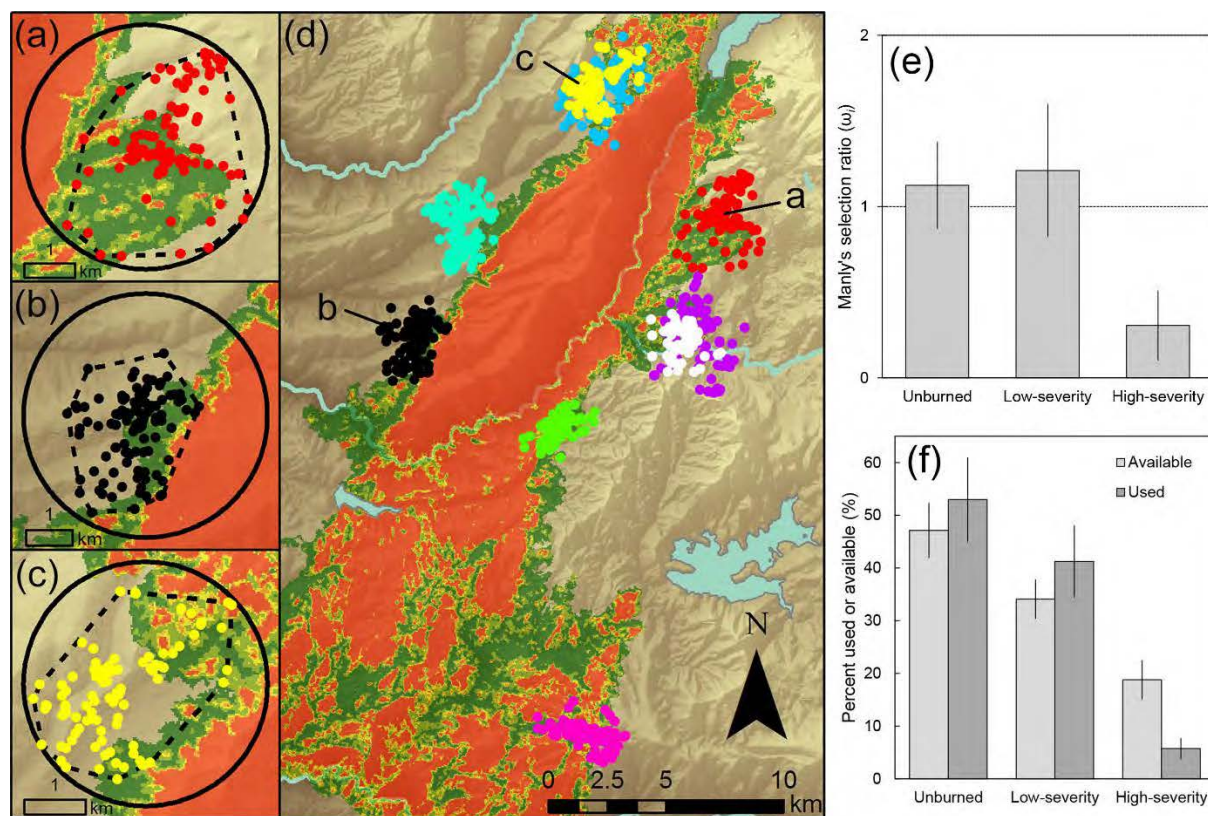


Figure 4.

Supplementary materials

Supplementary Table 1. Distribution of burn severities classes (% overstory canopy mortality) within the spotted owl demographic study area.

	None (ground fire)	> 0 to ≤ 25	> 25 to ≤ 50	> 50 to ≤ 75	> 75 to ≤ 100
Area (ha)	2969.35	1646.5	579.6	471.7	9926.7
Proportion	0.19	0.11	0.04	0.03	0.64

Supplementary Table 2. Model selection results for within-season detection probability (p) for spotted owls on the Eldorado Density Study Area in the central Sierra Nevada, California.

<i>Model</i>	<i>AIC</i>	ΔAIC	<i>w</i>	<i>K</i>
init + repro	3948.47	0	1	70
EL + repro	4044.74	96.27	0	70
T + repro	4047.04	98.57	0	70
lnT + repro	4047.34	98.87	0	70
TT + repro	4048.92	100.45	0	71
repro	4049.56	101.09	0	69
init	4064.01	115.54	0	69
EL	4159.52	211.05	0	69
T	4162.88	214.41	0	69
lnT	4163.72	215.25	0	69
TT	4164.86	216.39	0	70
(.)	4167.14	218.67	0	68

Notes: AIC, Akaike's information criterion; ΔAIC , difference in AIC compared to the model with the lowest AIC value; w , Akaike weight; K , number of parameters in the model.

Symbol definitions: an early-late season covariate (EL) where detection probability (p) for the first five survey periods was different from p for the second five survey periods; an initial detection covariate (init) where p was different for all surveys following the initial detection; a reproductive status covariate (repro) where p was different for owls that had produced offspring in a given year compared to owls that had not produced offspring; as well as linear (T), quadratic (TT), and log-linear (lnT) within-season time trends. We modeled within-season p with covariates but allowed p to vary by year.

Supplementary Table 3. Model selection results from continuous and categorical colonization and extinction BACI analyses.

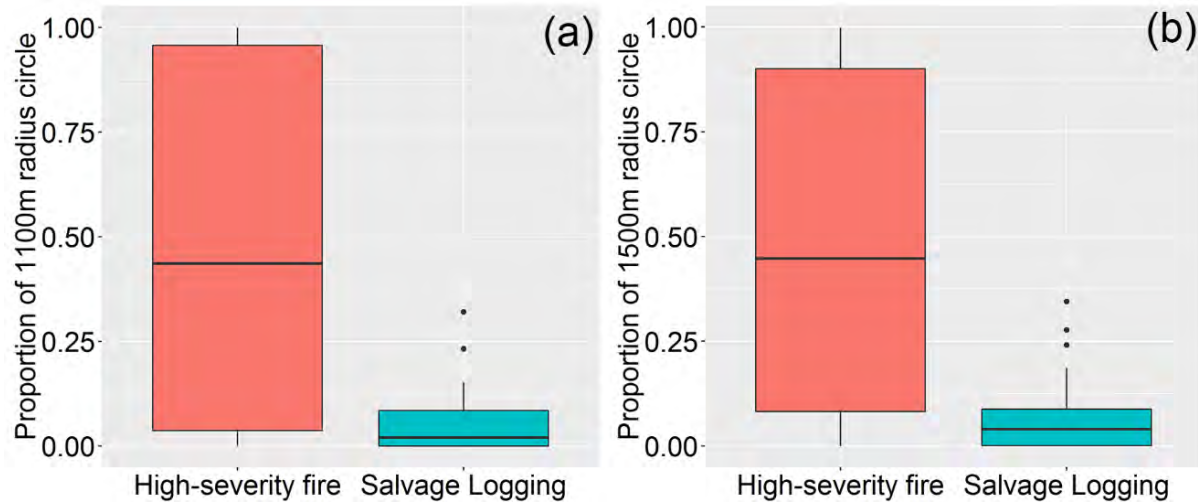
Colonization (γ)				
Continuous analysis				
<i>SiteTreat</i> + <i>SeasonBA</i>	<i>AIC</i>	ΔAIC	<i>w</i>	<i>K</i>
	3925.49	0	0.5205	51
<i>SiteTreat</i> + <i>SeasonBA</i> + <i>SeasonSiteTreat</i>	3926.61	1.12	0.2973	52
<i>Intercept-only</i> (.)	3927.59	2.10	0.1822	49
Categorical analysis				
	<i>AIC</i>	ΔAIC	<i>w</i>	<i>K</i>
<i>SiteTreat1</i> + <i>SiteTreat2</i> + <i>SeasonBA</i> + <i>SeasonSiteTreat1</i>	3924.65	0	0.4207	53
<i>SiteTreat1</i> + <i>SiteTreat2</i> + <i>SeasonBA</i> + <i>SeasonSiteTreat2</i>	3926.51	1.86	0.1660	53
<i>SiteTreat1</i> + <i>SiteTreat2</i> + <i>SeasonBA</i>	3926.56	1.91	0.1619	52
<i>SiteTreat1</i> + <i>SiteTreat2</i> + <i>SeasonBA</i> + <i>SeasonSiteTreat1</i> + <i>SeasonSiteTreat2</i>	3926.65	2.00	0.1548	54
<i>Intercept-only</i> (.)	3927.59	2.94	0.0967	49
Extinction (ϵ)				
Continuous analysis				
	<i>AIC</i>	ΔAIC	<i>w</i>	<i>K</i>
<i>SiteTreat</i> + <i>SeasonBA</i> + <i>SeasonSiteTreat</i>	3915.25	0	0.7249	52
<i>SiteTreat</i> + <i>SeasonBA</i> + <i>SeasonSiteTreat</i> + <i>SalvageLogging</i>	3917.19	1.94	0.2748	53
<i>SiteTreat</i> + <i>SeasonBA</i>	3931.40	16.15	0.0002	51
<i>Intercept-only</i> (.)	3934.41	19.16	0.0001	49
Categorical analysis				
	<i>AIC</i>	ΔAIC	<i>w</i>	<i>K</i>
<i>SiteTreat1</i> + <i>SiteTreat2</i> + <i>SeasonBA</i> + <i>SeasonSiteTreat2</i>	3915.86	0	0.7298	53
<i>SiteTreat1</i> + <i>SiteTreat2</i> + <i>SeasonBA</i> + <i>SeasonSiteTreat1</i> + <i>SeasonSiteTreat2</i>	3917.86	2.00	0.2685	54
<i>SiteTreat1</i> + <i>SiteTreat2</i> + <i>SeasonBA</i> + <i>SeasonSiteTreat1</i>	3929.34	13.48	0.0009	53
<i>SiteTreat1</i> + <i>SiteTreat2</i> + <i>SeasonBA</i>	3929.36	13.50	0.0009	52
<i>Intercept-only</i> (.)	3934.41	18.55	0.0001	49

Notes: AIC, Akaike's information criterion; ΔAIC , difference in AIC compared to the model with the lowest AIC value; *w*, Akaike weight; *K*, number of parameters in the model. *SiteTreat*: a "group" effect, which was a dummy variable that indicated whether a site was a control or impact site that accounted for background differences in occupancy rates at these sites; *SeasonBA*: a "time" effect, which was a dummy variable coding for before and after the fire, which accounted for differences in occupancy rates due to time and not the fire-related impact; *SeasonSiteTreat*: an "after-impact" effect, we included a term that represented impact sites after the fire occurred equivalent to a *SiteTreat* $\times$ *SeasonBA* interaction. We compared models with the *SeasonSiteTreat* term to models without the *SeasonSiteTreat* term to evaluate support for an effect of high-severity fire on occupancy rates (Popescu et al. 2012)

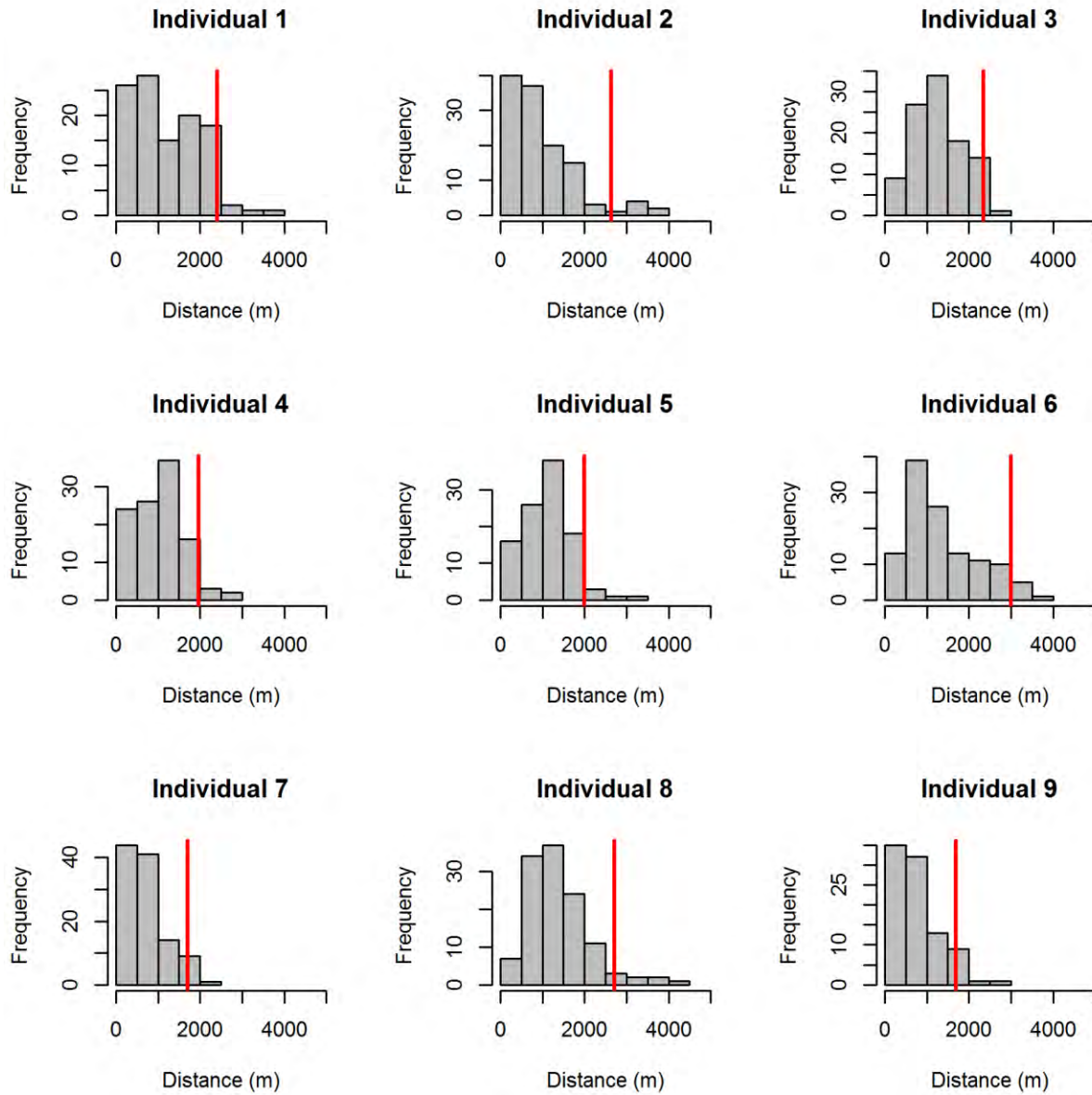
Supplementary Table 4. Model selection results from the annual occupancy trend analysis over the pre-fire years 1993-2014.

<i>Model</i>	<i>AIC</i>	ΔAIC	<i>K</i>	<i>RSS</i>	<i>n</i>
Segmented	-132.58	0.00	4	0.04	22
Quadratic	-126.62	5.95	4	0.05	22
Linear	-123.62	8.95	3	0.06	22
Log-linear	-114.60	17.97	3	0.09	22

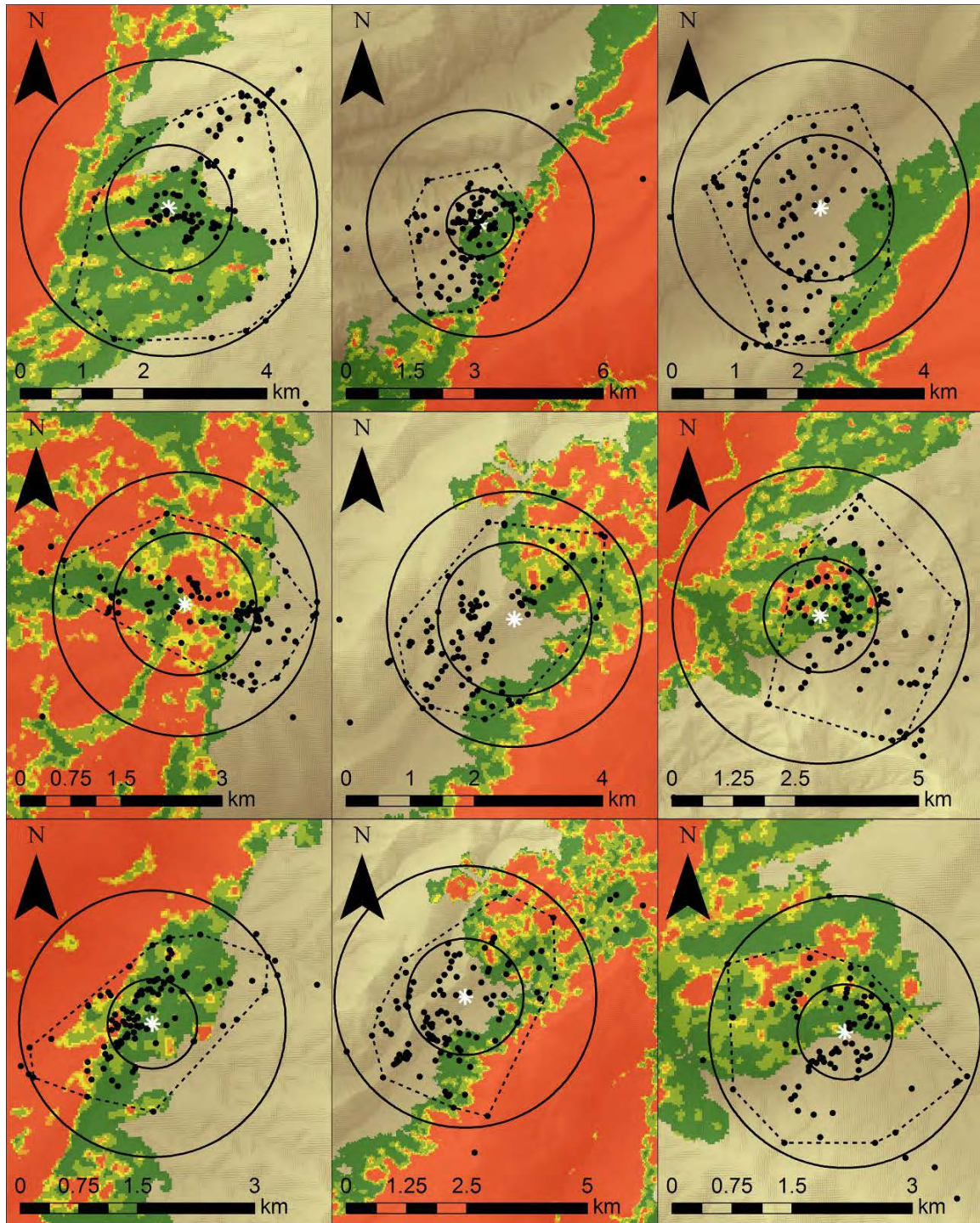
Notes: AIC, Akaike's information criterion; ΔAIC , difference in AIC compared to the model with the lowest AIC value; *K*, number of parameters in the model; *RSS*, residual sum of squares; *n*, number of data points (years) to which linear models were fitted. AIC was calculated manually using the residual sum of squares from each fitted model (Burnham and Anderson 2002).



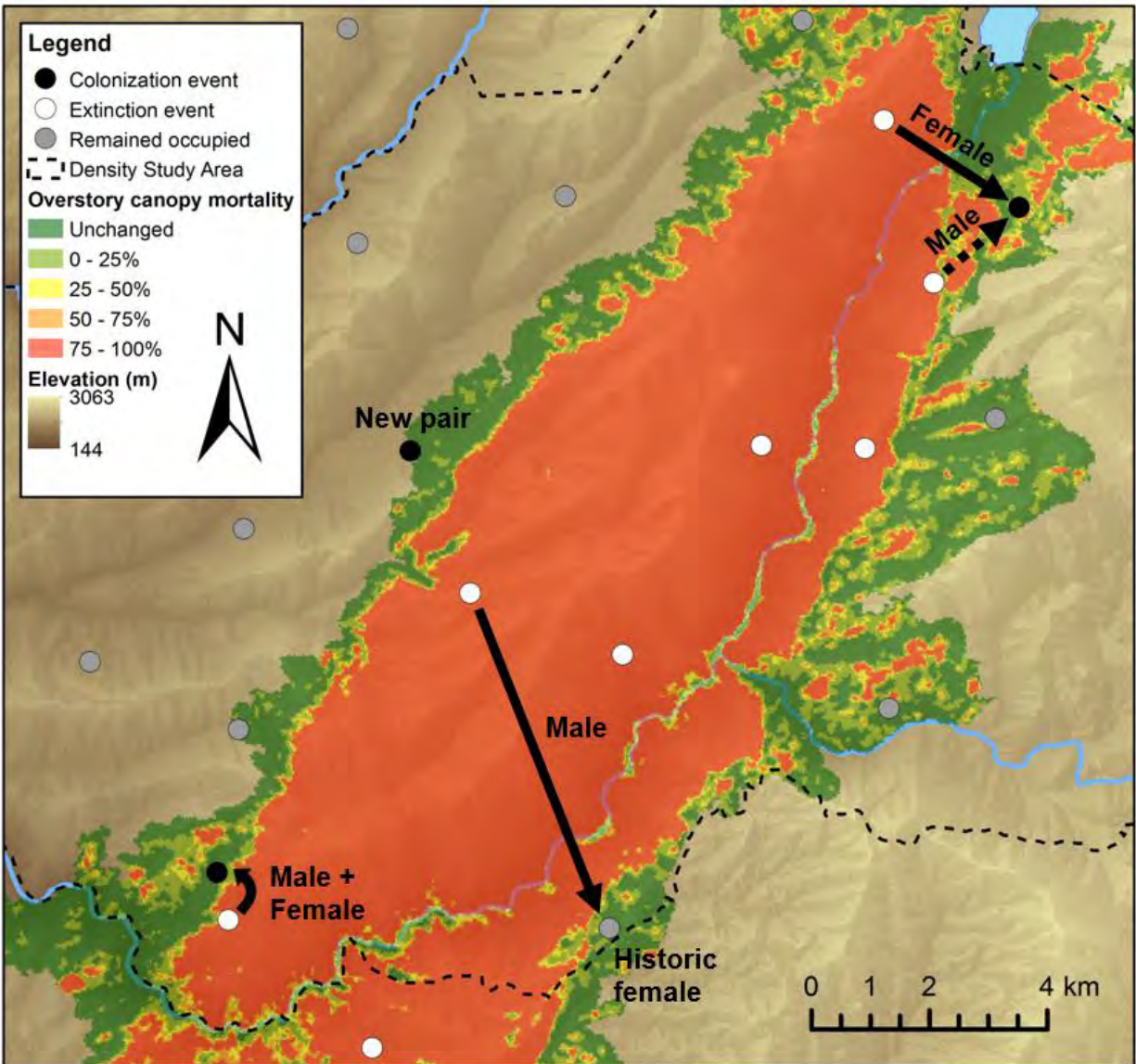
Supplementary Figure 1. Comparison of the extent of high-severity fire and salvage logging within 1100m (a) and 1500m (b) radius circles drawn around spotted owl site centers (long-term average of site nesting and roosting locations)). The circle with an 1100m radius represented the size of an actively defended spotted owl territory, equal to approximately one-half the mean nearest neighbor distance between owl territory centers on the Eldorado Density Study Area (Tempel et al. 2014a); the circle with a 1500m radius represented a larger home range that may support additional habitat use such as foraging activities (Bond et al. 2009, Lee and Bond 2015). We carried out our analysis of the effects on spotted owl site occupancy at the 1100m scale. Note that at both scales, high-severity fire affected a large proportion of territories relative to the proportion of territories affected by salvage activities. This, along with no empirical support for an effect of salvage logging on spotted owl site occupancy, supports the inference that high-severity fire—not post-fire salvage logging—appeared to drive declines in site occupancy.



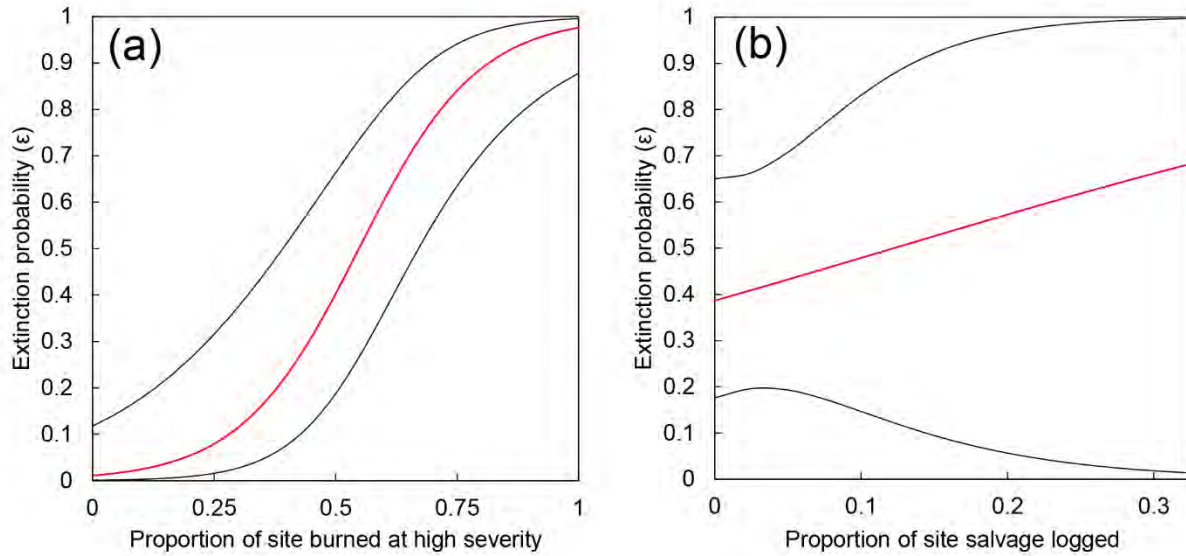
Supplementary Figure 2. Frequency distributions of foraging distance from activity center (i.e. geometric mean of 2015 roosting, nesting, and daytime capture locations) of nine GPS-tracked spotted owls. The red solid line on each graph represents the 95th percentile of foraging distances, which we used as the radius of a circle that defined available habitat for each owl in our habitat selection analysis.



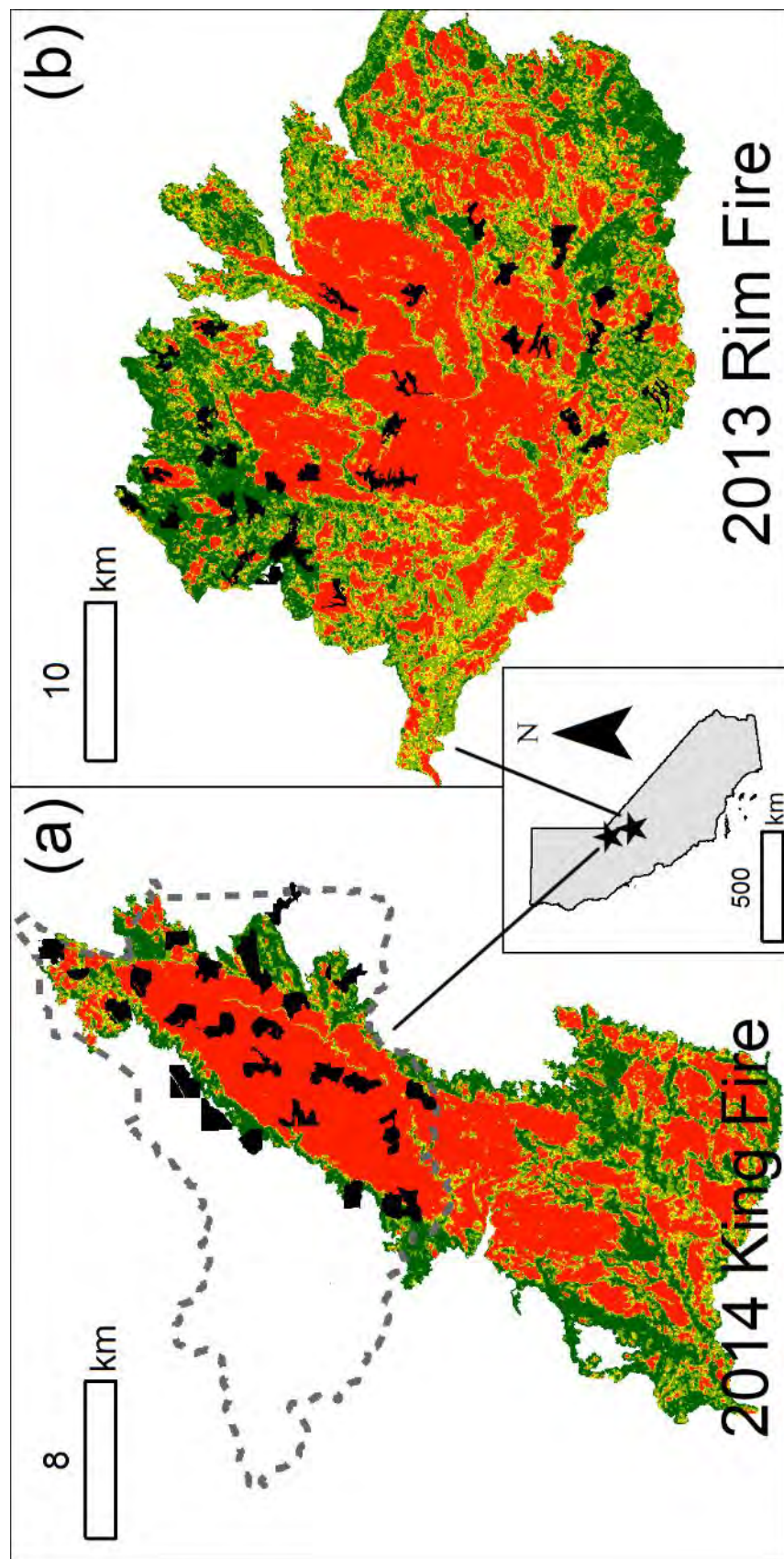
Supplementary Figure 3. Foraging locations for nine GPS-marked spotted owls following the 2014 King Fire (black dots). The largest black circle in each panel represents “available” habitat considered in our habitat selection analysis (i.e. a circle with a radius equal to the 95th percentile of foraging distances for each bird). The smallest black circle in each panel represents a circle with a radius equal to the 50th percentile of foraging distances (for illustrative purposes only). The black dashed polygon in each panel represents a minimum convex polygon fitted to all foraging locations within the 95th percentile of foraging distances.



Supplementary Figure 4. Relocation of marked spotted owls following the 2014 King Fire. Black arrows begin at the site occupied by a given owl in 2014 and end pointing to the site the same owl occupied in 2015. Solid black lines represent confirmed movements (via re-sighting of unique color bands). The single dashed line represents a putative relocation by a male spotted owl that was not confirmed by re-sight, but was thought to be the same male based on behavioral observations.



Supplementary Figure 5. A comparison of the influence of high-severity fire (a; see Fig. 1A in manuscript) and post-fire salvage logging operations (b) on site extinction probability following the 2014 King Fire. The proportion of a spotted owl site that burned at high-severity fire was a strong predictor of site extinction ($\beta_{\text{high-severity}} = 8.23$, 95% confidence interval [CI] = 0.92 to 15.54), while post-fire salvage logging was an uninformative parameter (see Table S2) with no statistical relationship with site extinction probability ($\beta_{\text{salvage}} = 3.77$, 95% confidence interval [CI] = -27.85 to 35.39). The plot in panel (a) was generated with coefficients from the extinction model from the continuous extinction analysis with the lowest AIC, while the plot in panel (b) was generated with coefficients from the extinction model from the continuous extinction analysis containing the ‘*SalvageLogging*’ term (second-lowest AIC) while holding the value for high-severity fire at 0.5. Red lines represent the mean point estimate and black lines represent the mean ± 1 SE.



Supplementary Figure 6. A comparison of the 2014 King Fire (a) and the 2013 Rim Fire (b). Burn severity is represented as overstory canopy mortality by the convention of Fig. S1. Black polygons represent ~121 ha spotted owl Protected Activity Centers (PACs) that were coincident with each respective study area (Lee and Bond 2015). Note that the burn pattern of the 2014 King Fire (a; present study) produced one large, contiguous patch of high-severity fire that left little intact habitat for spotted owls occupying severely burned PACs; while the 2013 Rim Fire (b) burned with greater heterogeneity, potentially leaving small, intact patches of suitable habitat for owls that may have occupied adjacent PACs that were severely burned. These differences in burn patchiness could partly explain the apparent differences in owl response to megafires.



Supplementary Figure 7. Fire-scorched tarsometatarsus bones of a California spotted owl and USFWS aluminum locking leg-band recovered from a historic spotted owl territory following the 2014 King Fire. When recovered, the bones were inside of the leg-band. The individual owl that apparently perished in the fire was a male identified as one of the most productive individuals (in terms of total number of offspring fledged) over the 23-year study period (M. Z. Peery, unpublished data). Photo by Sheila Whitmore.

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Chapter 2 - Declining old-forest species as a legacy of large trees lost

Gavin M. Jones¹, John J. Keane², R.J. Gutiérrez^{1,3}, M. Zachariah Peery¹

¹ *Department of Forest & Wildlife Ecology, University of Wisconsin-Madison, 237 Russell Laboratories, 1630 Linden Drive, Madison, WI 53706, USA;* ² *U.S.D.A. Forest Service, Pacific Southwest Research Station, Davis, CA 95618, USA;* ³ *Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, MN 55455, USA*

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Abstract

Global declines in large old trees from selective logging has degraded old-forest ecosystems, which could lead to delayed declines or losses of old-forest associated wildlife populations (i.e. extinction debt). We applied the declining population paradigm and explored potential evidence for extinction debt in an old-forest dependent species across landscapes with different histories of large tree logging. We tested hypotheses about the influence of forest structure on territory extinction dynamics of the spotted owl (*Strix occidentalis*) using detection/non-detection data from 1993-2011 across two land tenures: national forests, which experienced extensive large tree logging over the past century, and national parks, which did not. Our study area was located in montane forests of the Sierra Nevada, California, USA. Large tree/high canopy cover forest was the strongest predictor of extinction rates, and explained 26-77% of model deviance. Owl territories with more large tree/high canopy cover forest had lower extinction rates, and this forest type was ~4 times more prevalent within owl territories in national parks ($\bar{x} = 19\%$ of territory) than national forests ($\bar{x} = 4\%$ of territory). As such, predicted extinction probability for an average owl territory was ~2.5 times greater in national forests than national parks, where occupancy was declining ($\hat{\lambda} < 1$) and stable ($\hat{\lambda} = 1$), respectively. Large tree/high canopy cover forest remained consistently low, but did not decline, during the study period on national forests while owl declines were ongoing – an observation consistent with an extinction debt. In identifying a linkage between large trees and spotted owl dynamics at a regional scale, we provide evidence suggesting past logging of large old trees may have contributed to contemporary declines in an old-forest species. Strengthening protections for remaining large old trees and promoting their recruitment in the future will be critical for biodiversity conservation in the world's forests.

Introduction

Large old trees have declined across nearly all global ecosystems, in part because their high commercial value has led to logging pressure that outpaces sometimes centuries-long recruitment and development (Lindenmayer et al. 2012). Agriculture (Laurance et al. 2014), fire (Jones et al. 2016a, Westerling 2016), and disproportionate drought susceptibility (Bennett et al. 2015) also increasingly threaten large old trees and conservation of old-forest ecosystems (Lindenmayer and Laurance 2017). Loss of large old trees is a major contributor to habitat loss for many globally endangered old-forest dependent (hereafter ‘old-forest’) species such as the orangutan (*Pongo spp.*) in southeast Asia (Wich et al. 2003), the marbled murrelet (*Brachyramphus marmoratus*) and northern spotted owl (*Strix occidentalis caurina*) in western North America (Noon and Blakesley 2006, Raphael 2006), the Leadbeater’s possum (*Gymnobelideus leadbeateri*) in southeast Australia (Lindenmayer et al. 2013), and the Blakiston’s fish owl (*Bubo blakistoni*) in the Russian Far East and Japan (Slaght et al. 2013).

Like large old trees, many old-forest species have “slow” life histories with long generation times and high adult survival, which increases vulnerability when environments change rapidly (Webb et al. 2002). Long-lived individuals may persist for many years in marginal or degraded forests long after critical breeding habitat elements such as large old trees are lost or substantially reduced, but gradually these individuals die off and may not be replaced. Delayed population declines or local extinctions resulting from prior habitat loss or degradation is termed “extinction debt”, which can be assessed across different levels of organization (e.g., individual species vs. community) and may be evaluated at spatial scales ranging from local extirpation within a habitat patch to regional or global extinction of a species. Extinction debt challenges the ability of scientists to establish causal links between habitat loss and population declines of individual species (Kuussaari et al. 2009). Uncertainty about population status or

causes of decline, then, could delay implementing conservation measures for old-forest species and the restoration of degraded old-forest ecosystems. Moreover, this uncertainty creates political opportunities to undermine governmental or social responses to make corrective changes (Oreskes and Conway 2010).

Global challenges facing the conservation of large old trees and old-forest associated species (Lindenmayer and Laurance 2016) have led some to propose new and more rigorous policies for ensuring their protection and improving conservation outcomes (Lindenmayer et al. 2014). Nevertheless, if an extinction debt has already been created, population declines of old-forest species may continue to occur long after policies protecting large old trees are put into place. Here, we studied the potential long-term (multi-generational) impacts of large tree loss on an old-forest species, the spotted owl (*S. occidentalis*), across a large mountain ecosystem by comparing forest conditions and population dynamics between national parks (long-established protected areas) and national forests (areas that experienced widespread large tree logging but more recent protections). Following a century of extensive, intensive, and selective logging of very large trees on national forests (e.g., ~90-215 cm dbh; Laudenslayer & Darr, 1990; Stephens et al., 2015), forest policy was enacted immediately prior to our study to conserve remaining old-forest elements such as large trees and multi-layered canopy around spotted owl activity centres (Verner et al. 1992).

Despite these recent protections, we hypothesized that this historical loss of large trees on national forests could be associated with contemporary population declines, or an extinction debt, for spotted owls. In testing this hypothesis, we treated protected areas (national parks) as “contemporary reference landscapes” (Meyer 2015, Collins et al. 2016, Miller et al. 2016), because prohibition of logging within national park boundaries over the past century has largely

preserved historical forest structure and prevalence of very large and old trees (Beesley 1996, Lydersen and North 2012). Thus, in principle, contemporary forests characteristics in spotted owl territories on national parks (e.g., large trees) might more closely represent forests characteristics that might have existed on national forests if protections for large trees had been established long ago.

Comparing spotted owl populations on national forests and national parks, then, allowed us to diagnose causes of decline (Caughley 1994, Green 1995, Peery et al. 2004) for a species considered to be a barometer of old-forest wildlife community health in western North America (Simberloff 1998). Despite the fact that the spotted owl is one of the most intensively studied species in the world with 40 years of demographic and ecological research across its range, no definitive causal link between ongoing owl declines and changes in habitat has been established. Here, we offer insight into this elusive question by applying the concept of extinction debt and provide an unprecedented case study about the potential ecological legacies of large tree loss on increasingly rare global old-forest species and ecosystems (Lindenmayer et al. 2012, 2014).

Methods

Study areas and logging histories

Four spotted owl study areas – Lassen (LAS), Eldorado (ELD), Sierra (SIE), and Sequoia-Kings Canyon (SKC) – span nearly the entire latitudinal range of California’s Sierra Nevada (Fig. 1). Elevations range from 300–3,050 m across the four study areas, and the climate is Mediterranean (Tempel et al. 2016). LAS, ELD, and SIE study areas are primarily located within national forests (with intermixed private land), whereas SKC occurs within two national parks of the same name. While Sierran mixed-conifer montane forest is the primary vegetation type within owl territories across all study areas (Tempel et al. 2016), contemporary structure of these forests

has been strongly affected by different management legacies across the two land tenures (i.e., national forests vs. national parks).

Very large (e.g., >125 cm dbh) old trees were a dominant feature throughout the Sierra Nevada at the turn of the twentieth century (Safford & Stevens, 2017; McKelvey & Johnston, 1992). Several national parks including Sequoia (of SKC) were established in 1890 (Kings Canyon National Park adjoined in 1940), and the prohibition of logging within park boundaries over the following century largely acted to preserve historical forest structure and prevalence of very large and old trees (Beesley 1996, Lydersen and North 2012). In contrast, logging activities on what would eventually become Sierra Nevada national forest lands were well underway by 1900 (Beesley 1996, Thomas 2008). Commercial logging (i.e. selective removal of very large trees) on Sierra Nevada national forests increased from ~470,000 cubic meters (m^3) year^{-1} in the 1870s to its peak during the 1940s when timber production reached 4.5 million m^3 year^{-1} . Timber production remained reasonably high thereafter (generally between 2.8 and 3.8 million m^3 year^{-1}) for several decades before a near-historic peak in timber production in 1990 when production again neared 4.5 million m^3 year^{-1} (McKelvey and Johnston 1992).

Concern about the continued and cumulative loss of large trees required by spotted owls reached a highpoint around the same time and as a result, in 1992, logging of ≥ 76 cm dbh trees on national forests was restricted (with some allowable exceptions for equipment operability), as was almost all logging within 121 ha areas around known owl nest and roost sites (Verner et al. 1992, USFS 2004). Our study on spotted owls began in 1993, immediately following near-peak logging activity and subsequent restrictions. Recent work has established that national forest lands indeed contain greater prevalence of younger trees that are smaller in diameter and height (Laudenslayer and Darr 1990, Stephens et al. 2015) and significantly fewer trees in the largest

size classes compared to historical baselines (McIntyre et al., 2015; Stephens et al., 2015; Collins et al., 2017; Safford & Stevens, 2017). Given that SKC did not experience the same history of selective logging and forest structural change as the three study areas on national forests, we treated it as a contemporary reference landscape for evaluating differences in forest structure and owl population dynamics between land tenures.

Owl surveys

As part of prior work, we have established that temporal changes in occupancy rates of spotted owl territories (i.e., based on detection/non-detection data) can provide inferences regarding overall population trends that are comparably reliable to estimates of overall population trends based on changes in abundance (Tempel and Gutiérrez 2013, Tempel et al. 2014b, Conner et al. 2016). As such, we conducted detection/non-detection surveys for spotted owls at 275 owl territories located during breeding seasons (Apr-Aug on LAS and ELD; Mar-Sept on SIE and SKC) across the four study areas over a 19-year period (1993-2011). All study areas consisted of a core study area that we surveyed completely in each year of the study (i.e., both the areas containing owl territories and all areas not containing known owl territories within the core area were surveyed every year). In addition, we added some owl territories over time, either as an expansion of the core area (LAS) or as individual “satellite” territories (i.e., adjacent to, but not part of, the core area) to increase owl sample sizes for demographic analysis (LAS and ELD), and we dropped a portion of SKC in 2006 (Tempel et al. 2016). We surveyed all satellite territories used in our occupancy analyses for a minimum of 3 years; most territories in the core areas were surveyed for ≥ 15 years.

We located spotted owls by imitating their vocalizations (vocal lure) for 10 minutes at a survey station or used vocal lures while walking along a survey route. We then considered sites

to be a territory where owls responded to vocal lures, and were subsequently observed either roosting or nesting during diurnal hours. Some surveys occurred prior to 1993 but previous analyses have determined that survey coverage and effort required for population analyses (such as ours presented here) became adequate beginning in 1993 (Tempel and Gutiérrez 2013, Tempel et al. 2016). We did not survey all territories in all years of the study. However, of the 275 owl territories used in the study, ≥ 205 were surveyed in all but the first year of the study (in 1993, 187 owl territories were surveyed). The average number of owl territories surveyed annually was 239 (87% of all known territories; standard error = 21 territories), with a maximum of 263 territories surveyed in 2008 (95.6% of all known territories). Moreover, while most intervening area between territories was intensively surveyed each year, spotted owls on our study areas rarely established new territories outside of territories located in the early stages of the study. For example, the most recently located territory on the ELD was found in 1997. We included all surveys in our analyses but excluded nocturnal detections of unknown owls (i.e., owls that were not re-sighted by unique colour leg-bands as part of a concomitant mark-recapture study) that occurred outside of a delineated territory boundary (see below for information on owl territories) using a Geographic Information System (GIS) to eliminate potential spurious positive detections of owls not occupying the nominal territories. A survey in which no owls were detected needed a total duration of ≥ 30 min to be included as an absence record. Extensive details about each study area and additional survey details can be found in Tempel et al. (2016).

Sampling units and vegetation covariates

We treated owl territories as sampling units, where a territory had at least one owl detection during diurnal hours in ≥ 3 years. For quantifying habitat covariates within spotted owl territories, we first calculated the geometric centre of each territory as the average spatial coordinates of all

nest and roost locations across all years in the territory. We then calculated the mean nearest-neighbour distance among territory centres for each study area as the average distance between each territory centre and the centre of its nearest neighbouring territory. Thus, the location of owl territories was assumed to remain the same throughout the study period, and territories in each study area were assumed to be of equal size based on the nearest neighbour distance. In a recent meta-analysis (Tempel et al. 2016) we defined the spatial extent of a territory as a circle around each territory centre with a radius of half of the mean nearest-neighbour distance. The resulting territory size for each study area decreased along a north–south gradient: Lassen = 639.4 ha (1,427-m radius), Eldorado = 399.5 ha (1,128-m radius), Sierra = 301.6 ha (980-m radius), and Sequoia–Kings Canyon = 254.3 ha (900-m radius). This process nearly eliminated spatial overlap among adjacent territory circles. In the present paper, we defined territories as hexagons instead of circles with areas and geometric centres equal to those determined by Tempel et al. (2016) to facilitate integration into concurrent projects using spatial population models (e.g., HexSim; Schumaker, 2015).

We defined site-specific covariates based on two vegetation variables within owl territories using the ‘GNN’ (Gradient Nearest Neighbour) forest structural maps produced by the Landscape Ecology, Modeling, Mapping & Analysis (LEMMA) research group (Oregon State University, Corvallis, OR, USA). GNN is an imputation method used by LEMMA that integrates regional forest inventory plots with Landsat imagery to produce fine-scale (30-m resolution) and large-domain (currently the entire land area for the U.S. states of Washington, Oregon, and California) vegetation structure and species composition maps. The GNN approach is one variation of nearest neighbour imputation methods that uses (i) a neighbourhood value of $k=1$ as the number of neighbours imputed to each cell and (ii) direct gradient analysis as the ‘distance’

metric (see <https://lemma.forestry.oregonstate.edu/methods>). The first variable was the quadratic mean diameter of dominant and codominant trees in each 30×30 m pixel (“QMD_DOM”).

Quadratic mean diameter (QMD) is a commonly used metric in forestry that more strongly reflects the influence of large trees on stand tree size classifications than arithmetic mean (Curtis and Marshall 2000). The second variable was the percent canopy cover of live trees in each pixel (“CANCOV”).

Large trees are a key feature of spotted owl nest sites (Gutiérrez et al. 1992), and owl site occupancy has been positively correlated with large trees (> 61 cm dbh) and high canopy cover (> 70%) at nest areas (Blakesley et al. 2005). However, forests with intermediate canopy cover (40-70%) can constitute spotted owl nesting or roosting habitat if large, remnant trees are present (Moen and Gutiérrez 1997, Hunter and Bond 2001), and recent work found that both medium and high canopy cover were associated with spotted owl occupancy in the Sierra Nevada (Tempel et al. 2014a, 2016, Jones et al. 2016b). Thus, we estimated the proportion of each owl territory containing the following five covariates: large trees ($\text{QMD} \geq 61$ cm) regardless of canopy cover class; high canopy cover (> 70% cover) regardless of tree size class; as well as the spatial intersection ($\cap$; see Fig. 2) of large trees and high canopy cover, large trees and medium canopy cover (40-70% cover), and medium trees ($\text{QMD} = 30\text{-}61$ cm) and high canopy cover. These proportions were calculated by dividing the number of 30×30 m pixels in the territory for a particular variable divided by the total number of 30×30 m pixels in the territory. Several of the predictor variables were highly collinear (e.g., $r = 0.7\text{-}0.9$), so we developed models that contained a single predictor variable and used AIC to identify which predictor variables had the most explanatory power (see below).

We adopted the above tree size classes because they are commonly used by foresters (Verner et al. 1992, Blakesley et al. 2005), although the large old trees used by owls for nesting are typically larger than 61 cm dbh (e.g., 125-150 cm dbh; North et al., 2000). Median QMD in the ≥ 61 cm dbh size class was 75.5 and reached a maximum of 279 (Fig. S1). Finally, for each forest structure variable listed above, we averaged the within-territory covariate values across all years (1993-2011) to produce a single, static territory-level covariate that varied across space (but was averaged over time), because nearly all variation in the covariates was spatial rather than temporal (large among-territory differences). Ranges of covariate values for each study area are provided in Table 1.

Statistical analysis and model selection

We used multi-season occupancy models to assess territory occupancy dynamics on each study area separately (Tempel et al. 2016) using program PRESENCE 11.5. The models contained parameters for initial occupancy (ψ_1), local extinction (ϵ_t), local colonization (γ_t), and detection probability ($p_{t,j}$) (MacKenzie et al. 2003). Our primary sampling periods (t) were breeding seasons (i.e., years), and our secondary sampling periods (j) were bimonthly periods within each breeding season (April 1-15, April 16-30, etc.). No surveys were conducted on SKC in 2005 so we fixed p , ϵ , and γ for that year to zero. We allowed colonization to vary as a year-specific effect rather than a function of covariates because (i) colonization may be related more to site availability than site conditions, and (ii) we were interested in factors associated with elevated extinction rates.

We used multi-stage modelling (Tempel et al. 2016). At each stage, we ranked models using AIC (Burnham and Anderson 2002) to select the base model for the next stage. We first modelled p as a function of the above forest structure covariates and within- and among-year

temporal trends (i.e., linear, log-linear, or quadratic trends in p) while γ and ε varied by year. We then examined linear, logarithmic, and quadratic forms of covariates on ψ_1 while γ and ε varied by year. Finally, we examined the potential effects of covariates on ε while γ varied by year, again considering linear, logarithmic, and quadratic covariate forms because previous owl studies showed evidence of non-linear relationships (Dugger et al. 2005, Forsman et al. 2011). We used analysis of deviance to assess the amount of variation explained by model covariates. This approach compares deviance explained by the covariates in a model with the amount of deviance not explained by these covariates, thus providing an estimate of r^2 for the model (Skalski et al. 1993). The global model for the analysis of deviance consisted of the top-ranked model for the given study area with additional annual effects for ε , and the constant model consisted of the best detection structure with only an intercept for ε (Tempel et al. 2016).

We used the best p model from the first stage with year-specific γ and ε to obtain derived estimates of ψ_t which we used to calculate the geometric mean of the rate of change in occupancy ($\hat{\lambda}$) and estimated the realized change in occupancy (Δ_k) for each study area. We calculated variance for $\hat{\lambda}$ and Δ_k using the delta method (Powell 2007).

Results

We found that local extinction rates were high when owl territories contained less forest characterized by large trees (≥ 61 cm dbh) and high canopy cover ($>70\%$ cover), and extinction rates declined as this forest type increased (Fig. 3). Indeed, local extinction was best explained by the proportion an owl territory containing large trees/high canopy cover forest, as evidenced by the presence of this covariate in the top models on three of the four study areas (ELD, SIE, SKC) having nearly all (88-97%) of AIC weight (Table S1). The top three models for the fourth study area (LAS) were closely competing (within 1 AIC), containing parameters for large trees

only, large trees and high canopy cover, and high canopy cover only, respectively (Table S1), although the coefficient estimate for the high canopy cover only model was imprecise (Table S2).

No other models were competitive with the large trees/high canopy cover model for any study area (all >5 AIC from top model; Tables S1 and S3). However, models containing other forest structural covariates such as high canopy cover, medium trees and high canopy cover, and large trees and medium canopy cover sometimes outperformed the null model and yielded coefficient estimates with 95% confidence intervals that did not overlap zero (Table S2), suggesting they may be biologically meaningful. Analysis of deviance showed that the covariate for large trees/high canopy cover explained 28%, 26%, 77%, and 53% of the variation in local extinction rates on LAS, ELD, SIE, and SKC, respectively.

The median proportion of an owl site containing large trees/high canopy cover forest on national forests (LAS, ELD, SIE) was similar, ranging from 0.03-0.06 (Table 1). These values corresponded with higher predicted rates of local extinction ($\epsilon = 0.06-0.074$) and ongoing occupancy declines according to estimates of the geometric mean rate of change in occupancy ($\hat{\lambda} < 1$) and realized change in occupancy ($\Delta_k < 1$) over the period 1993-2011 (Table 2). By contrast, the median proportion of large trees/high canopy cover forest within owl territories on national parks (SKC) was 0.19 (Table 1), which was associated with much lower predicted extinction rates ($\epsilon = 0.027$) and stable occupancy ($\hat{\lambda} = 1$, $\Delta_k = 1$) (Fig. 3, Table 2). Thus, extinction probability at a “typical” owl territory was ~2.5 higher on average in national forests (LAS, ELD, SIE) than national parks (SKC). A post-hoc comparison showed that estimates of realized change in occupancy (Δ_k) for LAS, ELD, and SIE were not statistically different from one another, but all were significantly lower than SKC (Table 2).

The extent of large trees/high canopy cover forest within owl territories differed among study areas ($F_{3,271} = 38.3$, $P < 0.01$), and was ~4 times greater in national parks than in national forests on average (Table 1). Furthermore, this forest type did not appear to decline within owl territories on national forests over the study period (Fig. 3, Fig. S2), suggesting the considerable deficit of large tree/high canopy cover forest on national forests may have resulted from historical (as opposed to more recent) logging activities that selectively removed very large old trees (Laudenslayer & Darr, 1990; McKelvey & Johnston, 1992; Stephens et al., 2015; Collins et al., 2017).

Discussion

Extinction debt and restoration opportunities

Our work presents several key inferences suggesting ongoing declines in spotted owl populations on national forests are consistent with an extinction debt, or a legacy effect, resulting from logging of large trees prior to the initiation of our study. First, we found that local extinction rates were consistently higher across a large bioregion (the Sierra Nevada) when large tree/high canopy cover forest was less common in owl territories. Second, large tree/high canopy cover forest was far more common in owl territories in the national parks study area (SKC), where large trees have not been logged. Third, owl populations are declining on all national forest study areas, which contain far less large tree/high canopy cover forest in owl territories than national parks where the owl population is stable. Fourth, although logging activities prior to our study led to a deficit of large tree/high canopy forest on national forests, no further declines in this forest type were observed from 1993-2011 (Fig. S2) while owl populations experienced long-term declines over the same period. Together, these inferences suggest that past large tree logging on national forests, which removed key habitat elements for spotted owls, may have

created an extinction debt that led to contemporary owl declines long after policies were enacted to protect large trees (Fig. 3).

We note that other emerging threats to the spotted owl, such as large, severe wildfires (Jones et al. 2016a) and invasive barred owls (*S. varia*) (Wiens et al. 2014) did not contribute to observed declines given that our study areas did not experience significant severe fire or appreciable numbers of barred owls during the study period (Keane 2017). Secondary ingestion of anticoagulant rodenticides used to kill rodents on illegal marijuana (*Cannabis* sp.) cultivations has been documented in fishers (*Pekania pennanti*) and barred owls in the Sierra Nevada and north-western California (Gabriel et al. 2012, Keane 2017). However, we know of no documented cases of exposure in spotted owls, and it is currently unknown to what extent this stressor has contributed to observed changes in spotted owl populations.

The concept of extinction debt is defined by the idea that individuals, populations, or species can initially survive habitat change but later become locally extirpated or experience declines without any further habitat modification (Kuussaari et al. 2009). As such, it is important to note that by identifying the potential presence of an extinction debt in owl populations on national forests our inferences do not suggest that total population extinction is a foregone conclusion. On the contrary, it is possible (or even likely) that spotted owl occupancy on national forests will eventually reach a new, lower equilibrium once the extinction debt is paid (Hylander and Ehrlén 2013). In the present study, we did not explore when the extinction debt might be paid off (i.e., when the population will stop declining and persist at its new lower equilibrium level), nor did we attempt to identify an empirical extinction threshold (i.e., the minimum amount of habitat required in a territory for individuals to persist). Rather, we focused on

identifying potential mechanisms of extinction debt to guide more targeted conservation action (Hylander and Ehrlén 2013).

An emerging conservation paradigm for degraded old-forest ecosystems and, the many endangered species that inhabit them, centres on restoring forest structure and function (Chazdon 2008) thereby increasing forest resilience to disturbance from fire, disease, and drought (Millar and Stephenson 2015) and conserving wildlife habitat over the long term (Tempel et al. 2015b). The consistent relationship we identified between spotted owl extinction rates and large tree/high canopy cover forest across the latitudinal range of the Sierra Nevada has significant implications for developing meaningful ecosystem restoration targets at bioregional scales (Peery et al. 2017). In particular, high canopy cover is thought to increase severe fire risk and spread by creating fuel continuity, yet appears to be more relatively more prevalent within owl territories in national parks (SKC) that have been subjected to restored, lower-severity frequent-fire regimes for nearly half a century (van Wagendonk 2007). This indicates the potential that increased prevalence of large tree/high canopy cover forest types within owl territories in national forests may not be incompatible with fire resistance/resilience while at the same time providing conservation benefits to spotted owls.

The potential direct benefits to owls of increasing this forest type may be considerable. Employing our models, increasing this forest type (large trees with high canopy cover) from the median within-territory value of 0.03-0.06 to 0.10 (30-64 ha) on national forests reduced predicted local extinction rates by 36-79%. Increasing the median within-territory value further to 0.20 (60-127 ha), similar to the median value at SKC (0.19), reduced predicted extinction rates by 80-98%. Furthermore, because they are cornerstones of old-forest ecosystem stability, greater prevalence of large trees within owl territories and across the broader landscape probably would

provide direct benefits to both spotted owls and increase resilience of old-forest ecosystems to emerging stressors.

Forests in national parks representing contemporary reference landscapes generally contain less canopy cover and lower tree densities than fire-suppressed forests on average (Lydersen and North 2012). Why then do owl territories on national parks appear to contain considerably more large tree/high canopy cover forest than their counterparts on national forests? First, although national forests may contain higher densities of trees of all sizes, they contain significantly lower densities of trees in the largest diameter (i.e., > 91 cm dbh) (Collins et al., 2017) and height classes (> 48 m) (North et al. 2017). Second, forest patches characterized by both large trees and higher canopy cover are not a product of fire suppression, but occurred historically throughout Sierra Nevada forests within a diverse mosaic of forest types in systems maintained by mixed-severity fire regimes (Hessburg et al. 2016). Spotted owl territories likely contained disproportionately more large trees and higher canopy cover than the broader forested landscape because owls are known to select for these specific features (Lahaye et al. 1997, Moen and Gutiérrez 1997, North et al. 2017).

While areas managed for multiple uses including resource extraction (i.e., national forests) and protected areas serve different societal purposes and, for this reason and others, are unlikely to have convergent forest structure and function, we can still learn important lessons when protected areas contain stable populations of species of conservation concern. For example, protected areas often form refuges for ecosystems containing distinctive biological features such as large old trees (Miller et al. 2016) and, therefore, they can act as blueprints for ecological restoration (Boisramé et al. 2017). Furthermore, protected areas may contain tree sizes, age structure, and intact disturbance regimes (Lydersen and North 2012) characteristic of

ecologically resilient landscapes (i.e., landscapes that have the capacity to recover their ecological functioning following a disturbance) and that more closely reflect species' evolutionary environments (Moore et al. 1999). Thus, in certain cases, protected areas might act as contemporary reference landscapes (Meyer 2015, Collins et al. 2016) to provide a frame of reference for the goals of ecological restoration (White and Walker 1997) for large old trees and recovery of old-forest associated species across different land tenures.

Care should be taken, however, to acknowledge the potential limitations of using national parks and other protected areas as contemporary reference landscapes to inform conservation action at broader spatial scales. For example, protected areas do not necessarily represent a random sampling of area on the landscape, but instead are often biased towards places that are less likely to face land conversion pressures – areas characterized by higher elevations, steeper slopes, and greater distances to roads and cities (Joppa and Pfaff 2009). In our study, we treat Sequoia and Kings Canyon national parks (SKC) as a contemporary reference landscape, yet it is also most southerly of all study areas examined (Fig. 3). This raises the question of whether SKC can truly act as a reference, or if other fundamental differences related to differences in latitude (e.g., climate or vegetation types) could play a stronger role than past forest management on observed dynamics of spotted owls.

While this is a possibility, we present several lines of evidence to support our use of SKC as a contemporary reference landscape. First, average temperatures and annual precipitation in SKC fell within the range experienced by the other three more northerly studies (Franklin et al. 2004). Second, mixed-conifer forests characterized primarily by sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), and incense cedar (*Calocedrus decurrens*) was the dominant vegetation type on all four study areas. While SKC did contain ten groves of giant sequoia

(*Sequoiadendron giganteum*), these covered only 7% of the study area (Tempel et al. 2016).

Third, the two most southerly study areas, SIE and SKC, occur immediately adjacent to one another in the southern Sierra Nevada in a paired study design. Yet these two study areas exhibit the largest differences in population trends among all study areas according to estimates of $\hat{\lambda}$ and Δ_k (Table 2), suggesting differences in trajectory may be unrelated to underlying differences in climate or potential vegetation type.

Global conservation of large trees and forest policy

The case study presented here demonstrates globally informative principles for old-forest species and large tree conservation. Notably, our results are consistent with an extinction debt resulting from historical logging of large trees that yielded long-term declines in old-forest species populations even after policies protecting large trees were enacted, highlighting an urgent need to protect existing old-forest habitat and potential large tree refugia (Lindenmayer et al. 2014). Indeed, national and international environmental legislation often do not emphasize the protection of large trees and old-forest ecosystems (e.g., the European Union Habitats Directive; EU, 1992).

Regional-scale plans to protect and restore old-forest ecosystems allow exceptions to rules limiting removal of large old trees to meet needs for equipment operability in forest restoration projects (e.g., USFS, 2004), and the sale of larger trees is necessary to offset operational costs of ecological restoration activities in heavily managed or degraded forests ecosystems (North et al. 2015a). Therefore, alternative approaches for funding restoration may be required to prevent further large tree loss, which may lead to ecosystem collapse in landscapes with significant legacies of exploitive land use (Burns et al. 2015, Lindenmayer et al. 2016). Despite these global challenges and conservation gaps, an emerging paradigm is to emphasize

highly targeted and fine-scale conservation of large old trees as small (or sometimes individual) natural features (Lindenmayer 2017). Policies that emphasize the protection as well as the social and ecological value of individual large old trees will offer a new hope for the perpetuity of old-forest ecosystems and the increasingly rare biodiversity that depends on them.

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Tables

Table 1. Median (SD) proportion of a spotted owl territory^a containing GNN structure variables used to assess local extinction dynamics on four study areas^b in the Sierra Nevada, CA, USA.

The number of spotted owl territories identified on each study area is shown in the bottom row of the table.

Variable	Study area			
	LAS	ELD	SIE	SKC
Large trees ^c	0.07 (0.05)	0.11 (0.06)	0.13 (0.11)	0.33 (0.19)
High canopy cover ^d	0.46 (0.16)	0.54 (0.14)	0.25 (0.16)	0.48 (0.16)
Large trees and high canopy cover	0.03 (0.05)	0.06 (0.05)	0.04 (0.08)	0.19 (0.14)
Large trees and medium canopy cover	0.02 (0.02)	0.02 (0.03)	0.05 (0.06)	0.10 (0.08)
Medium trees and high canopy cover	0.28 (0.12)	0.32 (0.09)	0.15 (0.10)	0.18 (0.12)
	<i>n</i> = 90	<i>n</i> = 74	<i>n</i> = 66	<i>n</i> = 45

^aterritory areas (ha) for each study area were as follows: LAS (639.4), ELD (399.5), SIE (301.6), and SKC (254.3) (Tempel et al., 2016).

^bstudy area abbreviations: LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia-Kings Canyon.

^csummed across all canopy cover classes;

^dsummed across all tree size classes

Table 2. Estimates^a of model parameters^b and occupancy trends^c for California spotted owls on four study areas in the Sierra Nevada, CA, USA.

Study area	α	β_x	β_x^2	$\hat{\lambda}$	Δ_k
LAS	-2.35 [-2.74, -1.96]	-10.58 [-18.68, -2.48]	-	0.991 [0.9827, 0.9997]	0.853 [0.720, 0.987] †
ELD	-2.04 [-2.58, -1.50]	-11.84 [-20.25, -3.43] ^d	-	0.983 [0.9733, 0.9918]	0.728 [0.601, 0.855] †
SIE	-1.45 [-1.82, -1.08]	-26.24 [-36.28, -16.19]	-	0.981 [0.9717, 0.9904]	0.709 [0.583, 0.834] †
SKC	-1.47 [-2.08, -0.87]	-15.66 [-24.85, -6.47]	24.30 [1.86, 46.74]	1.005 [0.9997, 1.0105]	1.096 [0.990, 1.202] *

^a numbers square brackets represents the lower and upper boundaries of 95% confidence intervals for the point estimate, which precedes the square brackets.

^b α = intercept, β_x = model coefficients for the variable (x) representing the proportion of a spotted owl territory containing large trees and high canopy cover

^c $\hat{\lambda}$ = geometric mean of the annual rate of change in occupancy, Δ_k = realized change in occupancy (ψ_k/ψ_1) where k is the number of years in the study. Symbols following estimates and confidence intervals for Δ_k indicate groups resulting from pairwise comparisons where estimates that share the same symbol had Δ_k estimates that were not statistically different from one another at the $\alpha = 0.05$ level.

^d $\beta_{\ln(x)}$

Figure legends

Figure 1. Locations of owl territories across the four spotted owl study areas in the Sierra Nevada, California, USA.

Figure 2. An example showing how we produced covariates representing spatial intersections between GNN-derived canopy cover and tree size classes by overlaying classified pixels using a GIS. Here, we see the high canopy cover class ($>70\%$ canopy cover) and the large tree size class (≥ 61 cm dbh) combining in a spatial intersection ($\cap$) to produce a covariate called “large trees and high canopy cover” for an example spotted owl territory.

Figure 3. The relationship between large tree/high canopy cover forest and spotted owl occupancy dynamics. The left column of panels shows: (i) the modelled relationship between spotted owl territory extinction probability and the proportion of an owl territory containing forests with large trees and high canopy cover (x), where the solid coloured lines represents the modelled relationship and the dashed lines represent ± 1 SE, plotted over the range of observed values, and; (ii) the distribution of values for x present on each study area, which are represented by horizontal boxplots (corresponding to the x -axis). The right column of panels shows: (i) annual estimates of derived occupancy (solid circles) from a fully time-varying model (see Methods) on the primary (left) axis, where the solid line represents a linear trend to emphasize population trajectories (see Table 2) over the 19-year study period, and; (ii) the median annual proportion of large trees and high canopy cover (x ; open circles) on the secondary (right) axis, where the dashed line represents a linear trend to emphasize that this variable did not decline on national forests over the 1993-2011 study period (also see Fig. S2).

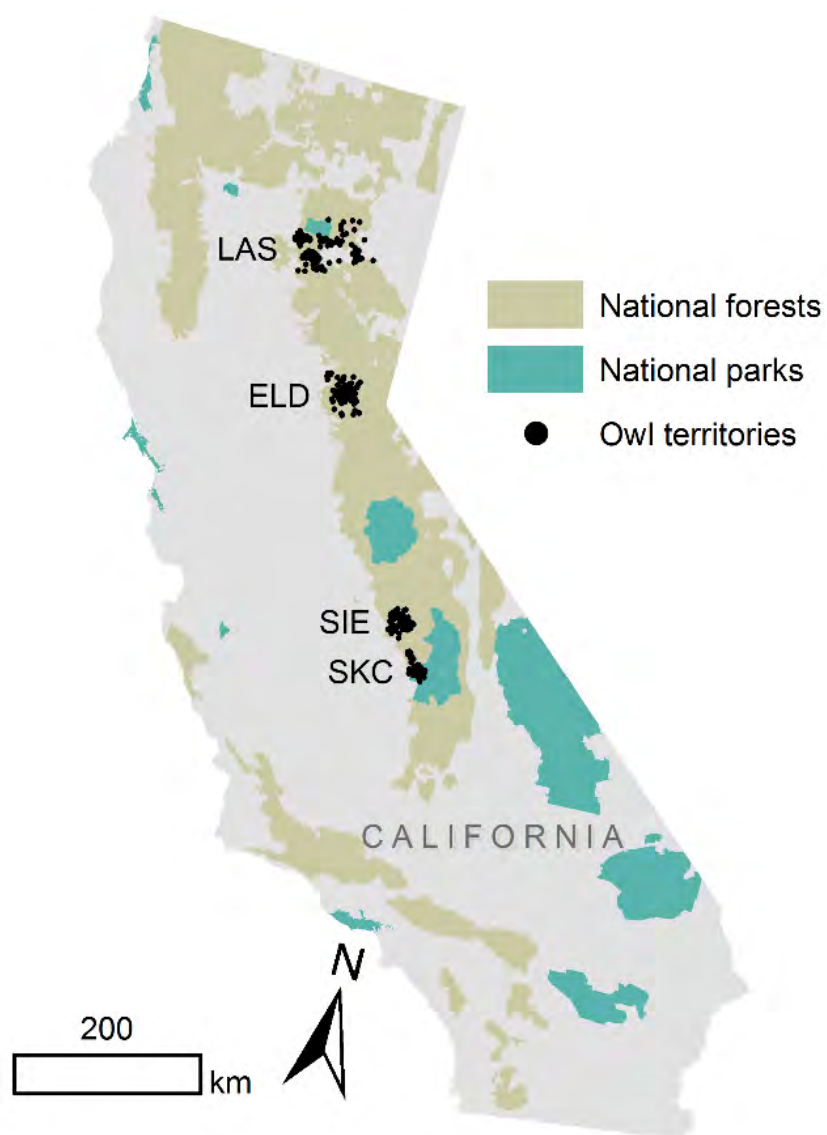
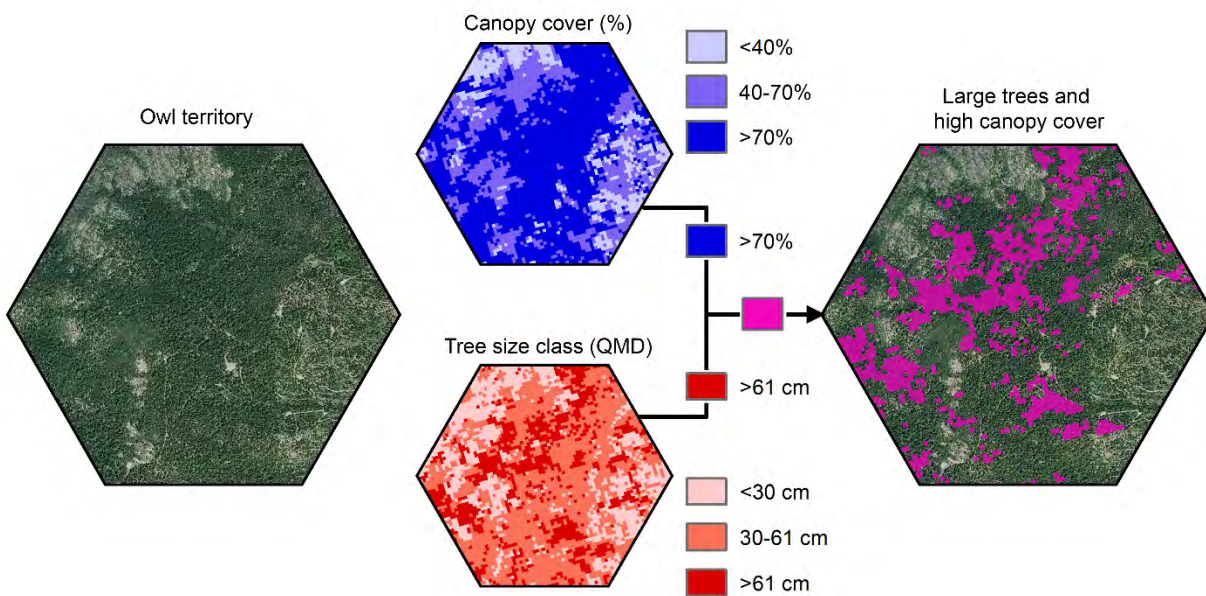


Figure 1

**Figure 2**

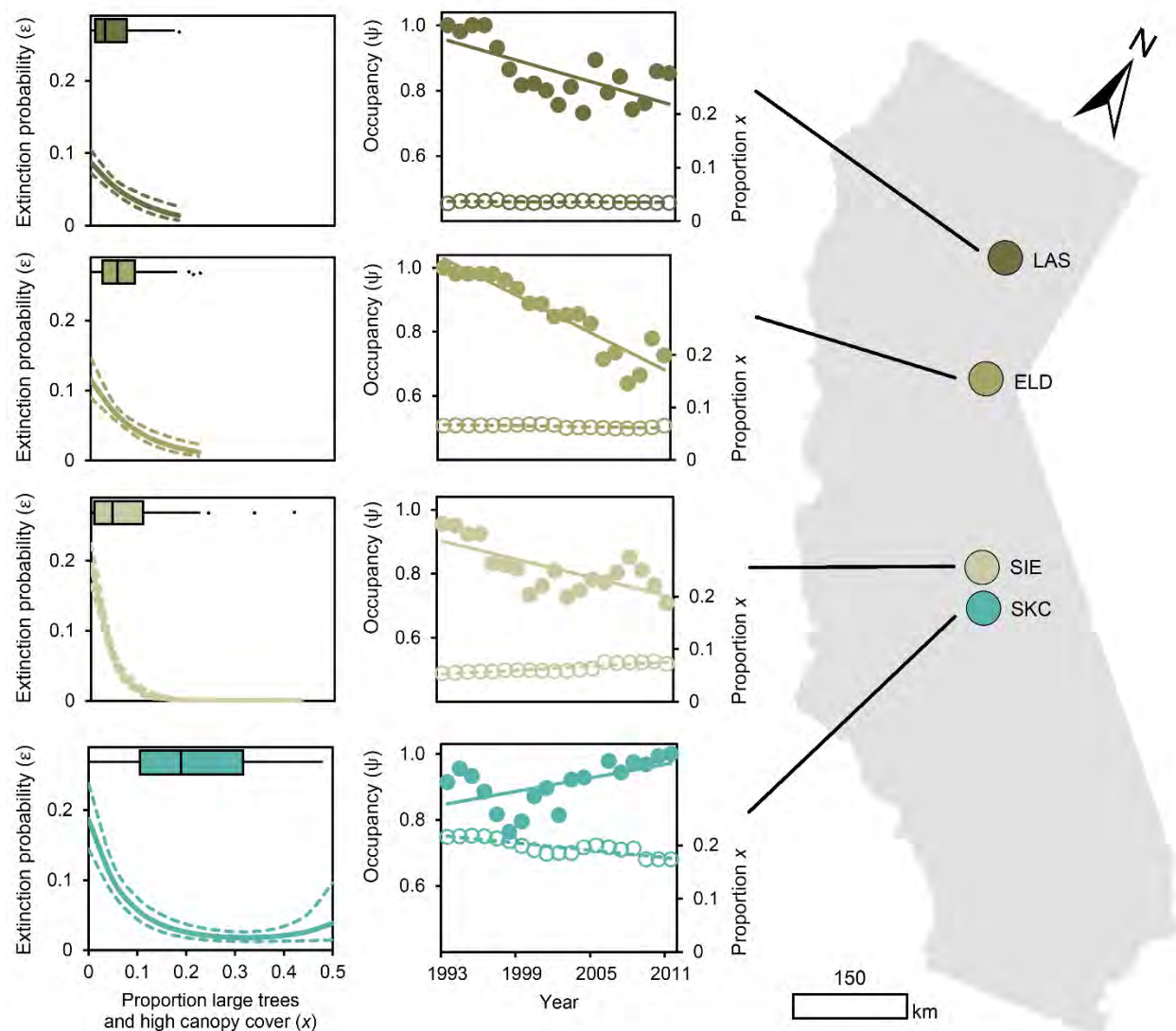


Figure 3

Supplementary materials

Table S1. Models relating tree size and canopy cover classes to California spotted owl territory extinction dynamics from 1993-2011 in the Sierra Nevada, CA, USA. Linear, logarithmic, and quadratic forms of each variable were evaluated; we displayed only the form for each variable that received the most empirical support in preliminary analyses. Study area abbreviations: LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia-Kings Canyon. The symbol “ $\cap$ ” indicates the intersection (spatial co-occurrence) of two variables.

LAS	AIC	Δ AIC	w_i	K
ln[large trees]	6741.75	0.00	0.40	42
large trees $\cap$ high canopy	6742.41	0.66	0.29	42
quad[high canopy]	6742.49	0.74	0.27	43
medium trees $\cap$ high canopy	6747.00	5.25	0.03	42
null	6749.08	7.33	0.01	41
large trees $\cap$ medium canopy	6750.43	8.68	0.01	42
year	6758.08	16.33	0.00	58
ELD	AIC	Δ AIC	w_i	K
ln[large trees $\cap$ high canopy]	4153.82	0.00	0.88	42
ln[large trees]	4160.21	6.39	0.04	42
high canopy	4160.44	6.62	0.03	42
null	4161.54	7.72	0.02	41
ln[medium trees $\cap$ high canopy]	4161.94	8.12	0.02	42
quad[large trees $\cap$ medium canopy]	4162.62	8.80	0.01	43
year	4163.05	9.23	0.01	58
SIE	AIC	Δ AIC	w_i	K
large trees $\cap$ high canopy	5319.37	0.00	0.97	28
ln[large trees]	5326.53	7.16	0.03	28
high canopy	5342.21	22.84	0.00	28
quad[medium trees $\cap$ high canopy]	5343.98	24.61	0.00	29
quad[large trees $\cap$ medium canopy]	5348.72	29.35	0.00	29
null	5368.04	48.67	0.00	27
year	5389.43	70.06	0.00	44
SKC	AIC	Δ AIC	w_i	K
quad[large trees $\cap$ high canopy]	4161.14	0.00	0.96	46

ln[large trees]	4168.76	7.62	0.02	45
quad[large trees $\cap$ medium canopy]	4170.25	9.11	0.01	46
high canopy	4171.00	9.86	0.01	45
quad[medium trees $\cap$ high canopy]	4173.72	12.58	0.00	46
null	4178.20	17.06	0.00	44
year	4189.29	28.15	0.00	61

Notes: AIC, Akaike information criterion; Δ AIC, difference in AIC compared to the model with the lowest AIC value; w_i , Akaike weight; K , number of parameters in the model.

Table S2. Coefficient estimates, standard errors (SE), lower (LCL) and upper (UCL) 95% confidence limits for the intercept (α) and covariates (β) used to model extinction probability (i.e., the final modeling stage) of spotted owls in the Sierra Nevada, CA. The symbol “ $\cap$ ” indicates the intersection (spatial co-occurrence) of two variables.

	ΔAIC	α				β_x				β_x^2			
		estimate	SE	LCL	UCL	estimate	SE	LCL	UCL	estimate	SE	LCL	UCL
Lassen (LAS)													
ln[large trees]	0.00	-2.05	0.26	-2.56	-1.54	-10.95	3.88	-18.55	-3.34	-	-	-	-
large trees $\cap$ high canopy	0.66	-2.35	0.20	-2.74	-1.96	-10.58	4.13	-18.68	-2.48	-	-	-	-
quad[high canopy]	0.74	-3.86	2.06	-7.89	0.17	9.38	10.92	-12.02	30.79	-14.61	13.61	-41.29	12.07
medium trees $\cap$ high canopy	5.25	-2.07	0.37	-2.79	-1.34	-2.66	1.40	-5.39	0.08	-	-	-	-
large trees $\cap$ medium canopy	8.68	-2.62	0.23	-3.08	-2.16	-5.62	7.25	-19.83	8.58	-	-	-	-
Eldorado (ELD)													
ln[large trees $\cap$ high canopy]	0.00	-2.04	0.28	-2.58	-1.50	-11.84	4.29	-20.25	-3.43	-	-	-	-
ln[large trees]	6.39	-2.17	0.36	-2.87	-1.46	-5.79	3.27	-12.20	0.61	-	-	-	-
high canopy	6.62	-1.77	0.57	-2.89	-0.65	-2.03	1.15	-4.29	0.23	-	-	-	-
ln[medium trees $\cap$ high canopy]	8.12	-1.94	0.68	-3.27	-0.62	-3.08	2.50	-7.98	1.81	-	-	-	-
quad[large trees $\cap$ medium canopy]	8.80	-2.50	0.33	-3.15	-1.86	-17.79	14.26	-45.74	10.15	158.65	96.26	-30.02	347.32
Sierra (SIE)													
large trees $\cap$ high canopy	0.00	-1.45	0.19	-1.82	-1.08	-26.21	5.17	-36.35	-16.07	-	-	-	-
ln[large trees]	7.16	-1.05	0.25	-1.54	-0.57	-13.93	2.54	-18.91	-8.96	-	-	-	-
high canopy	22.84	-1.44	0.23	-1.89	-0.99	-5.30	1.08	-7.41	-3.18	-	-	-	-
ln[medium trees $\cap$ high canopy]	24.61	-1.55	0.22	-1.98	-1.13	-9.12	1.90	-12.83	-5.40	-	-	-	-
quad[large trees $\cap$ medium canopy]	29.35	-1.54	0.23	-1.99	-1.08	-30.74	7.31	-45.08	-16.41	104.81	34.30	37.58	172.05

Sequoia-Kings Canyon (SKC)	ΔAIC	α				β_x				β_x^2			
		estimate	SE	LCL	UCL	estimate	SE	LCL	UCL	estimate	SE	LCL	UCL
quad[large trees $\cap$ high canopy]	0.00	-1.47	0.31	-2.08	-0.87	-15.66	4.69	-24.85	-6.46	24.30	11.45	1.86	46.75
ln[large trees]	7.62	-1.84	0.35	-2.52	-1.16	-4.66	1.37	-7.34	-1.99	-	-	-	-
quad[large trees $\cap$ medium canopy]	9.11	-1.88	0.34	-2.55	-1.21	-25.08	7.09	-38.96	-11.19	80.40	23.15	35.02	125.77
high canopy	9.86	-1.38	0.51	-2.38	-0.38	-3.89	1.26	-6.37	-1.42	-	-	-	-
quad[medium trees $\cap$ high canopy]	12.58	-1.58	0.46	-2.49	-0.67	-17.02	5.76	-28.30	-5.74	34.71	13.32	8.61	60.82

Table S3. Full model selection results from the multi-stage modeling procedure. The top model from each stage was advanced to the subsequent stage as the base model. Covariate abbreviations are as follows: lt=large trees (≥ 61 cm dbh), mt=medium trees (30-61 cm dbh), dc=dense canopy ($\geq 70\%$), mc=medium canopy (40-70%), year=annually varying time effect, T=linear time trend, TT=quadratic time trend, lnT=logarithmic time trend, repro=detection is different for reproducing owls, initial=detection is different after the first within-year detection at a site, survey=detection is different for each within-season survey period, (.)=intercept-only. The symbol “ $\cap$ ” indicates the intersection (spatial co-occurrence) of two variables.

Lassen (LAS)							
within-season detection probability (p)							
ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
(.)	year	year	year, repro+initial	6758.08	0	1	58
(.)	year	year	year, repro+survey	6823.35	65.27	0	66
(.)	year	year	year, repro+TT	6833.84	75.76	0	59
(.)	year	year	year, repro+T	6873.7	115.62	0	58
(.)	year	year	year, repro	6880.33	122.25	0	57
(.)	year	year	year, repro+lnT	6881.06	122.98	0	58
(.)	year	year	year, initial	7014.76	256.68	0	57
(.)	year	year	year, survey	7071.63	313.55	0	65
(.)	year	year	year, T	7123.83	365.75	0	57
(.)	year	year	year, (.)	7131.23	373.15	0	56
(.)	year	year	year, lnT	7131.87	373.79	0	57
among-season detection probability + covariates (p)							
ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
(.)	year	year	year, repro+initial	6758.08	0	0.9968	58
(.)	year	year	lnT, repro+initial	6770.06	11.98	0.0025	41
(.)	year	year	TT, repro+initial	6773.74	15.66	0.0004	42
(.)	year	year	T, repro+initial	6774.25	16.17	0.0003	41

(.)	year	year	(.), repro+initial	6789.85	31.77	0	40
(.)	year	year	lt, repro+initial	6830.04	71.96	0	41
(.)	year	year	dc, repro+initial	6831.07	72.99	0	41
(.)	year	year	mt∩dc + lt∩mc + lt∩dc, repro+initial	6832.99	74.91	0	43

initial occupancy probability (ψ_1)

ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
(.)	year	year	year, repro+initial	6758.08	0	0.3522	58
ln[lt∩mc]	year	year	year, repro+initial	6760.08	2	0.1296	59
lt∩dc	year	year	year, repro+initial	6760.08	2	0.1296	59
mt∩dc	year	year	year, repro+initial	6760.08	2	0.1296	59
lt	year	year	year, repro+initial	6760.08	2	0.1296	59
dc	year	year	year, repro+initial	6760.08	2	0.1296	59

extinction probability (ε)

ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
(.)	year	ln[lt]	year, repro+initial	6741.75	0	0.3967	42
(.)	year	lt∩dc	year, repro+initial	6742.41	0.66	0.2852	42
(.)	year	quad[dc]	year, repro+initial	6742.49	0.74	0.274	43
(.)	year	mt∩dc	year, repro+initial	6747	5.25	0.0287	42
(.)	year	(.)	year, repro+initial	6749.08	7.33	0.0102	41
(.)	year	lt∩mc	year, repro+initial	6750.43	8.68	0.0052	42
(.)	year	year	year, repro+initial	6758.08	16.33	0.0001	58

Eldorado (ELD)

within-season detection probability (p)

ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
(.)	year	year	year, repro+initial	4163.05	0.00	1.000	58
(.)	year	year	year, repro+survey	4307.27	144.22	0.000	66
(.)	year	year	year, repro+T	4309.20	146.15	0.000	58
(.)	year	year	year, repro+lnT	4310.45	147.40	0.000	58

(.)	year	year	year, repro+TT	4310.83	147.78	0.000	59
(.)	year	year	year, repro	4326.19	163.14	0.000	57
(.)	year	year	year, initial	4351.89	188.84	0.000	57
(.)	year	year	year, survey	4491.49	328.44	0.000	65
(.)	year	year	year, T	4498.21	335.16	0.000	57
(.)	year	year	year, lnT	4499.84	336.79	0.000	57
(.)	year	year	year, (.)	4516.76	353.71	0.000	56

among-season detection probability + covariates (p)

ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
(.)	year	year	year, repro+initial	4163.05	0	0.9418	58.00
(.)	year	year	T, repro+initial	4169.74	6.69	0.0332	41.00
(.)	year	year	TT, repro+initial	4171.15	8.1	0.0164	42.00
(.)	year	year	lnT, repro+initial	4172.44	9.39	0.0086	41.00
(.)	year	year	mt $\cap$ dc+lt $\cap$ mc+lt $\cap$ dc, repro+initial	4191.5	28.45	0	43.00
(.)	year	year	(.), repro+initial	4191.53	28.48	0	40.00
(.)	year	year	dc, repro+initial	4191.86	28.81	0	41.00
(.)	year	year	lt, repro+initial	4193.44	30.39	0	41.00

initial occupancy probability (ψ_1)

ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
(.)	year	year	year, repro+initial	4420.52	0	0.3522	58
lt $\cap$ dc	year	year	year, repro+initial	4422.52	2	0.1296	59
lt $\cap$ mc	year	year	year, repro+initial	4422.52	2	0.1296	59
mt $\cap$ dc	year	year	year, repro+initial	4422.52	2	0.1296	59
lt	year	year	year, repro+initial	4422.52	2	0.1296	59
dc	year	year	year, repro+initial	4422.52	2	0.1296	59

extinction probability (ε)

ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
(.)	year	ln[lt $\cap$ dc]	year, repro+initial	4153.82	0	0.8788	42

(.)	year	ln[lt]	year, repro+initial	4160.21	6.39	0.036	42
(.)	year	dc	year, repro+initial	4160.44	6.62	0.0321	42
(.)	year	(.)	year, repro+initial	4161.54	7.72	0.0185	41
(.)	year	ln[mt∩dc]	year, repro+initial	4161.94	8.12	0.0152	42
(.)	year	quad[lt∩mc]	year, repro+initial	4162.62	8.8	0.0108	43
(.)	year	year	year, repro+initial	4163.05	9.23	0.0087	58

Sierra (SIE)

within-season detection probability (p)

ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
(.)	year	year	year, repro+TT	5409.06	0.00	0.997	59
(.)	year	year	year, repro+survey	5420.74	11.68	0.003	70
(.)	year	year	year, repro+T	5433.64	24.58	0.000	58
(.)	year	year	year, repro+lnT	5470.03	60.97	0.000	58
(.)	year	year	year, repro+initial	5537.40	128.34	0.000	58
(.)	year	year	year, repro	5564.66	155.60	0.000	57
(.)	year	year	year, survey	5593.52	184.46	0.000	69
(.)	year	year	year, T	5619.05	209.99	0.000	57
(.)	year	year	year, lnT	5661.57	252.51	0.000	57
(.)	year	year	year, initial	5741.33	332.27	0.000	57
(.)	year	year	year, (.)	5770.69	361.63	0.000	56

among-season detection probability + covariates (p)

ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
(.)	year	year	dc, repro+TT	5392.88	0	0.6368	42.00
(.)	year	year	mt∩dc + lt∩mc + lt∩dc, repro+TT	5394.04	1.16	0.3565	44.00
(.)	year	year	lt, repro+TT	5402.07	9.19	0.0064	42.00
(.)	year	year	year, repro+TT	5409.06	16.18	0.0002	59.00
(.)	year	year	lnT, repro+TT	5411.52	18.64	0.0001	42.00
(.)	year	year	T, repro+TT	5414.44	21.56	0	42.00
(.)	year	year	TT, repro+TT	5415.83	22.95	0	43.00

(.)	year	year	(.), repro+TT	5433.1	40.22	0	41.00
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initial occupancy probability (ψ_1)

ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
quad[mt $\cap$ dc]	year	year	dc, repro+TT	5389.43	0	0.2875	44
quad[dc]	year	year	dc, repro+TT	5389.44	0.01	0.2861	44
quad[l $\cap$ mc]	year	year	dc, repro+TT	5389.44	0.01	0.2861	44
l $\cap$ dc	year	year	dc, repro+TT	5392.47	3.04	0.0629	43
l	year	year	dc, repro+TT	5392.84	3.41	0.0509	43
(.)	year	year	dc, repro+TT	5392.88	3.45	0.0512	42

extinction probability (ε)

ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
quad[mt $\cap$ dc]	year	l $\cap$ dc	dc, repro+TT	5319.37	0	0.9729	28
quad[mt $\cap$ dc]	year	ln[l $\cap$]	dc, repro+TT	5326.53	7.16	0.0271	28
quad[mt $\cap$ dc]	year	dc	dc, repro+TT	5342.21	22.84	0	28
quad[mt $\cap$ dc]	year	quad[mt $\cap$ dc]	dc, repro+TT	5343.98	24.61	0	29
quad[mt $\cap$ dc]	year	quad[l $\cap$ mc]	dc, repro+TT	5348.72	29.35	0	29
quad[mt $\cap$ dc]	year	(.)	dc, repro+TT	5368.04	48.67	0	27
quad[mt $\cap$ dc]	year	year	dc, repro+TT	5389.43	70.06	0	44

Sequoia-Kings Canyon (SKC)

within-season detection probability (p)

ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
(.)	year	year	year, repro+TT	4192.14	0.00	0.900	59
(.)	year	year	year, repro+T	4197.16	5.02	0.073	58
(.)	year	year	year, repro+survey	4199.18	7.04	0.027	70
(.)	year	year	year, repro+lnT	4215.99	23.85	0.000	59
(.)	year	year	year, repro+initial	4219.18	27.04	0.000	58
(.)	year	year	year, repro	4250.52	58.38	0.000	57
(.)	year	year	year, T	4365.19	173.05	0.000	57
(.)	year	year	year, survey	4368.48	176.34	0.000	69

(.)	year	year	year, lnT	4384.06	191.92	0.000	58
(.)	year	year	year, initial	4386.10	193.96	0.000	57
(.)	year	year	year, (.)	4423.27	231.13	0.000	56

among-season detection probability + covariates (p)							
ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
(.)	year	year	year, repro+TT	4192.14	0	0.7736	59.00
(.)	year	year	mt $\cap$ dc + lt $\cap$ mc+lt $\cap$ dc, repro+TT	4194.72	2.58	0.213	44.00
(.)	year	year	lt, repro+TT	4201.96	9.82	0.0057	42.00
(.)	year	year	dc, repro+TT	4202.11	9.97	0.0053	42.00
(.)	year	year	T, repro+TT	4205.59	13.45	0.0009	42.00
(.)	year	year	(.), repro+TT	4206.67	14.53	0.0005	41.00
(.)	year	year	TT, repro+TT	4206.8	14.66	0.0005	43.00
(.)	year	year	lnT, repro+TT	4207.1	14.96	0.0004	42.00

initial occupancy probability (ψ_1)							
ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
quad[lt $\cap$ mc]	year	year	year, repro+TT	4189.29	0	0.5114	61
ln[dc]	year	year	year, repro+TT	4191.58	2.29	0.1628	60
(.)	year	year	year, repro+TT	4192.14	2.85	0.123	59
lt	year	year	year, repro+TT	4193	3.71	0.08	60
lt $\cap$ dc	year	year	year, repro+TT	4193.15	3.86	0.0742	60
ln[mt $\cap$ dc]	year	year	year, repro+TT	4194	4.71	0.0485	60

extinction probability (ε)							
ψ_1	γ	ε	p	AIC	Δ AIC	w_i	K
quad[lt $\cap$ mc]	year	quad[lt $\cap$ dc]	year, repro+TT	4161.14	0	0.9597	46
quad[lt $\cap$ mc]	year	ln[lt]	year, repro+TT	4168.76	7.62	0.0213	45
quad[lt $\cap$ mc]	year	quad[lt $\cap$ mc]	year, repro+TT	4170.25	9.11	0.0101	46
quad[lt $\cap$ mc]	year	dc	year, repro+TT	4171	9.86	0.0069	45
quad[lt $\cap$ mc]	year	quad[mt $\cap$ dc]	year, repro+TT	4173.72	12.58	0.0018	46

quad[lt∩mc]	year	(.)	year, repro+TT	4178.2	17.06	0.0002	44
quad[lt∩mc]	year	year	year, repro+TT	4189.29	28.15	0	61

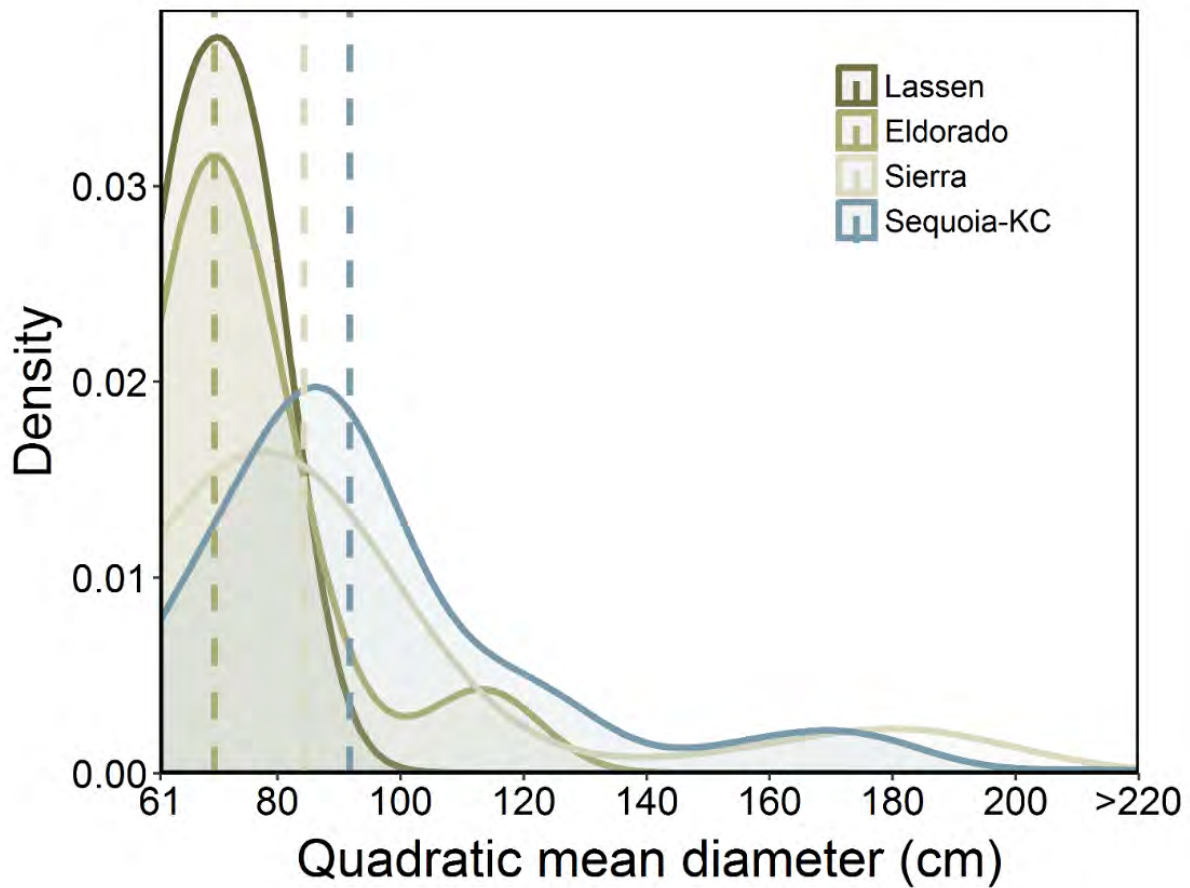


Figure S1. Density plot of quadratic mean diameter (QMD) values in the large tree class (≥ 61 cm) when co-occurring with $\geq 70\%$ canopy cover in spotted owl territories for the year 1993. The median QMD for each study area is represented by the vertical dashed line. QMD exceeded 220 cm in some cases (maximum value 279 cm, occurring on both SIE and SKC), but we truncated the x -axis to improve visualization. Units of observation were 30×30 m grid cells.

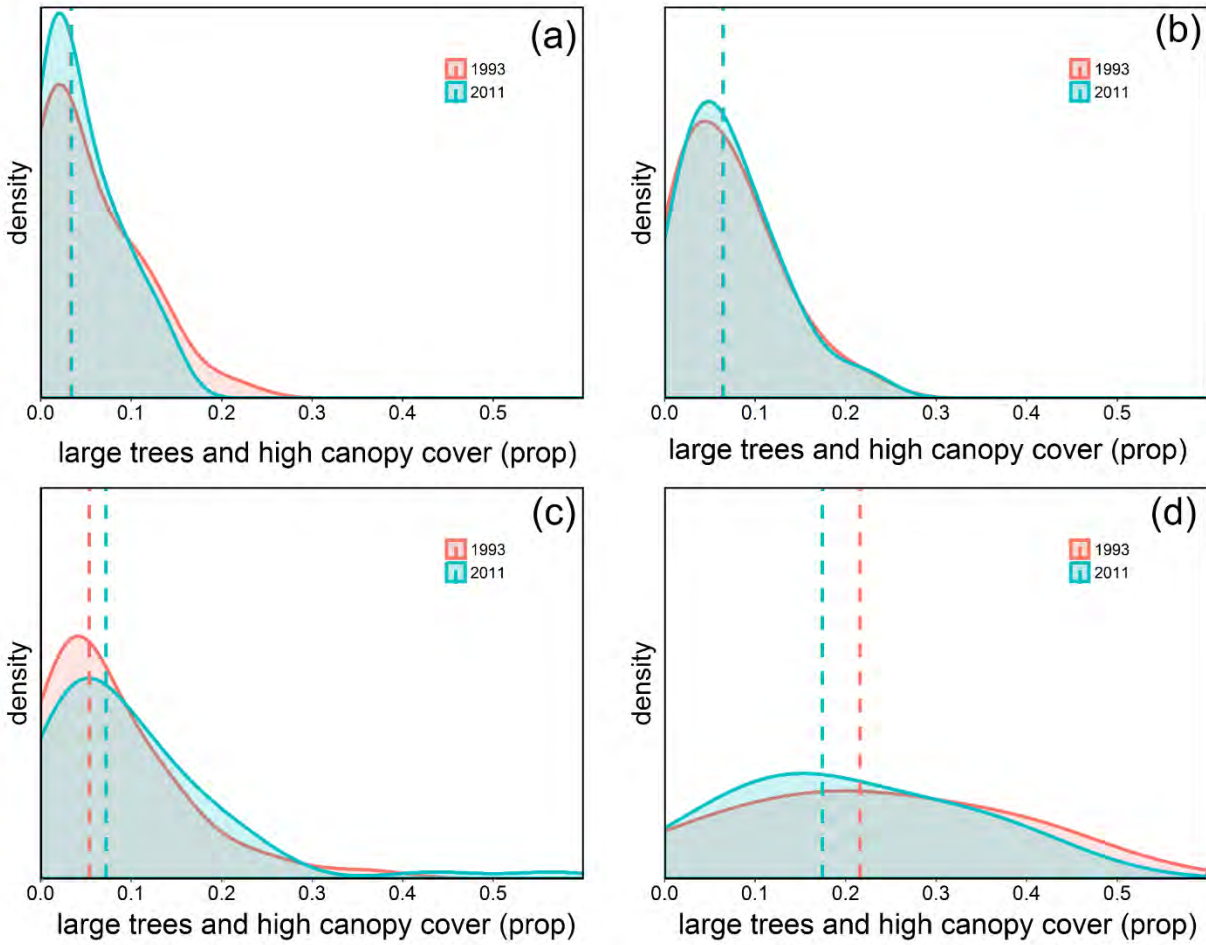


Figure S2. Density plots of the proportion of individual owl territories containing forests with large tree class (≥ 61 cm) and high canopy cover ($\geq 70\%$ canopy cover) for the year 1993 and 2011 for (a) LAS, (b) ELD, (c) SIE, and (d) SKC. Dashed vertical lines indicate the median value for each year. In panel (a) and (b), only one dashed line appears because the second line is approximately the same value. Units of observation were individual owl territories.

Chapter 3 - Bioregional-scale forest restoration limits megafires and supports rare species conservation in a changing climate

Gavin M. Jones¹, Alisa R. Keyser^{2,3}, A. Leroy Westerling², W. Jonathan Baldwin², John J. Keane⁴, Sarah C. Sawyer⁵, John D. J. Clare¹, R. J. Gutiérrez^{1,6}, M. Zachariah Peery¹

¹ *Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI, 53706;* ² *Sierra Nevada Research Institute, University of California, Merced, CA, 95343;* ³ *Department of Biology, University of New Mexico, Albuquerque, NM, 87131;* ⁴ *USDA Forest Service, Pacific Southwest Research Station, Davis, CA, 95618* ⁵ *USDA Forest Service, Pacific Southwest Region, Vallejo, CA, 94592;* ⁶ *Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, MN, 55108*

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Abstract

Climate change and fire suppression have altered disturbance regimes in forest ecosystems worldwide. In western North American dry forests, large-scale ecological restoration efforts may reduce severe fires and increase forest resilience to climate change, but restoration techniques may remove key structural habitat elements used by rare and declining old-forest species. We simulated bioregional-scale effects of forest restoration (i.e., fuel reduction treatments) on (1) future severe fire activity and (2) population dynamics of a focal old-forest species, the spotted owl (*Strix occidentalis*) in the Sierra Nevada, USA. We developed a predictive model of future severe fire coupled with a spatial occupancy model for spotted owls, with behavior of both models linked to fuel treatment location and extent. Our findings suggest restoring historical forest structure may mitigate future severe fire activity in the Sierra Nevada as the climate warms and dries, particularly when fuel treatments occur within spotted owl territories. On average, benefits provided by simulated fuel treatments to spotted owls (reducing severe fire activity) exceeded potential costs (direct habitat alteration) by mid-century at the bioregional scale. However, relative costs and benefits of fuel treatments to owls vary at finer scales, which will help to inform targeted restoration planning. Our study suggests that when large, old trees are maintained, fuel reduction and forest restoration in the Sierra Nevada is likely to benefit both old-forest species and forest ecosystem resilience under climate change.

Introduction

Climate change profoundly affects the distribution, structure, and disturbance regimes of forests worldwide (Seidl et al. 2017). Humans also continue to shape forests globally, such as in the seasonally dry forests of western North America, where a century of fire suppression and large-tree logging has changed forests from historical conditions. Forests that were historically “open”, with low tree densities maintained by frequent low- and mixed-severity fire regimes, now have high densities of small and medium-sized trees and a deficit of large trees (Safford and Stevens 2017). Consequently, these forests are at increased risk of high-severity fire and decreased resilience, defined as the capacity of an ecosystem to recover from disturbance while maintaining its characteristic structure and function (Hessburg et al. 2016). These altered forest structures—combined with warmer and drier conditions associated with climate change—have led to larger and more severe fires (Steel et al. 2015, Abatzoglou and Williams 2016, Westerling 2016, Stevens et al. 2017) and widespread drought-related tree mortality (Asner et al. 2015b, Diffenbaugh et al. 2015, Fettig et al. 2019) in western dry forests with substantial impacts both to humans and forests. While frequent low- and mixed-severity fire provides key ecological benefits to these fire-adapted systems, large areas of severe fire pose a significant threat to the persistence of these ecosystems and the species and services they support (Jones et al. 2016a). Post-disturbance forest regeneration may fail when disturbances exceed the natural range of system variability, which could lead to the persistent loss of forest ecosystems in some regions (Johnstone et al. 2016, Stevens et al. 2017, Shive et al. 2018). Both the current state of western North American dry forests and the potential for rapid changes in the near future that will lead to ecological novelty and altered provision of ecosystem goods and services to society are broadly considered to be undesirable (Rissman et al. 2018).

Landscape-scale fuels reduction and forest restoration treatments (Agee and Skinner 2005, Stephens et al. 2012) have the potential to increase dry forest ecosystem resilience (Hessburg et al. 2016). Treatments reduce accumulation and increase heterogeneity of landscape fuels through thinning and prescribed fire (Knapp et al. 2017), and promote the development of large, fire-resistant trees (Agee and Skinner 2005) that reduce risk of severe fire and drought-related tree mortality (Bradford and Bell 2016, Lydersen et al. 2017). However, treatments may simplify forests inhabited by rare and declining old-forest species that depend on large, old trees, high canopy cover, and complex vertical structure (Tempel et al. 2014a) and concern over these species and their habitat has limited the pace and scale of forest restoration efforts. Thus, restoring dry forest ecosystems while safeguarding vulnerable populations of old-forest species presents a conundrum to natural resource agencies: how can treatments occur without jeopardizing rare species that use “departed” forest conditions (Peery et al. 2017)?

A key to solving this conundrum is to first understand whether the potential negative impacts of treatments on old-forest species are outweighed by benefits to these species achieved by reducing habitat loss to future severe wildfires (Scheller et al. 2011, Tempel et al. 2015b, Stephens et al. 2016). Yet, our ability to model these theoretical trade-offs has been challenged by the following factors: existing process-based fire simulation models (e.g., LANDIS-II, FARSITE, FlamMap) are unable to reproduce large patches of severe fire that are becoming more common in western North America (Tempel et al. 2015b, Coen et al. 2018), our empirical understanding of the response of old-forest species to treatments and fire has, until recently, been limited (Tempel et al. 2016), and modeling wildfire and wildlife population dynamics at large spatial extents is computationally intensive (Scheller et al. 2011). To address these limitations, we used extreme value theory and random forests to develop a novel, empirically-based

probabilistic fire model (hereafter, “fire model”) that generated robust, fine-grain (30-m) predictions of future severe fire activity linked to changing climate and fuels conditions. Then, we modeled potential effects of fuels reduction treatments and future severe wildfire activity on old-forest species by simulating changes to fine-scale forest structure within a sensitivity analysis framework to bracket uncertainty. In doing so, we assessed the following central question: Do large-scale fuels reduction and forest restoration practices support or hinder conservation of declining old-forest species in the Sierra Nevada in a changing climate?

We coupled the fire model with a spatial occupancy model (“population model”) (Chandler et al. 2015) to evaluate relative and scale-dependent future effects of treatment and severe fire on an old-forest species, the spotted owl (*Strix occidentalis*), across the Sierra Nevada, USA (~120,000 km²). We fit the two empirical models independently over the period for which data existed (1984-2015), but we linked them together during forward simulations of treatment- and climate-induced changes in patterns of severe fire and owl population dynamics (through 2064) (Fig. S1). Climate change effects were assessed using two global circulation models, CanESM2 (relatively modest future warming and drying) and CNRM-CM5 (more extreme future warming and drying), to bracket uncertainty. The fire model produced annual spatially-explicit predictions of severe fire occurrence across the Sierra Nevada through mid-century (2064) that we introduced to the population model over the forecasting period; then the behavior of both models was linked to a factorial design that systematically varied fuel treatment total extent and location across the landscape. Fuel treatments were simulated across all landscapes deemed to be “treatable” (i.e., on public lands without significant operational constraints) (North et al. 2015a) with total treatment extent varying by equal intervals (18%, 36%, 54%, 72%, 90%) (Fig. S2). Treatable lands (i.e. 100% of “treatable” area) comprised ~35%

of the entire Sierra Nevada landscape (Fig. S4). A second set of treatment scenarios were then developed in which the same total landscape extent was treated, but treatments were excluded from owl territories (hexagons approximating the area defended by territorial individuals) (Jones et al. 2018) (Figs. S2 and S3). This design allowed us to explore how reducing fuel in owl territories affected future severe fire activity and assess the net costs and benefits of treatment to owls.

Methods

Fuels

Within the fire model, fuels were represented by fire regime current condition class (hereafter, “FRCC”) (Schmidt et al. 2002). FRCC describes ecosystem departure from historical conditions in terms of vegetation structure and composition and is an important predictor of fire activity in the region (Keyser and Leroy Westerling 2017, Keyser and Westerling 2019) (Supplemental materials). Although other factors can alter vegetation conditions, fire suppression was the principal driver of forest change in the Sierra Nevada in the past century (Collins et al. 2017).

We assumed that fuel reduction treatments, however implemented, would modify FRCC from a departed to non-departed state (Supplemental materials). Fuel treatments were randomly allocated to 30-m pixels in areas of the landscape meeting administrative constraints, with each scenario built sequentially using the previous scenario as a starting point (e.g., the pixels treated in the 18% scenario were nested within the 36% scenario). Within the population model, fuels were represented by canopy continuity of forest vegetation structure variables that strongly predict spotted owl occupancy dynamics (Jones et al. 2018, LEMMA 2018). We assumed that fuels reduction treatments would reduce canopy cover from $\geq 70\%$ to 40-70% while maintaining large trees, which follows basic principles of restoration treatments (Agee and Skinner 2005,

Stephens et al. 2014b). Fuel reduction treatments were introduced in the first year of the forward simulation and altered fuels remained static thereafter. We performed sensitivity analyses by varying the strength of treatment effects on spotted owl habitat (no habitat effects, weak habitat effects, strong habitat effects) to evaluate the degree to which our assumptions might affect inferences. Briefly, ‘no habitat effects’ assumed that treatment in owl territories did not modify large tree/high canopy cover forest; ‘weak habitat effects’ assumed that for each 1-ha treated within an owl territory, 0.25 ha of large tree/high canopy cover forest was changed to large tree/medium canopy forest; ‘strong habitat effects’ assumed that for each 1-ha treated within an owl territory, 1 ha of large tree/high canopy cover forest was changed to large tree/medium canopy forest (Supplemental materials).

Fire model overview

We downloaded fire severity polygons from United States Department of Agriculture Forest Service (USFS) Region 5 that classified burn severity as the percent change in basal area for 1984-2015. We used the 90% basal area (BA90) killed value as our measure of high severity fire occurrence (instead of a lower threshold such as 50% or 75%) for two reasons. First, there was a high certainty that BA90 represented acute ecological change relevant to spotted owls and old-forest ecosystems (JA Fites-Kaufmann, *personal communication*). Second, map accuracy is exceptionally high for BA90 (Miller and Quayle 2015). This fire severity data set was the response variable for both large (LS) and fine scale (FS) fire model development (Fig. S1).

Large scale (LS) fire model

We fit a spatially explicit logistic regression model (LR1) on a 1/16th degree latitude/longitude grid to estimate the monthly probabilities of the occurrence of at least one fire >400-ha as a function of topography, human population, vegetation fraction, and climate using the glm

function in R (Westerling 2018) (Supplemental materials, Table S3). Model specifications were compared using AIC to select for parsimonious models despite the presence of spatially auto-correlated variables (Akaike 1974, 1981). Specifications tested here extend models used in (Westerling et al. 2011a) to a finer spatial scale (1/16th degree latitude/longitude grid instead of 1/8th degree). The selected model was validated by applying parameters calculated with the first half of the data (1984-1999) to the full sample, and comparing Spearman's rank correlations over each period with correlations for the model estimated with the full 30-year sample (Westerling 2018).

For each fire >400-ha, the probability of >50-ha burning in BA90 was estimated by fitting a logistic regression (LR2) with climate covariates using the glm function in R. To estimate the conditional extent of BA90 burned area, for each fire with >50-ha BA90 burned, a generalized Pareto distribution (GPD) was fit with climate and FRCC covariates. Large-scale BA90 area burned was simulated for each climate and treatment scenario as follows: first, we repeated random draws from the binomial distribution using probabilities from LR1 to generate large (>400-ha) fire occurrence; second, for each simulated large fire, a random draw from the binomial distribution using probabilities from LR2 was used to generate BA90 occurrence >50-ha; third, for each BA90 occurrence >50-ha, a random draw from the GPD was used to generate total BA90 area.

Fine scale (FS) fire model

We used a presence/absence approach, similar to a species distribution model, to model the probability of high severity fire occurrence across the Sierra Nevada bioregion at 30-m resolution. We chose twenty fires from the fire severity dataset that met our modeling criteria to build the downscaled fire severity model, selecting fires that yielded the most complete coverage

of year, ignition month, fire size, and severity (Table S4). Individual pixels were classified as 0 or 1, where 1 represented a pixel that experienced 90% basal area killed (BA90). The training set of fires contained 556,444 pixels: 47.8% had a value of 1, 52.2% had a value of 0.

We used the classification and regression tree model Random Forests to predict occurrence of BA90 pixels on the landscape as a function of topography, vegetation, and fire size. To select the most parsimonious model for BA90 presence, we used the *rfUtilities* package in R (Murphy et al. 2010, Evans and Murphy 2018). We evaluated model accuracy using Cohen's Kappa and the area under the Receiver Operating Curve (AUC). Using the best-fit model, we produced a set of probability surfaces for seven fire size bins for the Sierra Nevada bioregion (Table S4); each 30-m pixel was assigned a probability of burning at high severity for fires in each fire size bin (Supplemental materials). The inclusion of fire size as a predictor in our classification model necessitated a separate probability surface for each fire size class. The remaining classification variables did not vary temporally so the same set of probability surfaces informed all management and climate change scenarios.

Spatial allocation of fire

The logit and generalized Pareto distribution models, driven by climate and fuel treatment scenarios, produced annual distributions of fire size and severity at the 1/16th degree scale (LS). We developed a spatial allocation algorithm to assign severely-burned pixels to the 30-m landscape surface (FS). Each projected LS fire occurrence was assigned to the appropriate fire size bin and subsequently allocated to the FS landscape using a Monte Carlo simulation drawing from the probability surface for the corresponding fire size bin. Starting with a randomly assigned ignition point within the LS modeling pixel, the algorithm assigned FS pixels as BA90 true/false in an iterative fashion based on the modeled probability surface until the predicted LS

fire size was reached. This procedure was repeated 100 times for each unique treatment/climate scenario; each individual simulation was delivered to the spatial occupancy model for spotted owls (see below). We utilized the MERCED high-performance computing cluster at University of California Merced to complete simulations.

To ensure that a BA90 pixel was not assigned to more than one fire each year or assigned a repeat fire in too short an interval, each pixel was deactivated for 9 years before it could burn again (at any severity). Limited information exists on the actual time interval between high-severity fires in the Sierra Nevada, but some research suggested previous fire occurrence limits high-severity fire for at least 9 years (Collins et al. 2009). After each fire was allocated to the landscape, the number of high severity pixels intersecting owl territories was calculated and passed to the population model (see below). See Supplemental materials for full model description, accuracy assessment, and allocation examples.

Owl population model

We modeled owl territory occupancy using a Bayesian dynamic spatial occupancy model (Chandler et al. 2015). The model was fitted using repeated within-season detection/non-detection surveys in $n=275$ spotted owl sites on four demographic study areas spanning the latitudinal range of the Sierra Nevada between 1993-2011 (Fig. S1) (Tempel et al. 2016, Jones et al. 2018). The spatial dependence in the model's structure allowed occupancy dynamics of the 275 surveyed sites to be modeled within a broader network of 1844 known or imputed sites that represented nearly all suitable habitat in the Sierra Nevada (Fig. S14). Covariates were selected *a priori* based on published information regarding spotted owl habitat-occupancy associations (Jones et al. 2018). Specifically, site extinction probability was modeled as a function of forest structural variables representing the proportion of each owl site containing large trees (quadratic

mean stand diameter ≥ 61 cm) and high canopy closure ($\geq 70\%$ canopy cover), and large trees and medium canopy closure (40-70% canopy cover), respectively (Fig. S1, Supplemental materials) (Jones et al. 2018). These same covariates were used to model detection probability.

We combined fire forecasts with posterior draws of parameter distributions to project the spotted owl population forward over the period 2012-2064 (Fig. S1; see Supplemental materials). Simulated treatment effects within individual owl territories were modeled by modifying forest structure covariate values (from above) in a manner consistent with expected changes in horizontal canopy structure due to fuel treatments (i.e., reducing fuel continuity by reducing canopy cover). Thus, when simulated fuel treatments occurred within portions of an owl site we re-allocated large tree/high canopy cover forest to large tree/medium canopy cover forest in proportion to the area treated, where the effects to owls were based on statistical associations between each forest cover type and local extinction probabilities (Supplemental materials). Severe fire effects were modeled by the addition of a parameter that represented an empirical effect of severe fire extent (proportion of territory area burned severely) on spotted owl local extinction rates determined by a before-after control-impact natural experiment (Jones et al. 2016a) (Fig. S1). To model potential semi-permanent vacancy of sites that experienced large amounts of severe fire (Jones et al. 2016a), we included a threshold effect in the colonization function that forced all future colonization probabilities to zero when exceeded (Supplemental materials). Simulations were conducted on the high-throughput computing platform HTCondor at the University of Wisconsin-Madison.

Results

Severe fire ($>90\%$ tree basal area mortality) was predicted to burn $\sim 23,500$ -ha/year in the Sierra Nevada by mid-century in the absence of fuel treatments, or $>680,000$ -ha during a 30-year mid-

century climate window (2035-2064) (Fig. S5). Landscape-scale fuel reduction treatments strongly reduced severe fire extent in the Sierra Nevada by mid-century. Treatments reduced predicted severe fire area by a minimum of 1.65% (11,200-ha) to a maximum of 30.5% (207,353-ha) from 2035-2064, depending on treatment extent, treatment location, and climate scenario (Fig. 1, Fig. S6, Table S1). More extensive fuel treatments consistently reduced severe fire area across the landscape, and this effect was proportionally larger when treatments were included in owl territories (Fig. 1B). Moreover, higher levels of treatment (e.g., >50% of the treatable landscape) appeared to reduce severe fire activity even in years when climate models produced extreme fire conditions, most notably when treatments were included in owl territories (Fig. S7).

The degree to which owl territories were exposed to extinction-inducing severe fire (Jones et al. 2016a) depended on the spatial extent of our simulated fuel treatments and whether treatments were or were not allowed within owl territories (Figs. S8 and S9). Population projections indicated that fuel treatments have the potential to provide net benefits to spotted owls inhabiting the Sierra Nevada by mid-21st century under all scenarios considered (Fig. 2, Fig. S10). When landscape fuel treatments were excluded from owl territories (Fig. 2A), owl populations experienced net benefits that increased with more treatment but the long-term benefits were generally lower compared to scenarios where owl territories received fuel treatments (Fig. 2B-D). **Owls benefited most when fuel treatments occurred within territories but treatments were designed to avoid modifying large tree/high canopy cover forest** (Fig. 2B). When fuel treatments occurred inside territories and owl habitat was modified (Fig. 2C-D), a downward pressure was imposed on owl populations over the initial years of the simulation but varied in degree depending on assumptions made about strong versus weak effects of treatment

on owl habitat (see also Methods and Supplemental materials). The downward pressure on owl populations eased following the initial years of the simulation, and the net costs of treatment were offset by the cumulative benefits of reduced severe fire exposure by the 2040s and 2050s for all treatment scenarios (Fig. 2C-D).

When averaged across the entire Sierra Nevada, treatment effects on population occupancy were apparent but modest in magnitude (e.g., -0.01 to $+0.04$) (Fig. 2). However, larger effects that varied considerably in space emerged when outcomes were mapped to individual territories across the Sierra Nevada (e.g., ± 0.30) (Fig. 3, Figs. S11 and S12). When treatments were excluded from owl territories, there were relatively uniform benefits to mid-century territory occupancy compared to a no-treatment scenario (e.g., -0.06 to $+0.11$; range of 99th percentile of values) (Fig. 3A). These benefits grew (e.g., -0.07 to $+0.20$) when treatments were simulated to occur within owl territories but were designed to avoid modifying large tree/high canopy cover forest (Fig. 3B). When simulated treatments were applied in owl territories and treatment modified owl habitat, strong regional-scale patterns in trade-offs emerged (e.g., -0.11 to $+0.22$) (Fig. 3C). Owls in the northern Sierra Nevada were predicted to experience larger benefits from treatment in territories across all treatment levels, with mid-century occupancy probability expected to rise by >0.20 for many territories in this region compared to a no-treatment scenario. Owls in a portion of the central Sierra Nevada were also expected to experience net benefits if treatment occurred within territories, but clear benefits tended to accrue only at higher levels of treatment (~ 50 - 90%) (Fig. 3C). Owls in the north-central and southern Sierra Nevada were predicted to experience net costs of treatment in territories across all treatment levels when we assumed treatment would have negative habitat effects (Fig. 3C).

Discussion

Severe fires are increasing due to climate change and fuel buildup from historical fire suppression, and have the potential to disrupt forest ecosystems and destroy human communities. Our simulations show that bioregional-scale fuel treatments have the potential to substantially reduce future severe fire extent and therefore increase dry forest resilience to climate change. These treatments also appear to support the conservation of a focal old-forest species, the spotted owl, in the Sierra Nevada, USA. In our simulations, the relative costs and benefits of treatments to owl populations varied across space and through time, particularly when treatments occurred in owl territories (Fig. 3). Owls experienced relatively large benefits from treatment (Fig. 3) in areas where treatments considerably reduced future severe fire (Fig. 1). Conversely, areas where owls experienced net negative treatment effects (Fig. 3) were characterized by lower future exposure to severe fire (Fig. 1), more pronounced direct treatment impacts on predicted territory extinction rates because of regionally-varying treatment effects (Supplemental materials, Table S2), or both. When fuel treatments occurred in owl territories, but were simulated to have no effects on key owl habitat (e.g., because treatment designs that avoided modifying large tree/high canopy forest), benefits were nearly universal and larger than alternative scenarios (Figs. 2B and 3B). Optimal management strategies might entail a mixed approach where treatments are excluded from owl territories, or designed to maintain high-quality owl habitat, in certain regions where negative impacts are greatest, and included elsewhere where costs are less or benefits are predicted to be positive (Fig. 3). Compatibilities may exist between cost-benefit trade-offs to owls and feasibility of treatment in some regions. For example, steeper and more remote terrain in national forest lands of the southern Sierra Nevada make implementation of treatments more difficult (North et al. 2015a), but owls in this region also show strong negative costs of within-

territory treatment. In our simulations, we considered an owl territory to be that area surrounding the owl's central activity center (nest, roost), which ranged from ~250-640 ha (Jones et al. 2018).

Mechanistic simulation studies (Moghaddas et al. 2010, Collins et al. 2011) and empirical observations (Safford et al. 2012, Lydersen et al. 2017, Tubbesing et al. 2019) have suggested fuels reduction can significantly reduce severe fire activity in the Sierra Nevada. Our results, obtained using a novel modeling approach that drew on empirical data to reproduce larger severe fire patches, corroborate these general conclusions but did so at a much larger spatial extent than was previously possible. We used 31 years of empirical fire records and a probabilistic forecasting approach to show that restoring Sierra Nevada forest structure to historical conditions reduced predicted severe fire extent by mid-century (Figs. 1 and 2). Although this was an expectation for fuel-limited dry forest ecosystems (Stephens et al. 2013), there is concern that fuels management may be inadequate to alter severe wildfire in a changing climate when extreme fire conditions become more common on an annual basis (Schoennagel et al. 2017). Indeed, we observed some degree of increase in severe fire activity under all treatment scenarios with climate warming (e.g., Fig. S7). However, as more of the landscape was treated, future severe fire extent was reduced (Fig. 1). Importantly, treating more of the landscape also reduced severe fire activity even in years with extreme fire weather, an effect that was particularly notable when larger proportions of landscapes were treated (e.g., >50%, Fig. S7). These results suggested that large-scale forest restoration efforts have the potential to alter severe fire activity and reduce fire-related risk to spotted owls in a changing climate.

The primary mechanism by which severe fire negatively affects spotted owls and other old-forest species is through the elimination of nesting and denning habitat (Scheller et al. 2011, Ganey et al. 2017). The availability of nesting habitat and thermally beneficial roosting sites

(large, old trees and high canopy cover) is a limiting factor for spotted owl populations in the Sierra Nevada because of historical selective logging activities that removed large, old trees (Collins et al. 2017, Jones et al. 2018). Moreover, regression analyses suggest that in the next 75 years, the cumulative amount of spotted owl nesting habitat in the Sierra Nevada predicted to experience significant severe fire effects (>50% tree basal area mortality) will exceed the total existing habitat amount (Stephens et al. 2016). Indeed, although we used a more conservative severity threshold (>90% tree basal mortality) (see Methods), loss of nesting habitat to extensive severe fire was the key driver of future population declines within our model (Fig. S13). Moreover, by explicitly linking habitat changes from fire and treatment effects to a demographic model, we were able to rigorously evaluate trade-offs in a population viability context. Previous studies that have applied demographic models to evaluate fuel treatment trade-offs in the Sierra Nevada have also showed that the indirect benefits of treatment (reducing severe fire activity) may outweigh direct costs of habitat manipulation (Scheller et al. 2011, Tempel et al. 2015b). Our results generally support these findings (Fig. 2), while broadening inferences to the entire Sierra Nevada ecosystem and providing insights about how costs and benefits might vary in space across a large bioregion experiencing climate change (Fig. 3, Figs. S19 and S20).

Forest restoration and fuels reduction treatments now occur at levels below those desired by managers (North et al. 2015b) because implementation is constrained by legal, administrative, and financial factors (Collins et al. 2010, North et al. 2015a). So we examined fuel treatment scenarios that ranged from highly feasible (e.g., 18% of the treatable landscape) to relatively less feasible (90% of the treatable landscape) to bracket the hypothetical range of uncertainty regarding fuel treatment effects on fire activity and owl populations. When treatments occurred across much of the landscape (e.g., >50%), future occurrence of severe fire was reduced in the

region. However, even low levels of treatment appeared to provide benefits to owls by modifying severe fire area in some regions, even when treatments were restricted from owl territories.

Although owl territories made up a small proportion (~10%) of treatable area in the Sierra Nevada (North et al. 2015a), scenarios that permitted within-territory treatment resulted in less severe fire activity than scenarios treating the same total area but outside of owl territories. We think this finding can be explained by two factors. First, the vegetation within owl territories is particularly productive because of soil and moisture conditions and therefore contains large amounts of fuel compared to the broader landscape (Spies et al. 2006, Collins et al. 2010). Second, some areas (e.g., northern and central Sierra Nevada) have relatively high densities of owl territories and therefore treatment restrictions result in relatively large contiguous areas of untreated forest with high risk of severe fire (Figs. S3 and S14). Over the past several decades, treatments have sometimes been implemented within portions of owl territories (~300-600 ha), but generally not in the “core” areas of the territory corresponding with management units called protected activity centers (PACs; ~121 ha) (Peery et al. 2017). Our study treated the entire territory as the management unit (including the smaller PAC) and therefore we did not estimate potential effects of fuels management at the PAC scale alone. However, previous syntheses have recommended lower-intensity fuel treatments at the scale of the activity center (nest, roost) to reduce potential habitat-related negative effects to owls (Peery et al. 2017).

While our model offers a robust starting point for forecasting wildfire and population dynamics across this large bioregion (e.g., Dietze et al., 2018), it has limitations. We assessed the sensitivity of our results to several modeling decisions and assumptions (Supplemental materials), but potential limitations of our study include aspects of our characterization of fuel treatments and fire effects on owls. In both the fire model and spotted owl population model, we

only considered how the expected changes in forest structure resulting from treatment interacted with models, not potential effects of the treatment method itself (e.g., prescribed burning, hand-removal of small trees, thinning and/or logging of medium-sized trees). Within the fire model, the effect of treatment on forest structure was represented by simulated changes to fire regime condition class (Schmidt et al. 2002) (see Methods and Supplemental materials), which is a coarse depiction of vegetation change. Within the owl model, treatments reduced canopy cover in some scenarios (Fig. S1), but we were unable to assess how other changes (e.g., understory vegetation or increase in mean tree diameter size) might affect spotted owl occupancy dynamics. We modeled treatment effects to owls by altering a specific habitat type, large tree/high canopy cover forest (Jones et al. 2018), within owl territories (Fig. S1). However, given that large tree/high canopy cover habitat generally makes up a small proportion of each territory (mean = 0.05), it is likely possible to design treatments that avoid canopy reduction in this habitat (Figs. 2B and 3B) even when treatments occur across large portions of the territory and/or landscape. Vegetation and fuels within our models were static, and treatments were introduced once at the beginning of forward simulations. Recent work suggests that temporally dynamic treatments reduce severe fire area in a changing climate more than static treatments (Hurteau et al. 2019), meaning that we may have underestimated the benefits of treatments to owls by using a static approach. Future efforts therefore may benefit from using dynamic treatment models. Whereas treatments were placed randomly across the landscape in our model, strategic placement in areas with high baseline fire risk might make treatments more effective at lower treatment extents in the real world (Tubbesing et al. 2019). We assumed that the probability of spotted owl territory extinction would relate to the proportion of the territory that burned severely, consistent with findings from field studies (Jones et al. 2016a). However, spotted owl response may also depend

on either the spatial configuration of severe fire, latitudinal and/or elevational gradients, or specific pre- and post-fire vegetation conditions. Finally, our simulations assumed larger trees (>61 cm dbh) would be retained (not removed intentionally either before or after treatment), although the trees used by owls for nesting are usually much larger (e.g., mean 157 cm dbh) (North et al. 2000, Jones et al. 2018).

Sierra Nevada forests face an increased probability of disturbance-initiated transition to non-forest landscapes without active management to restore ecologically-appropriate forest conditions and reduce accumulated fuels (Stephens et al. 2013, Rissman et al. 2018). Although owls inhabit forests with high tree densities, these conditions also increase the risk of severe fire and drought-related tree mortality (Bradford and Bell 2016, Stephens et al. 2018, Fettig et al. 2019) that results in loss of ancient trees (Jones et al. 2016a). Broadening forest restoration efforts in the Sierra Nevada has the potential to enhance forest resilience and reduce risk of severe fire that negatively impacts forests, carbon storage, water supply, air quality, and local communities as the climate changes. Moreover, our simulations predicted that forest restoration appears to be largely compatible with conservation of an old-forest species. Yet, to minimize the effects of fuel reduction and forest restoration on spotted owls and other old-forest species including the Pacific fisher (*Pekania pennanti*), northern goshawk (*Accipiter gentilis*), and American marten (*Martes americana*), it is essential that large, old trees and core nesting/roosting areas within territories be maintained (Peery et al. 2017, Jones et al. 2018). When large, old trees are maintained and recruited (Hessburg et al. 2016), fuel reduction and forest restoration in the Sierra Nevada can benefit both old-forest species and forest ecosystem resilience under climate change.

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Figure legends

Figure 1. Expected annual changes in severe fire (90% basal area killed) extent from 2035-2064 relative to the baseline no-treatment (0%) scenario. (A) Treatments excluded from owl territories. (B) Treatments included in owl territories. Results are summarized from the large-scale fire model (6-km) (see Methods).

Figure 2. Summary effects of treatment on spotted owls in the Sierra Nevada showing annual range-wide occupancy for each treatment scenario relative to the baseline no-treatment scenario (red line). (A) Occupancy when treatments are excluded from owl territories. (B-D) Occupancy when treatment occurs inside owl territories but vary in their assumptions about how treatments affect owl habitat (no effects, weak effects, strong effects). Trajectories were averaged across 50,000 simulations (Supplemental materials) using the CRNM-CM5 global circulation model (see Supplemental materials for CanESM-2).

Figure 3. Spatial effects of the location and extent of fuel treatments on spotted owl territory occupancy. Map shows the mean change in mid-century occupancy (at year 2064) across all 1844 spotted owl territories in the Sierra Nevada, relative to a no-treatment scenario. (A) Occupancy when treatments are excluded from owl territories. (B-D) Occupancy when treatment occurs inside owl territories but vary in their assumptions about how treatments affect owl habitat (no effects or strong effects; see Supplemental materials for weak effects). Averaged across 50,000 simulations (Supplemental materials) using the CRNM-CM5 global circulation model (see Supplemental materials for CanESM-2).

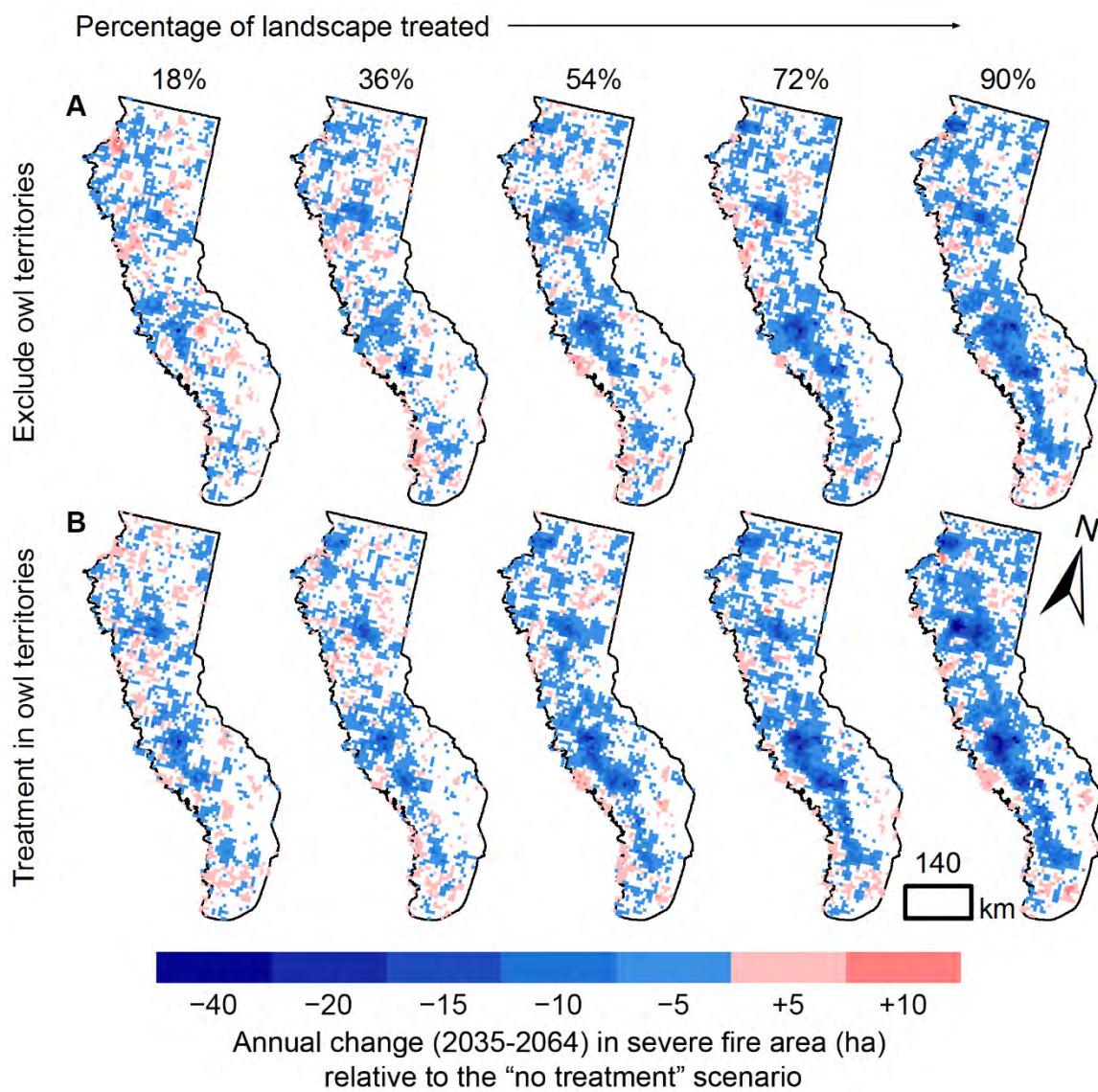


Figure 1.

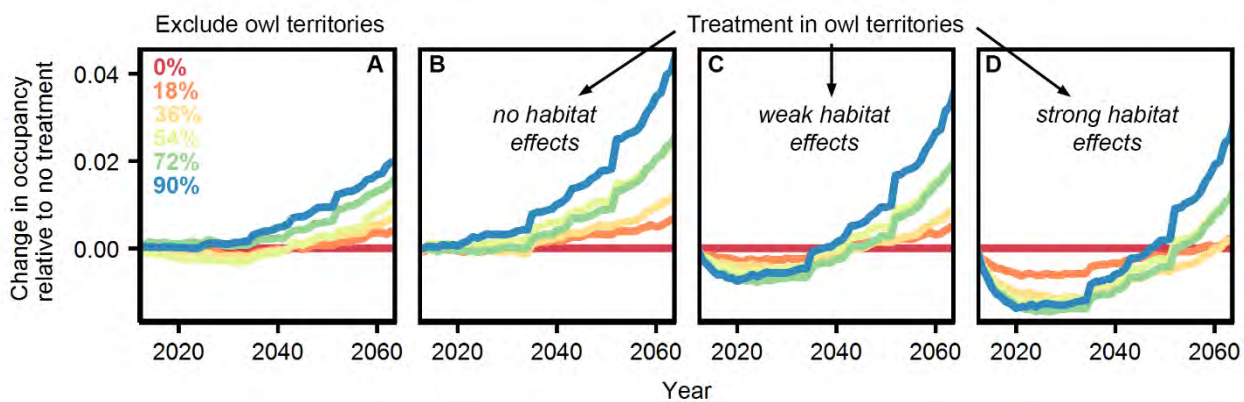


Figure 2.

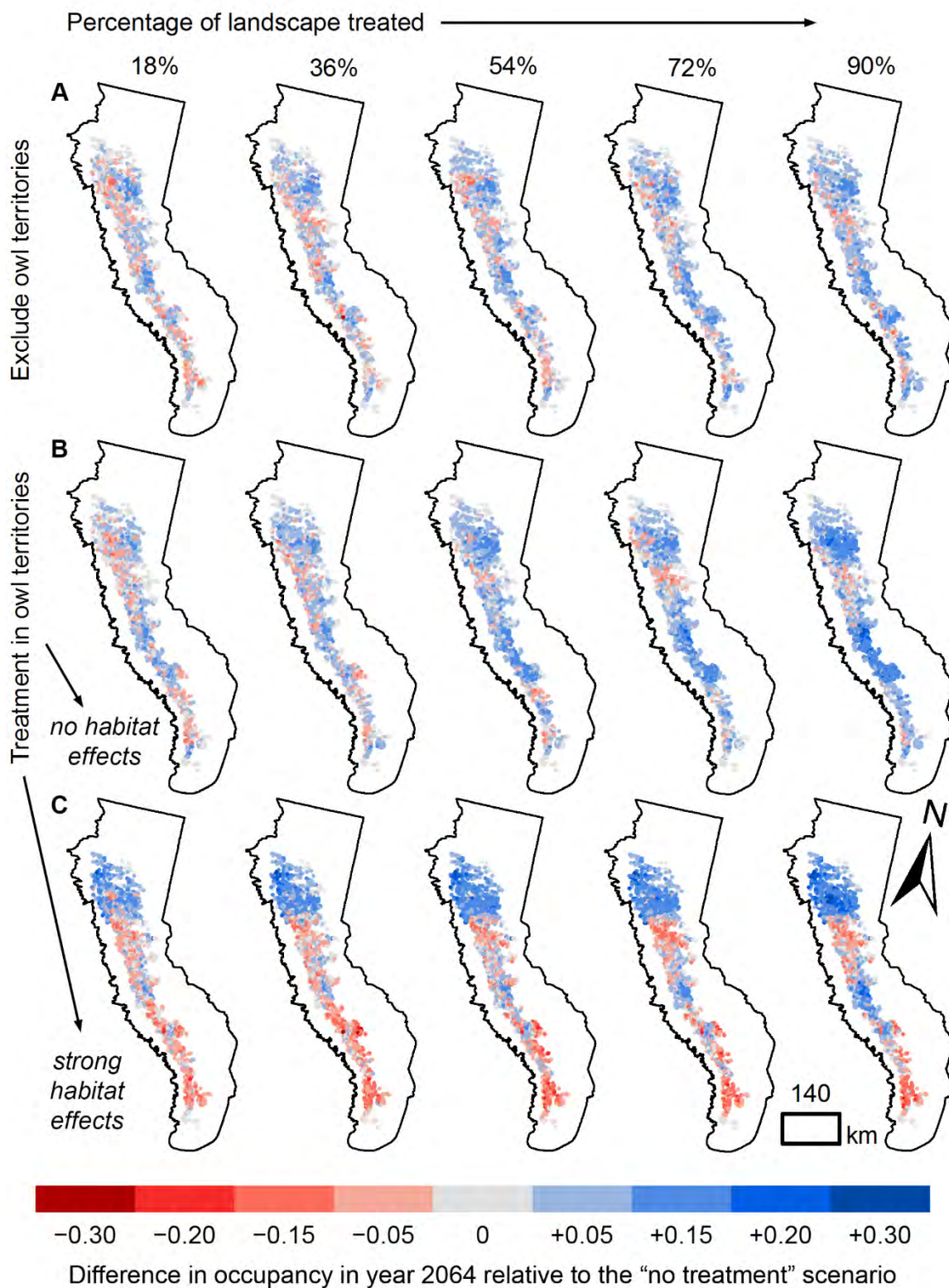


Figure 3.

Supplementary materials

Fire model

Fuels. Within our fire model, we used fire regime current condition class (FRCC) as a proxy for the effects of fire suppression (i.e., accumulation of fuels and altered stand structure/composition). We acknowledge that other factors can alter vegetation condition, but fire suppression has been the major driver of vegetation change in the Sierra Nevada over the past century (Collins et al. 2017). FRCC is a metric that characterizes how land management decisions have affected ecosystems (LANDFIRE project; www.landfire.gov). Specifically, FRCC quantifies the degree to which current vegetation differ from the historical range of variability (HRV) under a natural fire regime on a continuous scale of 0–100% (Keyser and Westerling 2019). This continuous departure metric, which refers to changes in vegetation composition, are categorized into three groups: FRCC1, which represents areas within HRV (<33% departure); FRCC2, which represents areas that are moderately departed HRV (33 to 66% departure); and FRCC3, which represents areas that are highly departed and outside HRV ($\geq 67\%$ departure).

We used two sets of FRCC treatments within an existing mask defining areas where mechanical fuel reduction treatments are feasible (Collins et al. 2010) on non-subalpine federal lands in the Sierra Nevada bioregion. A federal ownership administrative mask provided by USDA Forest Service Pacific Southwest Region (PSW) defined the first treatment set. Fuel reduction treatments were simulated by modifying FRCC classes 2 or 3 to class 1 (Westerling 2018). Six treatment layers were produced with 18% increments between treatment extents for our analysis: 0% (i.e., no treatment), 18%, 36%, 54%, 72%, and 90% (Fig. S2). Each treatment

layer was nested within the mask of the next highest percentage treatment layer. As an example, the 18% layer was randomly sampled from the 36% layer, not the 90% layer. As noted in the main text, treatment levels (18%, 36%, 54%, 72%, and 90%) refer to the percentage of treatable lands (public lands without significant operational constraints) that are restored to FRCC class 1, which reflect a fraction (~36%) of the entire Sierra Nevada landscape (Fig. S4).

The second treatment set excluded mapped owl territories within the administrative mask, resulting in a 10% reduction in total treatable area. For the treatments excluding owl territories, we started with the 100% administrative treatment layer and masked out all owl territories to create a new maximum potential treatment layer, which represented 90% of the treatable landscape. In order for each scenario to match the total treatment extent from the first treatment set, we used the new out of territory (OOT) 90% treatable layer and sequentially selected 72, 54, 36, and 18% of pixels as treatment pixels. As in the first treatment set, each fractional layer nests within the mask of the next higher percentage treatment layer. We used map algebra to change FRCC values in the treatment mask from FRCC 2 or 3 to 1 from the original FRCC values. With the exclusion of the owl territories, it was not possible to treat the same pixels in the two FRCC treatment sets, but we treated an equivalent number of pixels in the 18-90% treatment layers. The effect of excluding owl territories on the potential area treated is evident at the fine scale (see Fig. S3 for inset images from Fig. S2). In some areas, owl territories made up large proportions (up to 0.8) of large-scale ($1/16^{\text{th}}$ degree) modeling pixels (Fig. S15), which strongly limited the potential for treatment to reduce severe fire activity in our model when treatments were excluded from territories.

Fire occurrence data. We downloaded fire severity polygons from USDA Forest Service Region 5 that classified burn severity as percent change in basal area for years 1984-

2015. We used the 90% basal area (BA90) killed value as our measure of high severity fire occurrence (USDA 2017). This dataset was the dependent variable for all fire modeling.

Large scale (LS) model. We fit a spatially explicit logistic regression model (m1; Fig. S1) on a 1/16th degree latitude/longitude grid to estimate the monthly probabilities of the occurrence of at least one fire >400-ha as a function of topography, human population, vegetation fraction, and climate using the glm function in R (Westerling 2018). Human population and vegetation data were obtained from ref. (Sleeter et al. 2017). Climate data were obtained from the Livneh Research Group at the University of Colorado, Boulder (B. et al. 2013). Additional details about LS data can be found in ref. (Westerling 2018). Model specifications were compared using AIC to select for parsimonious models despite the presence of spatially auto-correlated variables (Akaike 1974, 1981). Specifications tested here extend models used in (Westerling et al. 2011a) to a finer spatial scale (1/16th degree latitude/longitude grid instead of 1/8th degree). The selected model was validated by applying parameters calculated with the first half of the data (1984-1999) to the full sample, and comparing Spearman's rank correlations over each period with correlations for the model estimated with the full 30-year sample (Westerling 2018). For each fire >400-ha, the probability of >50-ha burning in BA90 was estimated by fitting a logistic regression (m2; Fig. S1) with climate covariates using the glm function in R. To estimate the conditional extent of BA90 burned area, for each fire with >50-ha BA90 burned, a generalized Pareto distribution (GPD) was fit with climate and FRCC covariates (m3; Fig. S1).

Large-scale BA90 area burned was simulated for each climate and treatment scenario as follows. First, we repeated random draws from the binomial distribution using probabilities from LR1 to generate large (>400-ha) fire occurrence. For each simulated large fire, a random draw

from the binomial distribution using probabilities from LR2 was used to generate BA90 occurrence >50-ha. For each BA90 occurrence >50-ha, a random draw from the generalized Pareto distribution using probabilities from the GPD was used to generate total BA90 area.

The logit, defined as $\ln(\mathbf{p}/(1 - \mathbf{p}))$, where $\mathbf{p}$ refers to the probability of large fire (>400-ha) occurrence, was modeled as follows:

$$\ln\left(\frac{\mathbf{p}}{1 - \mathbf{p}}\right) = \boldsymbol{\beta}_m \times g(AETmu_i, CWDmu_i) + \sum \boldsymbol{\beta}_m \times g(AETmu_i, CWDmu_i) \\ \times q_m(X_{mij}) + \sum \boldsymbol{\beta}_m \times X_{mij}$$

where X_{mij} is the m th explanatory variable for location i and month j (see Table S3 for further description), $g(AETmu_i, CWDmu_i)$ was a semiparametric function g of the interaction between long term average evapotranspiration ($AETmu_i$) and long-term average climatic water deficit ($CWDmu_i$), $q_m(X_{mij})$ was a parametric or semiparametric function of the m th explanatory variable (Hastie et al. 2001), and $\boldsymbol{\beta}$ are estimated parameters (Westerling 2018). Semiparametric functions are splines and thin-plate splines expanded into basis functions that can be used linearly in the regression (Preisler and Westerling 2007). Similar mixed parametric and semiparametric models have been used by for seasonal forecasting and climate change impact assessment (Preisler and Westerling 2007, Preisler et al. 2008, 2011, Westerling et al. 2011b, 2011a). Long-term average climatic water deficit and evapotranspiration best predict the occurrence of coarse vegetation types on the landscape (Stephenson 1998), which in turn shape the frequency, extent and severity of fire in response to shorter term climatic variability (Westerling 2009, Westerling et al. 2009, Krawchuk and Moritz 2011). Prior work has extended

this to modeling fire presence/absence using cumulative moisture deficit (Westerling et al. 2011b, 2011a).

The best fit presence/absence model for 50-ha or more of BA90 area conditional on a 400-ha fire being present was a generalized linear model using cumulative monthly climate water deficit (CWD_{ij}), cumulative monthly actual evapotranspiration (AET_{ij}), cumulative water year climate water deficit ($CWD0_{ij}$), and June-July-August (JJA) average temperature ($Tjja_{ij}$). The extent of BA90 area conditional on 50-ha BA90 being present was estimated using a generalized Pareto distribution fit to climate and vegetation characteristics as covariates. Model specifications were assessed using AIC (Akaike 1974, 1981, Burnham and Anderson 2002).

The best fit generalized Pareto distribution for BA90 extent had a constant shape parameter and a scale parameter modeled as a linear function of monthly climate water deficit (CWD_{ij}) and the interaction between cumulative current water year climate deficit and grid cell fraction in fire regime current condition (FRCC) classes 2 and 3 ($CWD0_{ij} \times FRCC23_i$), where $FRCC23_i$ was normalized to provide a continuous variable not bounded by [0,1] as:

$$FRCC23_i = \log((f23_i)/(1 - f23_i))$$

In order to make this model relevant to spotted owl territories, we developed a framework to downscale our predictions of high severity fire from 1/16th (LS) degree to 30-m resolution fine-scale model (FS) (see below).

We obtained gridded downscaled climate simulations for 1950-2099 from two global climate models using the Representative Concentration Pathway (RCP) 8.5 emissions scenario (see ref. (IPCC AR5 WG1 2013)) via Scripps Institution of Oceanography, including global models from Centre National de Recherches Météorologiques (CNRM-CM5, see ref. (Voldoire et al. 2013)), the Canadian Centre for Climate Modeling and Analysis (CanESM2, see refs.

(Arora and Boer 2010, Christian et al. 2010)). These climate models represent a subset of models selected by California's Fourth Climate Change Assessment (CCCA4) (<http://www.climateassessment.ca.gov/>). A set of filters were applied by CCCA4 at global, regional, and California scales to obtain models that realistically represent variability for California in selected hydrologic variables and the climatological drivers of that variability. RCP 8.5 describes a world where emissions rise rapidly in coming decades. Climate scenarios were downscaled to a 1/16 degree lat/lon grid using the Localized Constructed Analogs (LOCA) statistical downscaling methodology (Pierce et al. 2014).

Fine scale (FS) model. We used historical fire severity data for the Sierra Nevada with vegetation and topography to develop a static presence/absence model of high severity fire at 30-m scale. We then used this model to create a set of 30-m probability surfaces of high severity fire for a range of fire size classes for the Sierra Nevada bioregion. Previous work found that topography was the most important predictor of high severity fire occurrence when sampling individual 30-m pixels (Dillon et al. 2011). We developed a suite of topographic variables from a 30-m digital elevation model (DEM). We transformed aspect to calculate the heat load index (HLI) and topographic radiation aspect index (TRASP) using the Geomorphometry and Gradient Metric toolbox in ArcGIS (Evans et al. 2014). We created topographic position indices (Jenness 2013) in four and six classes with 1-km and 2-km radii. We also created layers of elevation and percent slope. We used three hierarchical levels of vegetation information taken from the Landfire v.1.4.0 existing vegetation type (EVT) layer: EVT, existing vegetation type physiognomy (EVT_PHYS; e.g., conifer, hardwood, grassland), and plant functional type (PFT). PFT is the coarsest classification and results in 97 EVTs in the Sierra Nevada aggregated to six PFT's: forest, grass, shrub, riparian, exotic, and non-vegetated.

For all fires >400-ha, we calculated the distribution of fires where the total fire size was greater than or equal to 85% of the average vegetated area of the LS grid cells (1/16th degree) to align with prior Sierra Nevada modeling efforts (Westerling 2018). This produced a minimum fire size of 3290-ha. We ordered the fires that intersected the Sierra Nevada bioregion by total area burned. Applying the minimum fire size limit left 264 fires that we separated into seven fire size bins. With the exception of the largest bin, each bin includes fires that span the length of the fire severity record, 1984-2015. The largest fires have occurred since 2002, resulting in the largest bin including only the most recent fires. We chose 2-3 fires from each size class to build the downscaling model (Table S4). While we attempted to be as objective as possible in selecting fires for model development, a degree of subjectivity was necessary to achieve full spatial and temporal coverage of the study area. All fires selected for model development occurred after 2000 (the Landsat acquisition year for the imagery used in the Landfire existing vegetation and FRCC layers), and where possible, each bin contained fires that were distributed North-South. We selected twenty fires to train and test our downscaling model, choosing fires that produced the fullest coverage of year, ignition month, total fire area and fraction of BA90 (Table S4).

We used a presence/absence approach to model presence of high severity fire pixels in each fire. Individual fire pixels were classified as 0 (absent) or 1 (present), where 1 represented pixels that burned at BA90. The set of fires selected for training the downscaling model resulted in 556,444 pixels with nearly equal representation of presence and absence (47.8% of these had a value of 1, 52.2% had a value of 0). Having true absence values, especially when equivalent in number to presence ensures that accuracy assessments are unbiased and more robust. We used all training pixels to sample the independent variables and used the rfUtilities package in R (Murphy et al. 2010, Evans and Murphy 2018) to select the best model using a classification and

regression tree approach, Random Forest (Breiman 2001). We evaluated model accuracy using Cohen's Kappa and the area under the Receiver Operating Curve (AUC) using the rfUtilities package in program R (Evans and Murphy 2018). The best fit model included existing vegetation type (EVT), heat load index (HLI), elevation, percent slope, total fire size (ha), and six class topographic position index (Cohen's Kappa = 0.8175, AUC = 0.9085, percent correctly classified = 90.88%) (Figure S16). We used the best model to create a set of probability surfaces corresponding to seven fire size class bins; each 30-m pixel was assigned a probability of burning at BA90 for fires in each bin. The remaining classification variables did not vary temporally so the same set of probability surfaces were used for all management and climate change scenarios.

The logit and generalized Pareto distribution models (LS), driven by GCM and fuel treatment scenarios, produce annual distributions of fire size and severity at 1/16th degree (LS). Each fire occurrence was assigned to the appropriate fire size bin and allocated to the 30-m landscape (FS) with a Monte Carlo simulation drawing from the probability surface for the corresponding fire size bin. Starting with a randomly assigned ignition point within the LS modeling pixel, FS pixels were allocated as BA90 (true/false) in an iterative fashion based on the probability surface until the predicted fire size was reached. This process was repeated 100 times for each unique treatment/climate combination. Tests of the simulation approach revealed that simulated BA90 probabilities very closely approximate empirical BA90 patterns from real fires (Fig. S17). To ensure that a pixel was not assigned to more than one fire in a given year or assigned a repeat fire in too short an interval, each pixel was deactivated for 9 years before it could be burned again. There is limited information on the actual time interval between high severity fires in the Sierra, but research suggests previous fire occurrence limited high severity

fire for 9 years (Collins et al. 2009). After each fire was allocated to the landscape, the number of BA90 pixels intersecting owl territories was estimated for each year and passed to the spatial occupancy model.

We note that while the simulated probability of BA90 closely approximated the observed BA90 pattern (Fig. S17), there was a tendency within individual simulations for the simulated BA90 patches to have a more evenly sprinkled “salt shaker” type distribution, whereas the observed pattern would be expected to be more clumped. That is, spatial autocorrelation was relatively weak at fine spatial scales. We expect that the effects of that lack of clumping would average out over the 100 simulations of the FS model that were delivered to the spotted owl spatial occupancy model, but ultimately may have resulted in more conservative (less negatively impactful) severe fire effects to owls than would be expected (Jones et al. 2016a). Nevertheless, future revisions to the spatial allocation algorithm could include a spatial autocorrelation parameter that enforces clumping patterns that even more closely approximate real observed BA90 patches.

Population model

Spatial occupancy model for spotted owls. We completed repeat within-season detection/non-detection surveys in $n=275$ spotted owl sites on four demographic study areas between 1993-2011 (Tempel et al. 2016, Jones et al. 2018). On all study areas, Sierran mixed-conifer montane forest was the dominant vegetation type, elevations ranged from 300-3050 m, and climate was Mediterranean (Tempel et al. 2016). We used vocal lures during surveys to detect owls. A survey in which no owls were detected needed a total duration of ≥ 30 -min to be included as an absence record. We excluded nocturnal detections of unknown owls (i.e., owls that were not re-sighted by unique color leg-bands as part of a concomitant mark-recapture study) that occurred outside of a

delineated territory boundary using a Geographic Information System (GIS) to eliminate potential spurious positive detections of transient owls not occupying the nominal sites. Extensive details about each study area and additional survey details have been published (Tempel et al. 2016).

We modeled site occupancy dynamics using a Bayesian multi-season spatial occupancy model (Chandler et al. 2015). The spatial dependence in the model's structure allowed occupancy dynamics of the 275 surveyed sites to be modeled within a broader network of 1844 known or imputed sites that represented nearly all suitable habitat in the Sierra Nevada. The process model defines dynamics in the binary occupancy state of spotted owls across $i = 1, 2, \dots, R = 1800$ sites and years $k = 1, 2, \dots, K = 53$ as

$$z_{ik} \sim \begin{cases} \text{Bernoulli}(\psi_i), & \text{if } k = 1 \\ \text{Bernoulli}(\gamma_{i,k-1}(1 - z_{i,k-1}) + (1 - \varepsilon_i(1 - \gamma_{i,k-1}))z_{i,k-1}), & \text{if } k > 1 \end{cases}$$

where $z_{i,k} = 1$ denotes that site i is occupied in year k and $z_{i,k} = 0$ denotes that site i is not occupied in year k . In the initial year of the model, $z_{i,k}$ depends only upon the initial occupancy, ψ_i . In subsequent years $z_{i,k>1}$ is dependent upon the previous occupancy state of site i and its neighbors n_{ih} : it is sampled from the function $h(\gamma_{i,k-1}, \varepsilon_{i,k-1}, z_{i,k-1})$ where $\varepsilon_{i,k-1}$ and $\gamma_{i,k-1}$ respectively describe probabilities for extinction (transitioning from occupied to unoccupied) and colonization (transitioning from unoccupied to occupied). Covariates were selected *a priori* based on published information regarding spotted owl habitat-occupancy associations (Jones et al. 2018). Extinction probability ($\varepsilon_{i,k-1}$) was modeled as

$$\begin{aligned} \text{logit}(\varepsilon_i) = & \beta_0 + \beta_1 \text{central}_i + \beta_2 \text{south}_i + \beta_3 \text{lgTree.hiCanopy}_i + \beta_4 \text{lgTree.medCanopy}_i \\ & + \beta_5 (\text{lgTree.hiCanopy}_i \times \text{central}_i) + \beta_6 (\text{lgTree.hiCanopy}_i \times \text{south}_i) \\ & + \beta_7 (\text{lgTree.medCanopy}_i \times \text{central}_i) + \beta_8 (\text{lgTree.medCanopy}_i \times \text{south}_i) \end{aligned}$$

where β_{0-2} were intercepts that varied by latitudinal bioregion (*north* was the reference category); β_{3-4} were forest structural variables representing the proportion of each owl site containing the spatial intersection ($\cap$) of large trees (quadratic mean stand diameter ≥ 61 cm) and high canopy closure ($\geq 70\%$ canopy cover), and large trees and medium canopy closure (40-70% canopy cover), respectively (Jones et al. 2018); and β_{5-8} were interactions that allowed the slopes of β_{3-4} to vary across bioregions.

Defining colonization $\gamma_{i,k-1}$ began by defining the probability that site i was colonized by an individual from site h in year k as

$$\rho_{ik,h} = \rho_0 \exp\left(-\frac{d_{i,h}^2}{2\sigma^2}\right) z_{i,k-1} n_{ih}$$

where ρ_0 was the baseline colonization probability for coincident sites, $d_{i,h}$ was the Euclidean pairwise distance between sites, σ was the scale parameter determining the decay rate in colonization probability from ρ_0 as a function of distance, n_{ih} was an $i \times h$ neighborhood matrix that limited colonizing sites to those occurring within the approximate 95th percentile of breeding dispersal distances for spotted owls (25-km, ref. (Blakesley et al. 2006)). We used the neighborhood matrix to limit the number of potential colonizing sites, which helped facilitate model fitting; we note that truncating the dispersal distance is not likely to bias results (Zhao et al. 2017). This parameterization enforced the condition that site i could not be colonized by site h if $z_{h,k-1}=0$ (i.e., an unoccupied site does not contribute potential colonizers). The probability of a colonization event was thus

$$\gamma_{ik} = 1 - \left\{ \prod_{h=1}^M 1 - \rho_{ik,h} \right\}$$

where M was the total number of sites in i 's neighborhood. Like ref. (Chandler et al. 2015) we also allowed for a pseudo-rescue effect (Brown and Kodric-Brown 1977) in which extinctions were less likely to be observed at highly connected sites than at isolated sites, because the former sites have a greater chance of being colonized immediately after extinction. The pseudo-rescue effect was modeled as

$$\phi_{i,k-1} = 1 - \varepsilon_i(1 - \gamma_{ik})$$

indicating that the probability that an occupied site remains occupied ($\phi_{i,k-1}$) was one minus the probability that it went extinct and was not recolonized.

The observation model was

$$y_{ik} = \text{Bernoulli}(z_{ik} * p_i)$$

$$\text{logit}(p_i) = \alpha_0 + \alpha_1 \text{lgTree.hiCanopy}_i + \alpha_2 \text{lgTree.medCanopy}_i$$

where p_{ijk} was the probability of detecting an individual when it was present, α_0 was the intercept, α_1 and α_2 were the regression coefficients for detection, and covariates were the same as those used to model the extinction process above. We included the same covariates when modeling detection as we did modeling extinction to account for potential detection biases associated with habitat covariates.

We chose flat prior distributions for all model parameters: *Uniform*(−40, 40) for all α and β coefficients because habitat-related covariate values were proportions ranging from 0 to 1; *Uniform*(0, 1) for ψ_1 and ρ_0 ; and *Uniform*(0, 40) for σ . After an adaptation phase of length 5000, we sampled posterior distributions using three Markov chains each of length 15,000. Markov-Chain Monte Carlo simulation was conducted using JAGS (Plummer 2003) in program R (v

3.3.2) using the package jagsUI (v 1.4.4) (Kellner 2016). Convergence was assessed using the Gelman-Rubin diagnostic ($\hat{R}$), where we considered values <1.1 to indicate convergence. We also assessed trace plots to ensure chains were not still moving toward the stationary distribution.

Development of the patch network. We developed a network of ($n = 1844$) California spotted owl sites spanning the Sierra Nevada, which acted as patches in the metapopulation model (Fig. S14). The metapopulation network began with $n = 1422$ known spotted owl protected activity centers (PACs) delineated by the USDA Forest Service (USFS) during 1993-2011. PACs represent approximately 121-ha of the highest quality surrounding the known location of every territorial owl, or pair of owls, that have been detected at any time on USFS land in the Sierra Nevada. Other ownerships, such as national parks or private lands, do not have PACs but still contain areas that are used by spotted owls throughout the Sierra Nevada. With additional known owl territories from non-USFS ownerships, we identified a total of ($n = 1494$) previously delineated PACs and territories in the Sierra Nevada (Fig. S14).

The spatial area that spotted owls actively defend is commonly referred to as the “territory”, which is larger in size than the 121-ha PAC (254-639 ha) and increases with latitude (Tempel et al. 2016). For the sake of clarity we hereafter refer to all areas that were (a) originally delineated as PACs, (b) identified as owl territories but had no associated PAC, or (c) randomly generated *potential* spotted owl PACs/territories (see below) as “owl sites” or “patches” interchangeably. However, and as is described in more detail below, we collected site-specific covariate information at the scale of the owl *territory* to be used in our spatial occupancy model in part because habitat and disturbance covariates of interest in the present study have been strongly linked to owl occupancy dynamics at the territory scale (Jones et al. 2016a, 2018).

Therefore, the spatial extent of an “owl site” or “patch” is here best interpreted to be equivalent to an owl territory.

Some gaps were present within the known patch network, but it was unclear whether these gaps were ecologically meaningful or a sampling artifact because owl sites were identified incidentally, not systematically. We used a Sierra Nevada-wide spotted owl habitat suitability index (HSI; JJ Keane *unpublished data*) to identify areas most likely to contribute to the owl population where no patches were currently known to exist. To fill gaps in the patch network, we generated $n = 350$ of points at random locations across the Sierra Nevada, but constrained their locations to occur (1) at least the mean nearest neighbor distance from existing owl site centers in the network ($\bar{x}_{NND} = 2423.6$ m) and (2) in areas with HSI values above the 50th percentile (i.e., of putative higher quality). These points represented site centers, so we buffered the new points to match region-specific territory sizes for covariate estimation. The generation of $n = 350$ new territories yielded territory densities that approximately matched densities from regions with known territory locations (Fig. S14).

Influence of treatments on owls. The current scientific literature lacks strong empirical evidence regarding temporal treatment effects on spotted owls. The detection of such effects might be obscured by the owl’s long lifespan and high site fidelity; that is, spotted owls may continue to occupy territories long after they become sub-optimal (Jones et al. 2018). On the other hand, a number of empirical studies suggest spotted owl territories that contain greater amounts of large trees and/or high canopy cover tend to have higher occupancy, higher survival, and higher reproduction than territories that contain less of this forest type (Blakesley et al. 2005, Tempel et al. 2014a, 2016, Jones et al. 2016b, Gutiérrez et al. 2017). One approach for modeling potential treatment effects on spotted owls, therefore, involves a space-for-time substitution,

positing that future processes can be predicted from existing spatial patterns (Pickett 1989). Using this approach we might reasonably assume, for example, that because owl territories with higher canopy cover have lower extinction rates, then extinction rates would be expected to increase if canopy cover is reduced as part of a treatment (Tempel et al. 2015a). Thus, in the present study, we approximated the effect of treatment on owls based on empirical relationships between forest characteristics and spotted owl occupancy rates (see below for additional details).

A primary proximate goal of treatments is to reduce the continuity of available fuels on the landscape. Treatments can act to reduce fuel continuity in at least two ways: decrease vertical continuity by removing ladder fuels that connect the understory to the canopy (increased vertical canopy separation), and decrease horizontal continuity by reducing overstory canopy cover (increased horizontal canopy separation) (Hessburg and Agee 2003, Agee and Skinner 2005). Changes in vertical continuity are more difficult to quantify than changes in horizontal continuity, and thus most approaches for measuring canopy cover estimate horizontal overstory closure. Therefore, although treatments that affect vertical continuity may alter important understory forest structures preferred by spotted owls, we focus hereafter on potential treatment effects to horizontal continuity and total canopy cover. In the Sierra Nevada, treatments often reduce total canopy cover in stands from greater than 70% to between 40% and 70% (North et al. 2007, Stephens et al. 2009).

The amount of forest in an owl territory characterized by both high total canopy cover (>70% overstory closure) and larger trees (>61 cm dbh) is the best predictor of spotted owl occupancy dynamics across the Sierra Nevada bioregion (Jones et al. 2018). Thus, one empirically-based approach to linking the potential effects of treatments to owl dynamics could involve re-allocating large tree/high canopy cover forest to large tree/medium canopy forest in

proportion to the extent of treatment that is applied (Marc Meyer, *personal communication*).

Preliminary analyses suggested local extinction probabilities were less positively (or sometimes negatively) associated with large tree/medium canopy cover forest compared to large tree/high canopy cover forest. Therefore, using this approach to approximate treatments would be expected to incur a mean negative effect on owl dynamics in the absence of any potential benefits related to the reduction of severe fire activity.

Treatment scenarios were applied to the entire Sierra Nevada using an algorithm that reduced FRCC classes 2 and 3 (i.e., forests outside of HRV) to FRCC class 1 (i.e., representative of HRV). When FRCC changed from class 2 or 3 to class 1 within portions of an owl site, we approximated potential effects to owls by re-allocating large tree/high canopy cover forest to large tree/medium canopy cover forest in proportion to the area treated. For example, if an owl site contained 100 ha of large tree/high canopy cover and 100 ha of large tree/medium canopy cover forest prior to treatment, and 25 ha of the owl site changed from FRCC 2 or 3 to FRCC 1, then following treatment the owl site would contain 75 ha of large tree/high canopy cover forest and 125 ha of large tree/medium canopy cover forest. Thus, we assumed that treatment would preferentially target large tree/high canopy cover forest. However, in practice, treatment likely targets a suite of forest types (not just large trees/high canopy cover), with particular focus on medium and small tree dominated types, so we also created scenarios that were more conservative where treatment effects were proportionally smaller (e.g., only 25% of treatments occurred in large tree/high canopy cover forest). We refer to the first and second scenarios as having “strong habitat effects” and “weak habitat effects”, respectively.

Forward projections of the population model. All posterior distributions achieved convergence ($\hat{R} < 1.1$) (Table S2). For each forward projection, we originally planned to

combine each iteration of the FS fire model output ($n = 100$) with each posterior parameter draw ($n = 45,000$) to ensure projections covered the full range of variation from the two data sources. However, this resulted in a computationally intractable number of simulations for each treatment/climate scenario ($100 \text{ fire runs} \times 45,000 \text{ posterior draws} = 4,500,000 \text{ simulations per scenario}$). Thus, to make forward projections computationally tractable, we sampled from a thinned posterior distribution ($n_{\text{sampled}} = 500$; $n_{\text{full}} = 45,000$). We used each posterior draw ($n_{\text{sampled}} = 500$) and FS fire output ($n = 100$) to project the spotted owl population forward $500 \times 100 = 50,000$ times over the period 2012-2064 for each treatment/climate scenario. Treatment effects within individual owl territories were modeled by modifying forest-structure covariate values in a manner consistent with expected changes in horizontal canopy structure due to fuel treatments (i.e., reducing fuel continuity by reducing canopy cover). Thus, when fuel treatments occurred within an owl's site (FRCC values within a pixel changed from FRCC 2 or 3 to FRCC 1), we approximated potential effects to owls by re-allocating large tree/high canopy cover forest to large tree/medium canopy cover forest in proportion to the area treated (see above). Severe fire effects were modeled by the addition of a parameter within the extinction function that represented an empirical effect of severe fire extent (proportion of territory area burned severely) on spotted owl local extinction rates determined by a natural before-after control-impact experiment (Jones et al. 2016a) (Fig. S1):

$$\begin{aligned} \text{logit}(\varepsilon_{ik}) = & \beta_0 + \beta_1 \text{central}_i + \beta_2 \text{south}_i + \beta_3 \text{lgTree.hiCanopy}_i + \beta_4 \text{lgTree.medCanopy}_i \\ & + \beta_5 (\text{lgTree.hiCanopy}_i \times \text{central}_i) + \beta_6 (\text{lgTree.hiCanopy}_i \times \text{south}_i) \\ & + \beta_7 (\text{lgTree.medCanopy}_i \times \text{central}_i) + \beta_8 (\text{lgTree.medCanopy}_i \times \text{south}_i) \\ & + \beta_9 \text{propSevere}_{ik} \end{aligned}$$

where β_9 was defined by a mean value of 8.23 (SD = 3.73) (Jones et al. 2016a), and *propSevere* was the proportion of an owl territory that experienced BA90 in a given year as determined by the FS fire model. Note that β_9 from ref. (Jones et al. 2016a) was generated using a broader definition of severe fire (75% mortality) than we use in this paper (90% mortality). We expect this means our simulations will yield severe fire effects on owls that are slightly more conservative (smaller in magnitude) than would be expected in reality. We generated a normal distribution of length $n=45,000$ for β_9 to match the length of posterior distributions for the other parameters used in the forward projection. To model potential semi-permanent vacancy of sites that experienced large amounts of severe fire (Jones et al. 2016a), we included a threshold effect (q) in the colonization function:

$$\gamma_{ik} = \begin{cases} 1 - \{\prod_{h=1}^M 1 - \rho_{ik,h}\} & \text{if } s_{i,1:k-1} < q \\ 0 & \text{if } s_{i,1:k-1} \geq q \end{cases}$$

where s was the proportion of the spotted owl site that experienced severe fire in year k of the forward simulation (via the fire model), and q was a threshold value (0.4, 0.5, or 0.6) that forced all future colonization probabilities to zero when exceeded. This parameterization allowed for (1) delayed extinction following high-severity fire because of the high site fidelity in spotted owls, which was observed following the 2013 Rim Fire (JJ Keane, *unpublished data*), and (2) severely-burned sites experiencing catastrophic habitat loss to be removed from the site network over the modeling period. For all inferences made in the paper, we used $q = 0.5$. However, we show the sensitivity of owl model results to varying the value of q to 0.4 or 0.6 in under the CNRM-CM5 GCM scenario in Figs. S18-S20.

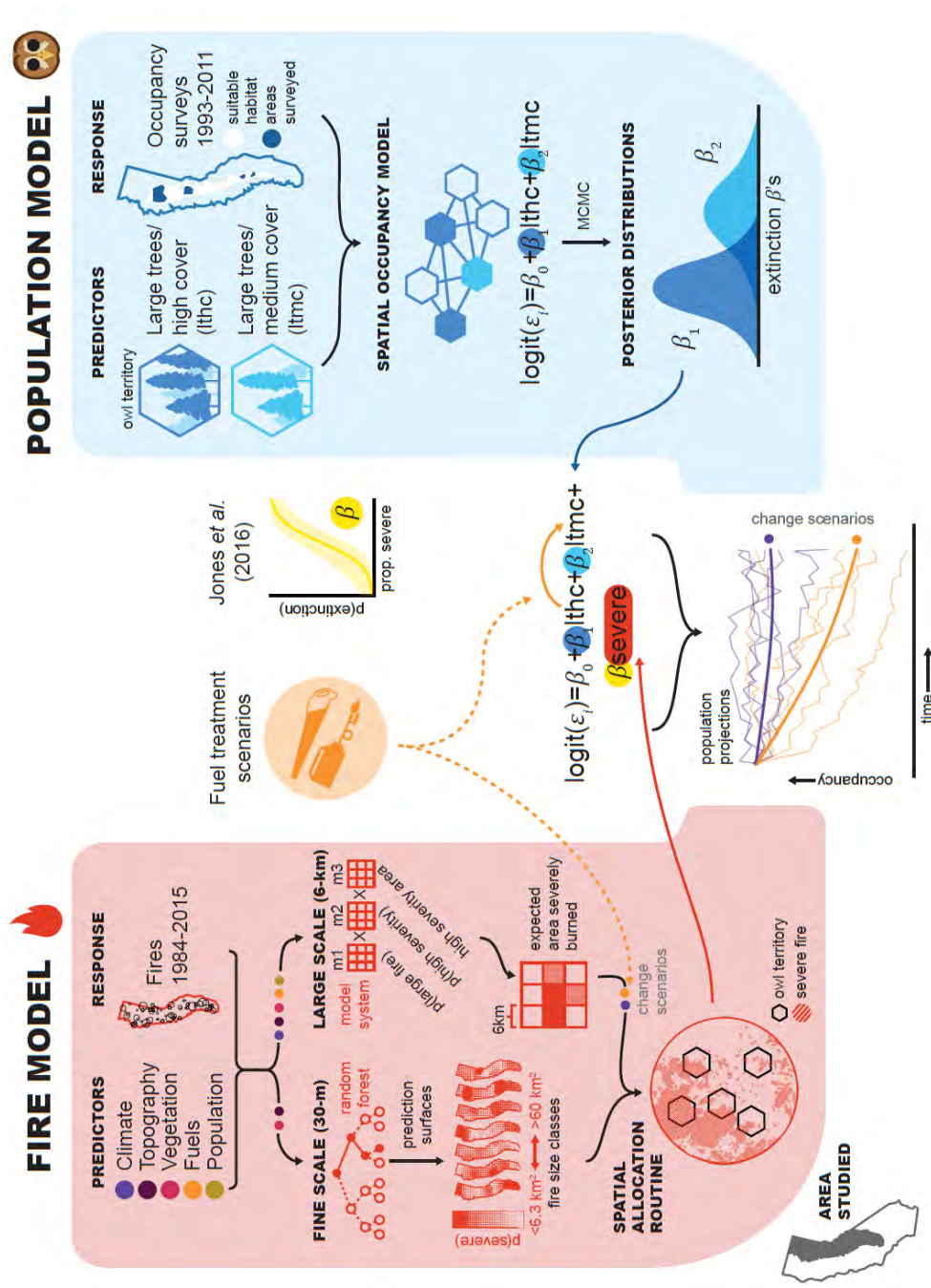


Fig. S1. Conceptual diagram showing the flow of information through the fire and population models and how they were linked during forward simulations.

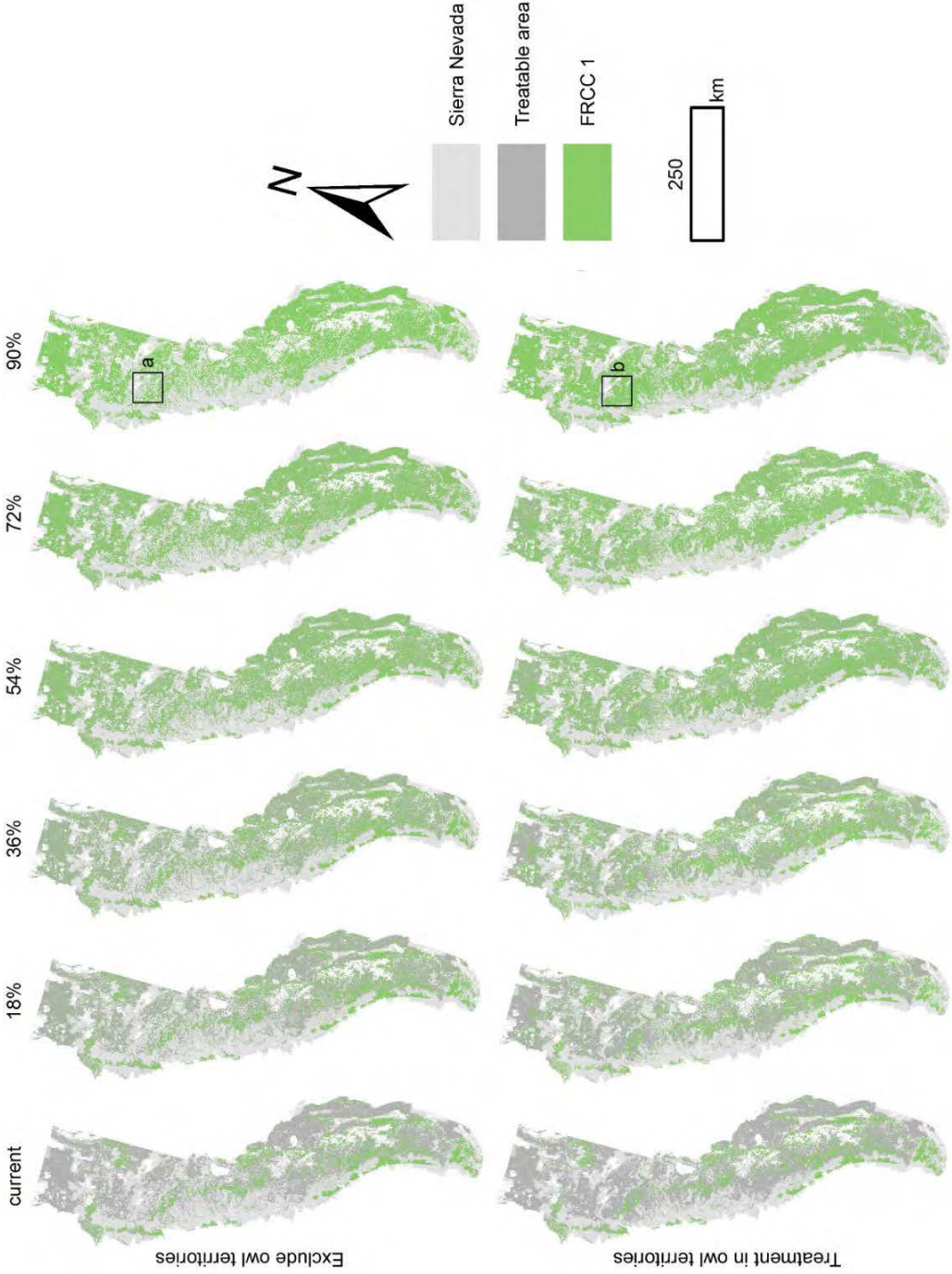


Fig. S2. Fuel treatment data that served as input data to the fire and population models.

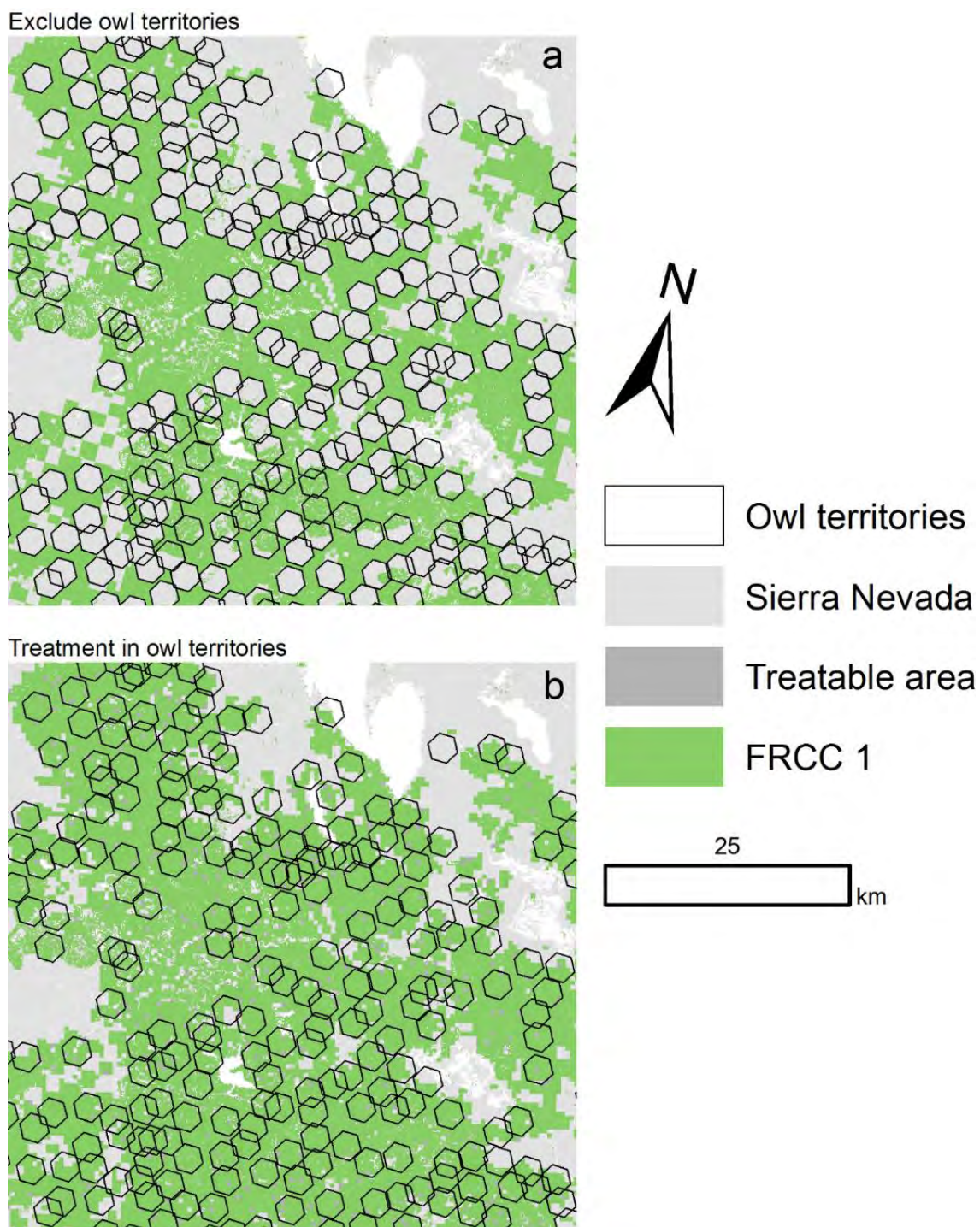


Fig. S3. Zoomed in figure showing fine scale effects of fuel treatment exclusion (corresponding with insets a and b from Figure S2).

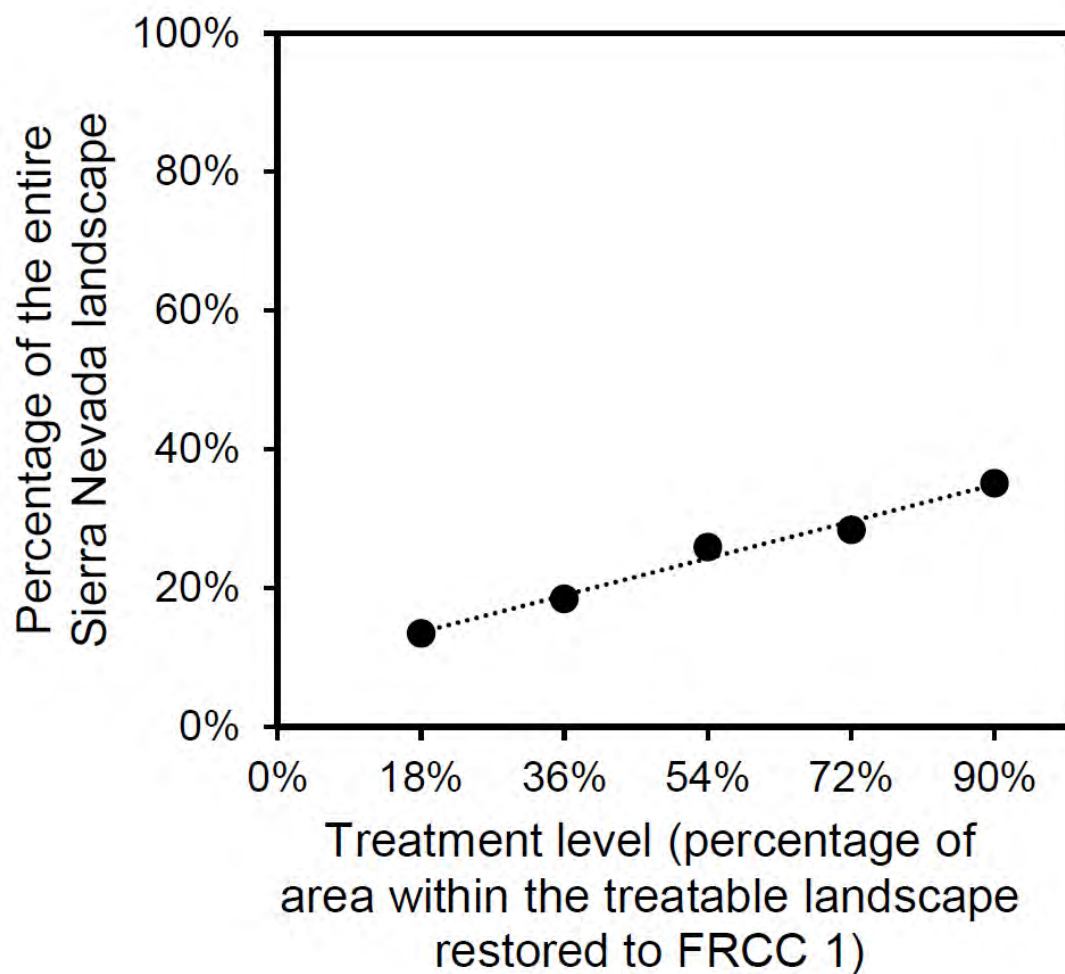


Fig. S4. Relationship between treatment levels (18%, 36%, 54%, 72%, 90%) and the percent area of the total Sierra Nevada landscape that each level comprises.

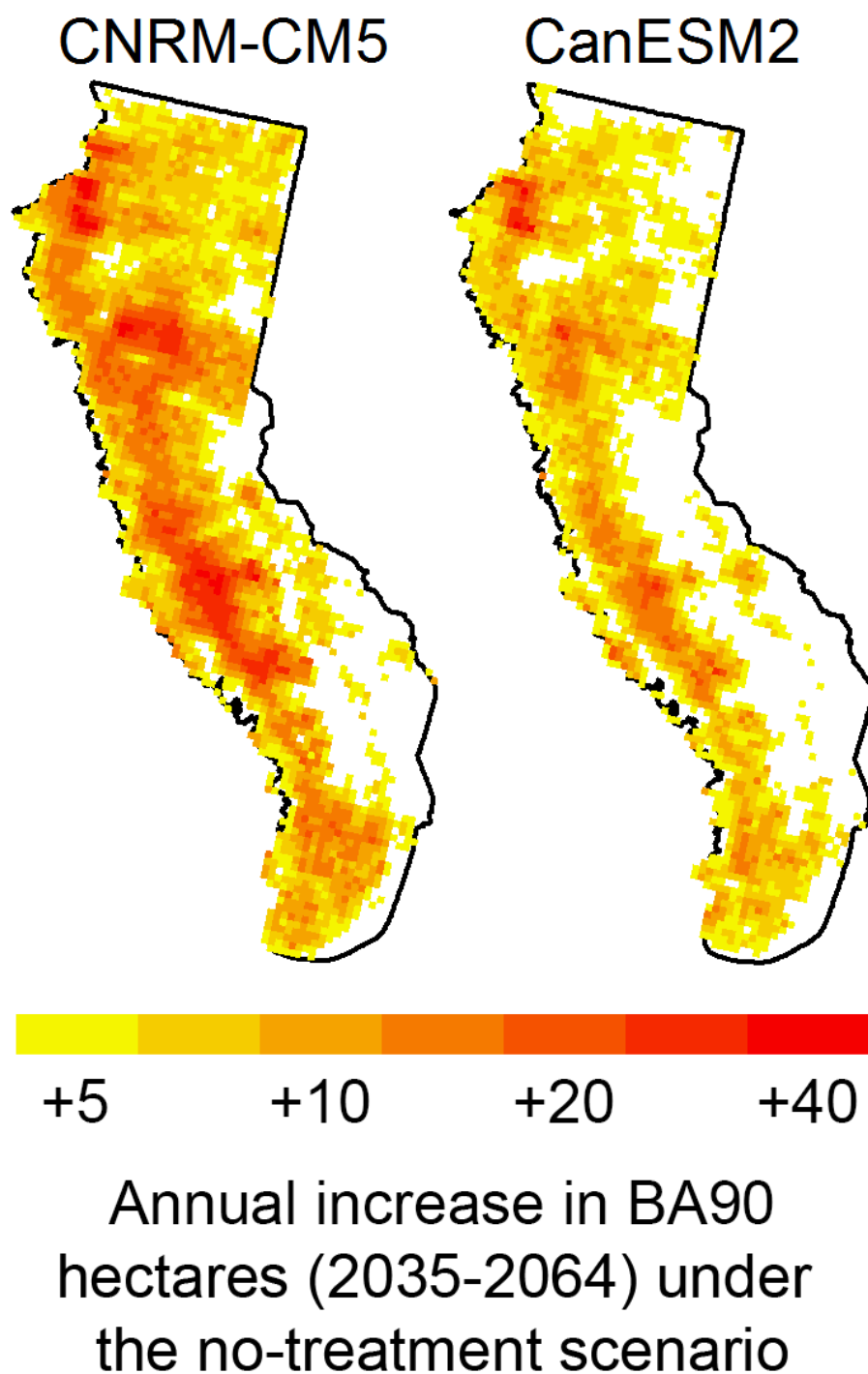


Fig. S5. Annual rate of change in BA90 area (hectares) from 2035-2064 under the no-treatment scenario for each GCM (CNRM-CM5 and CanESM2).

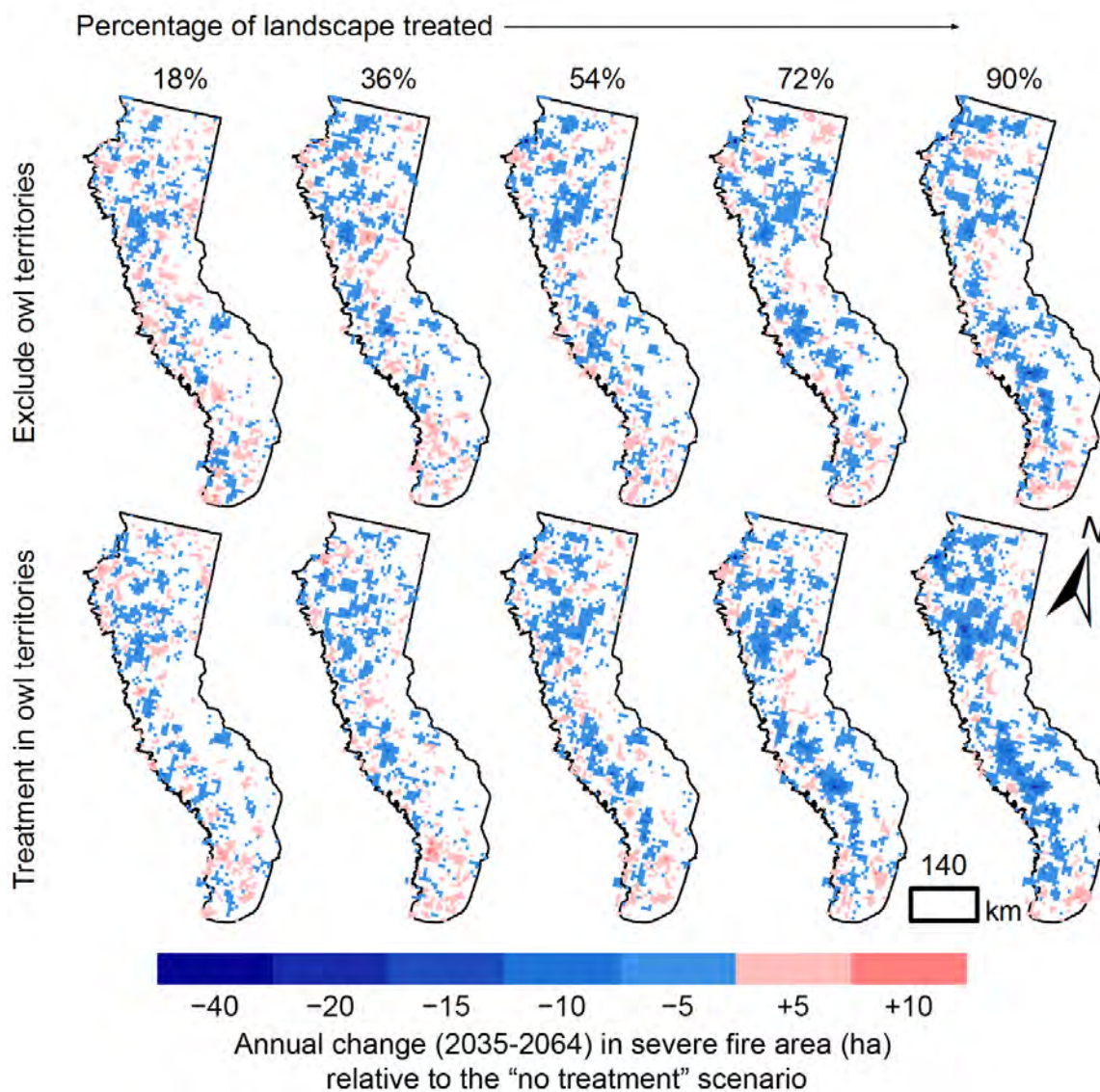


Fig. S6. Changes in severe fire (BA90) extent by mid-century (2035-2064) compared to the baseline no-treatment (0%) scenario. This figure is a repeat of Fig. 1 from the main text but for the CanESM2 GCM.

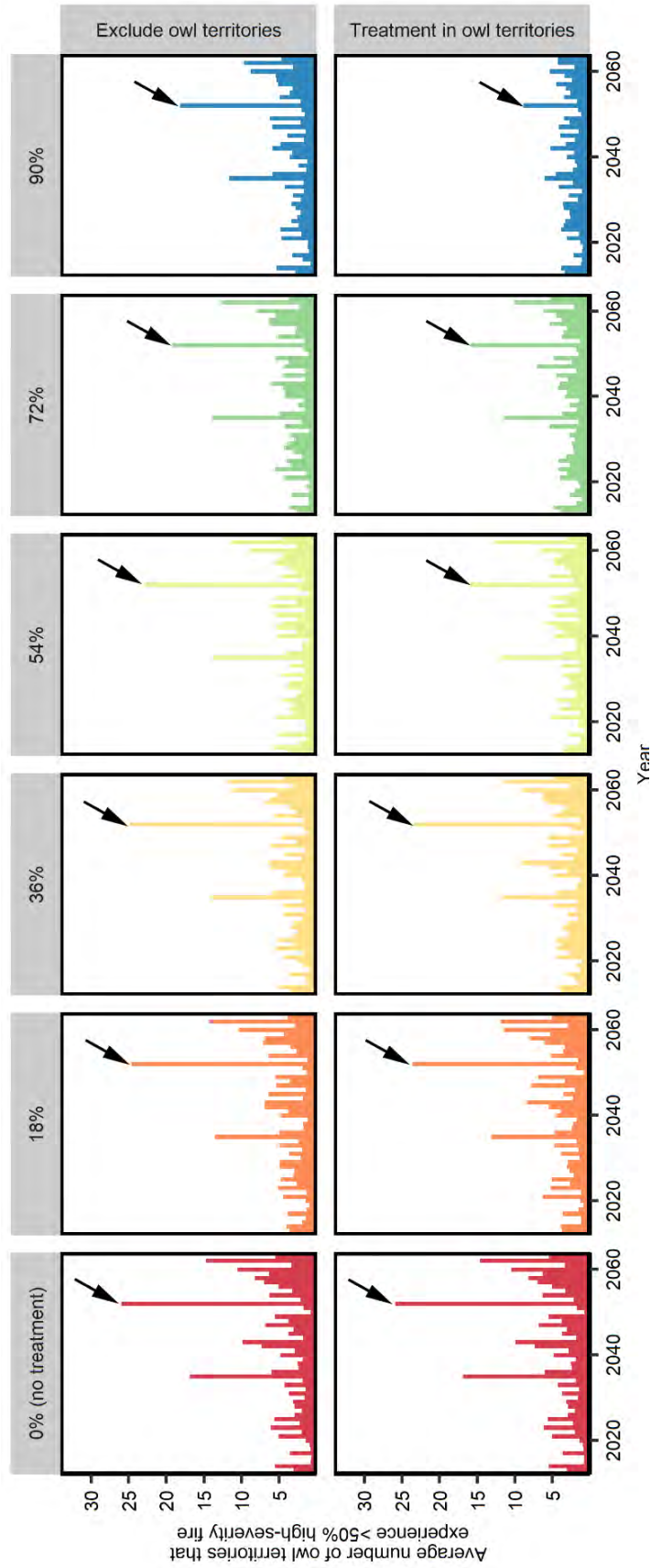


Fig. S7. Predicted changes in spotted owl territory exposure to extinction-inducing severe fire (>50% territory area burned at BA90) in the Sierra Nevada from 2012-2064. Each bar represents the number of owl territories per year affected by >50% severe fire averaged across 100 simulations of the fire model. The CRNM-CM5 global circulation model was used. Arrows point to an extreme fire year (2052).

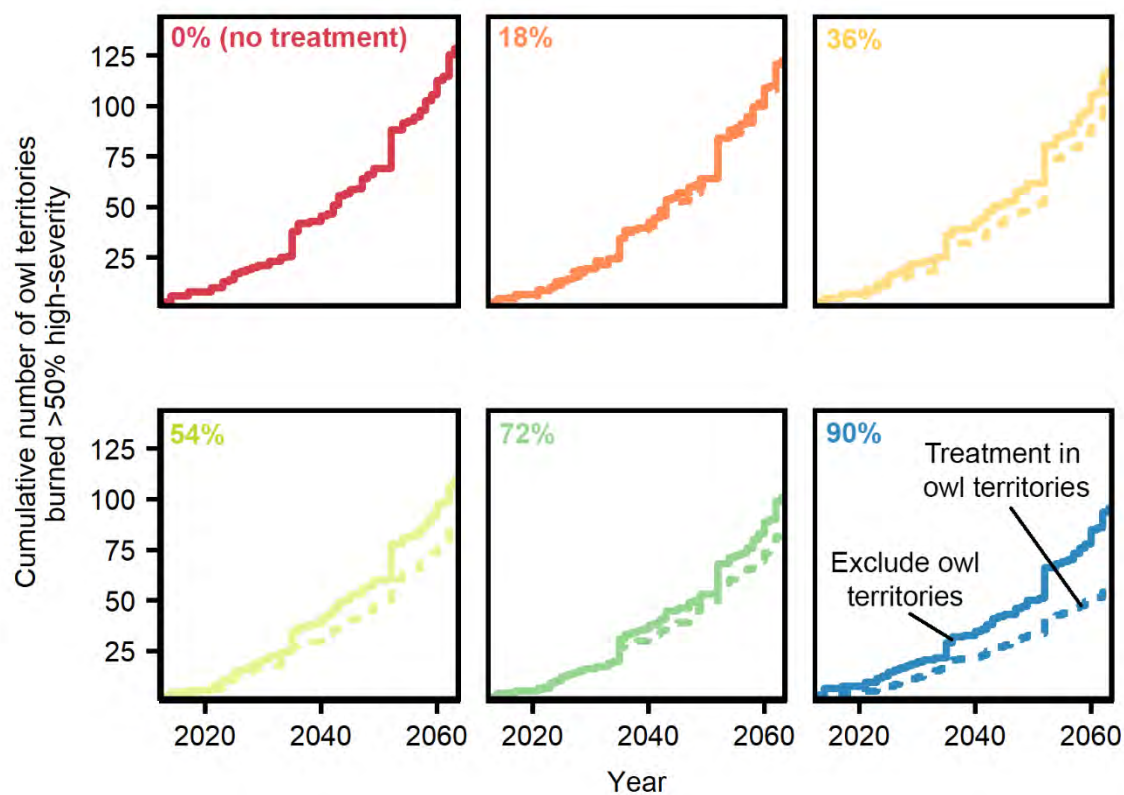


Fig. S8. Expected cumulative number of spotted owl territories exposed to extinction-inducing severe fire (>50% territory area burned severely) in the Sierra Nevada from 2012-2064 for each treatment level, averaged across 100 simulations of the fire model. Results produced using CNRM-CM5 GCM.

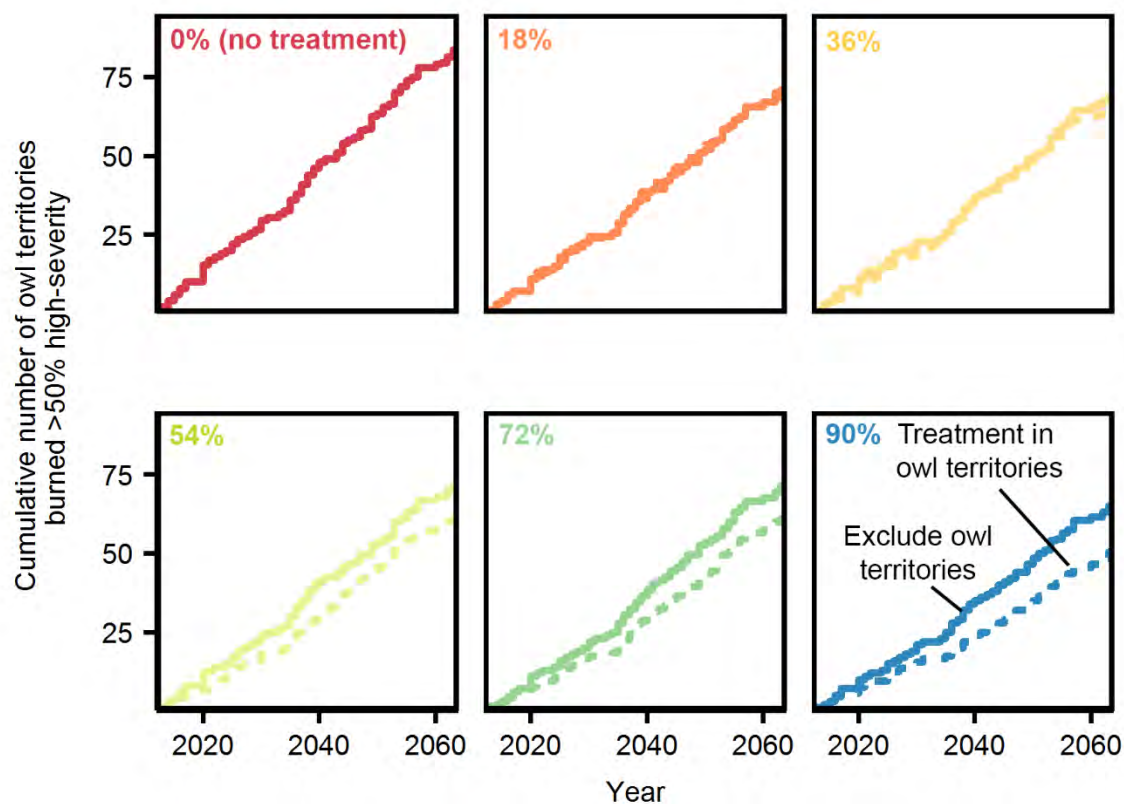


Fig. S9. Expected cumulative number of spotted owl territories exposed to extinction-inducing severe fire (>50% territory area burned severely) in the Sierra Nevada from 2012-2064 for each treatment level, averaged across 100 simulations of the fire model. This is a repeat of Figure S8 but for the CanESM2 GCM.

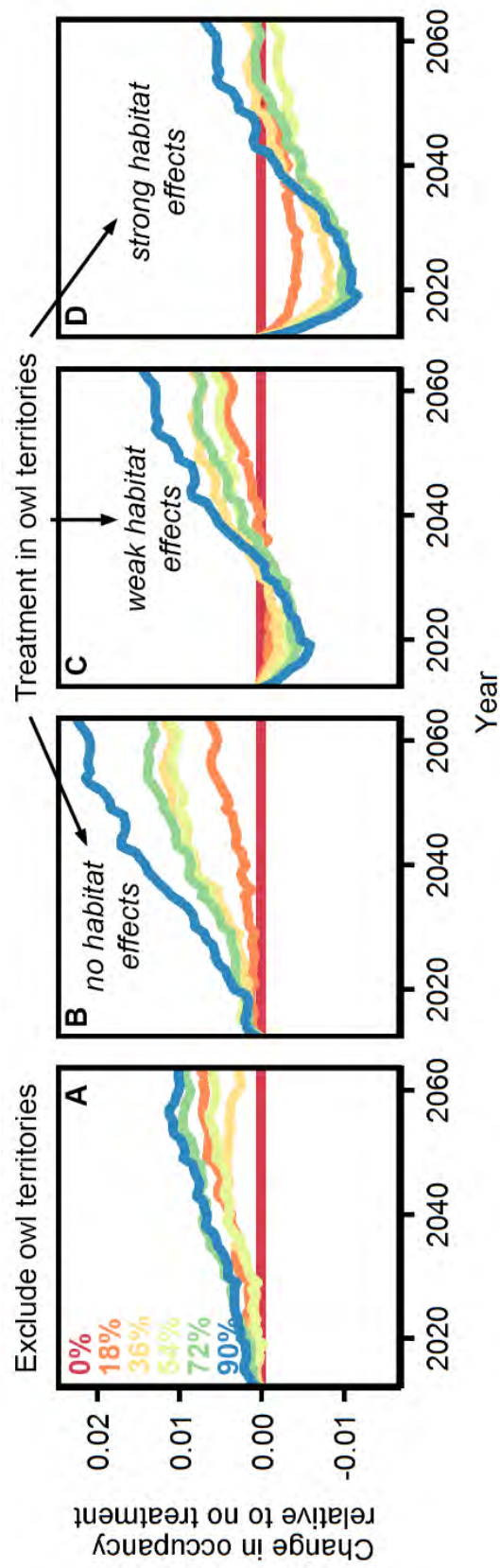


Fig. S10. Summary effects of treatment on spotted owls in the Sierra Nevada showing annual range-wide occupancy for each treatment scenario relative to the baseline no-treatment scenario (red line). This is a repeat of Figure 2 from the main text but for the CanESM2 GCM.

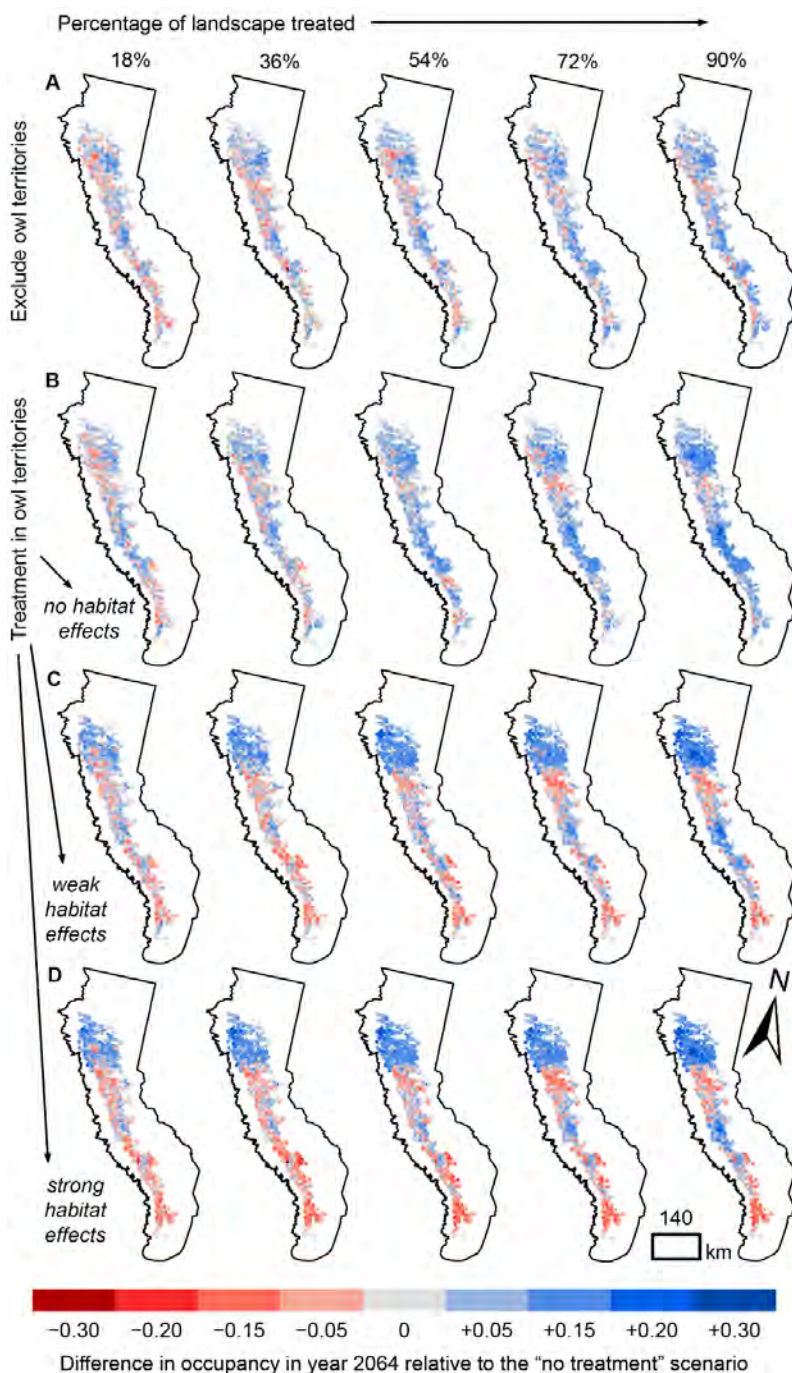


Fig. S11. Spatial effects of the location and extent of fuel treatments on spotted owl territory occupancy. Map shows the mean change in mid-century occupancy (at year 2064) across all 1844 spotted owl territories in the Sierra Nevada, relative to a no-treatment scenario. This is an expanded version of Figure 3 from the main text, but also showing results from simulations that assumed “weak” habitat effects of fuel treatments (middle row). Figure 3 in the main text shows the top row (exclude treatment) and the bottom row (“strong” habitat effects).

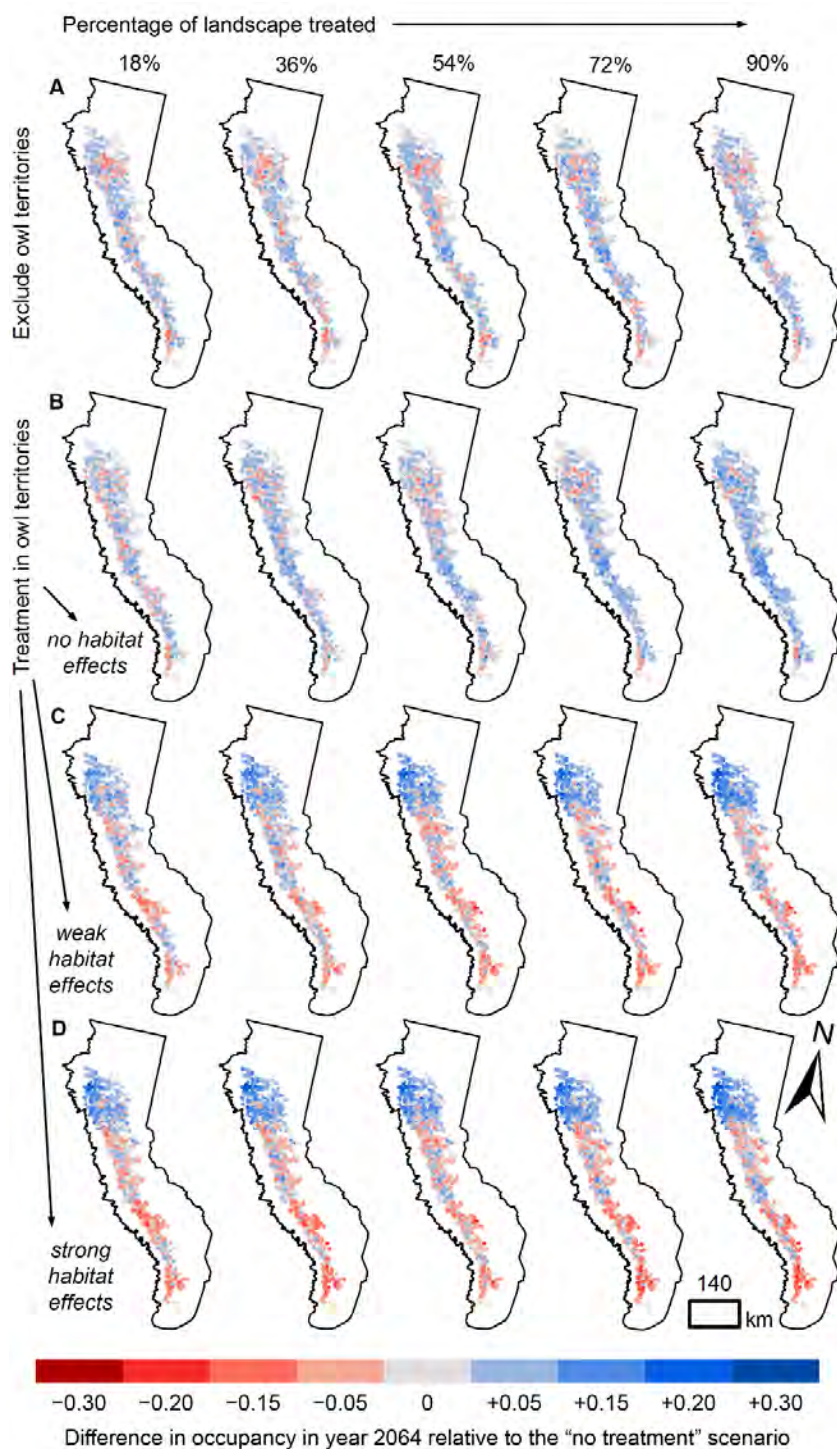


Fig. S12. Spatial effects of the location and extent of fuel treatments on spotted owl territory occupancy. Map shows the mean change in mid-century occupancy (at year 2064) across all 1844 spotted owl territories in the Sierra Nevada, relative to a no-treatment scenario. This is a repeat of of Figure S11 text but for the CanESM2 GCM.

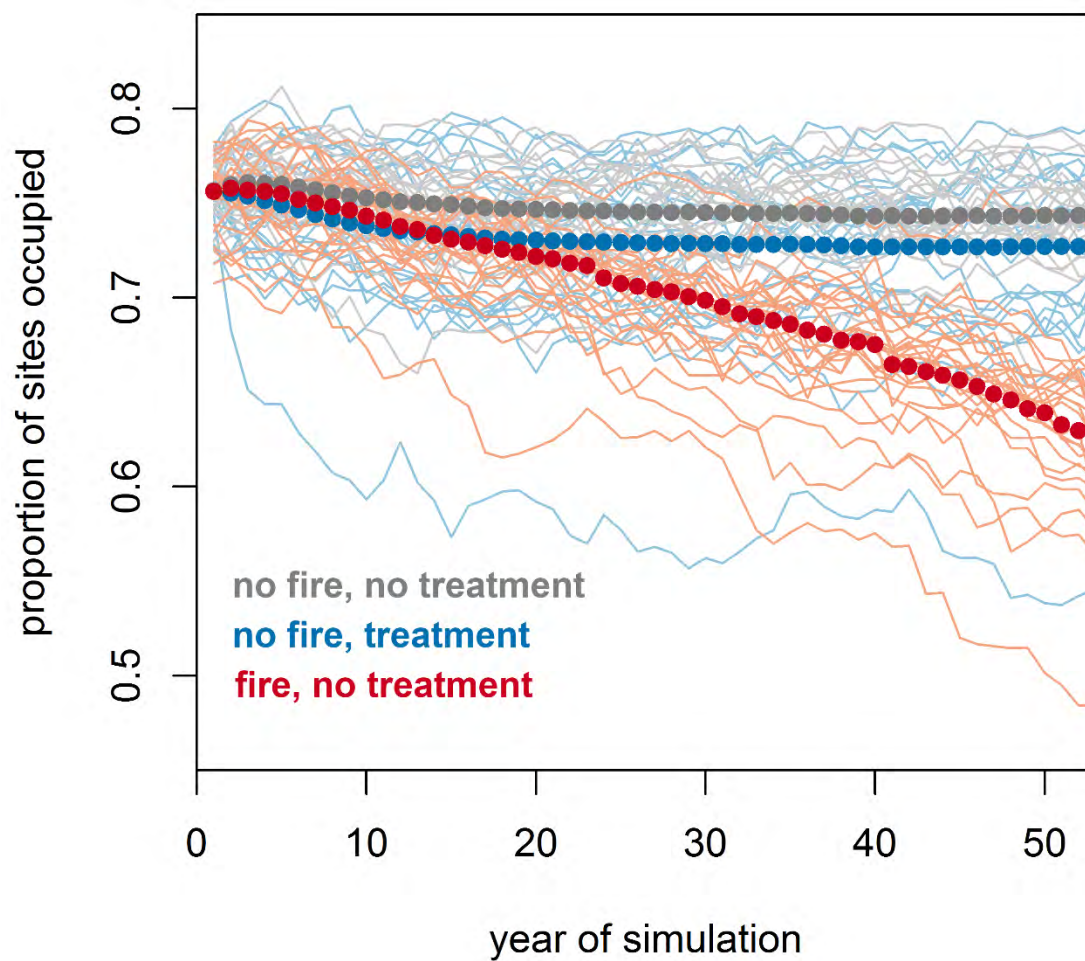


Fig. S13. Relative influence of fire and treatment on projected spotted owl occupancy compared to a baseline “no fire, no treatment” scenario. Projections were run using the CNRM-CM5 GCM.

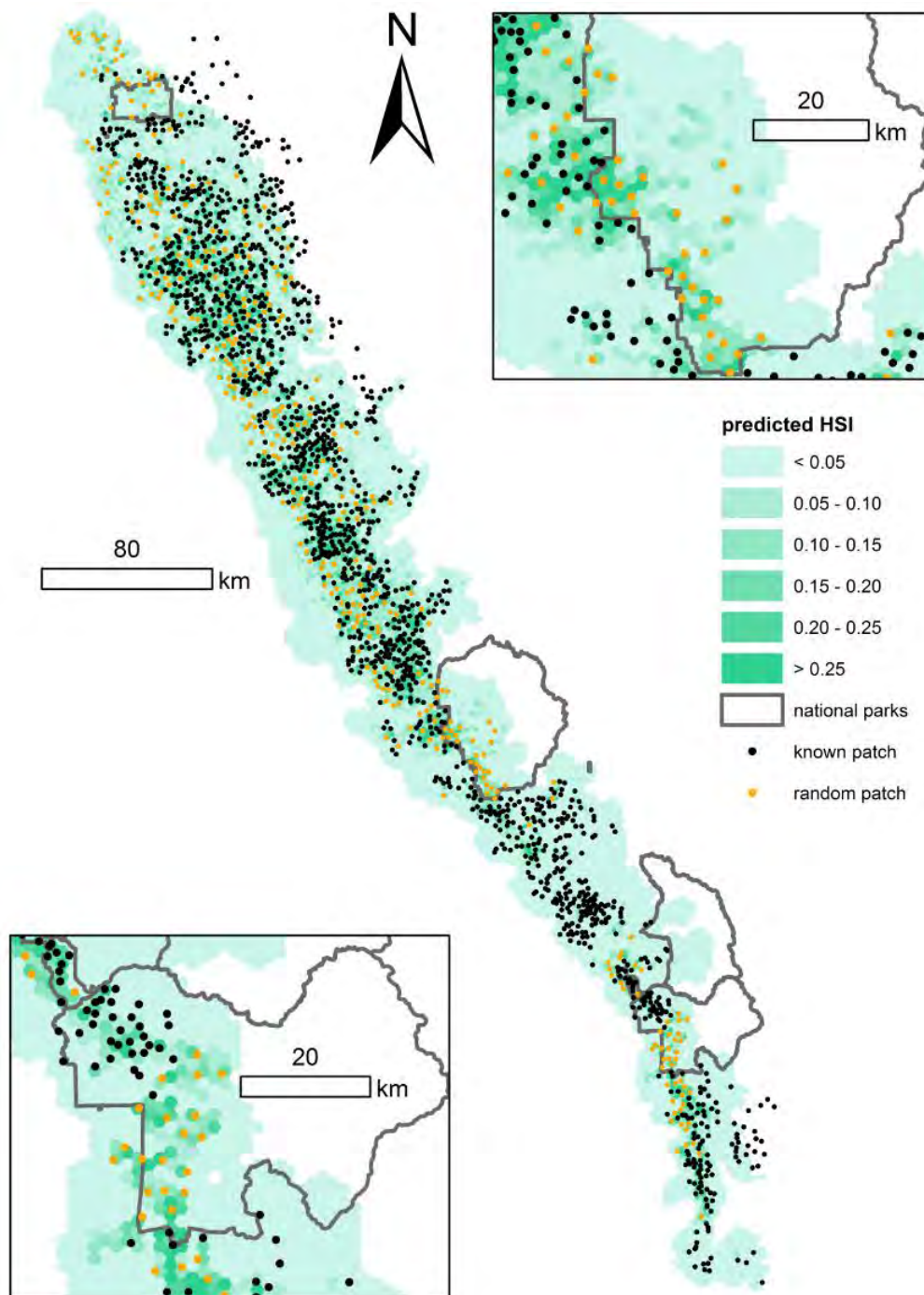


Fig. S14. Patch network used in the spatial occupancy model for spotted owls. Random patches (orange dots) were placed in areas with above-average habitat suitability and that were located at least the mean nearest neighbor distance from known patches. HSI = habitat suitability index (green shading) predicts the probability of spotted owl presence in each ~324-ha hexagonal grid cell across the Sierra Nevada bioregion (JJ Keane, unpublished data).

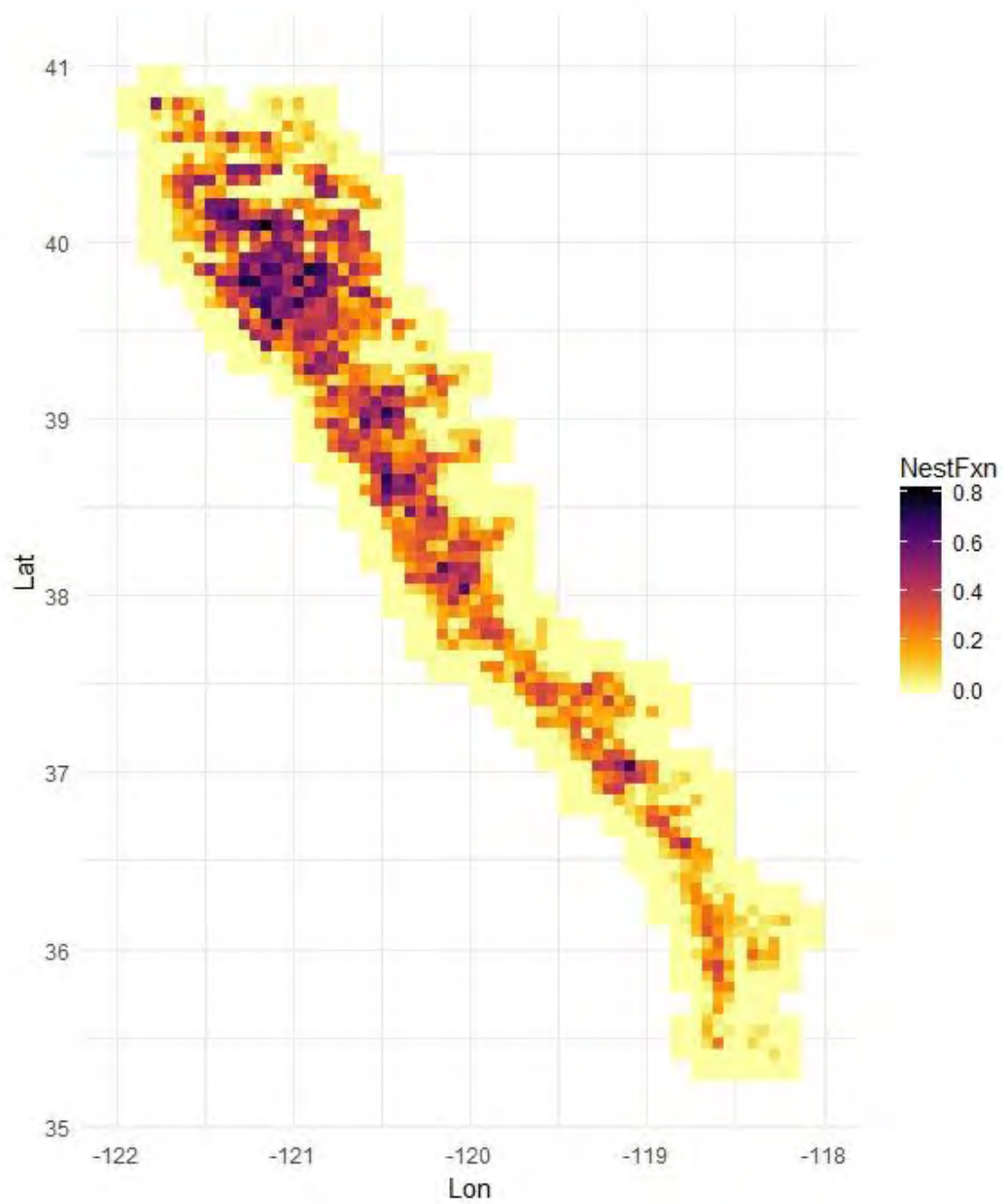


Fig. S15. Proportion of each 6-km grid cell filled by spotted owl territories.

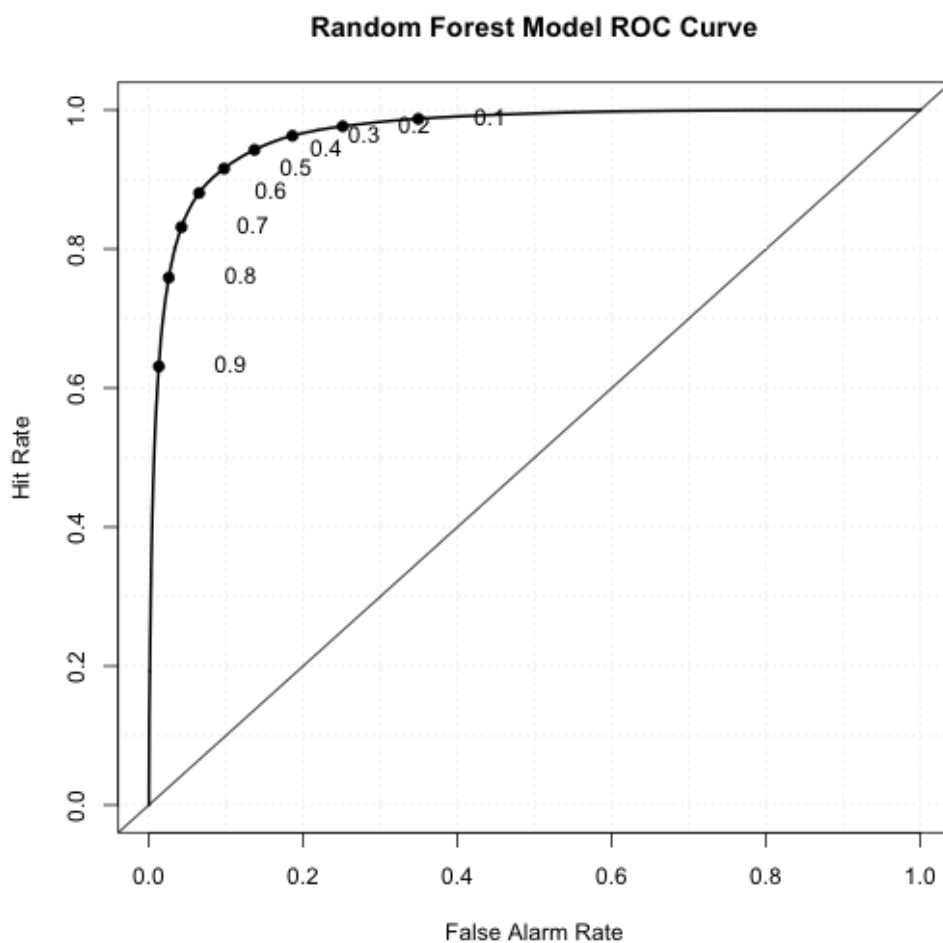


Fig. S16. Area under the receiver-operating curve (AUC) for the downscaling model. AUC = 0.9085. An area of 0.50, a curve corresponding to the 1:1 line, indicates a hypothetical model with skill equivalent to chance.

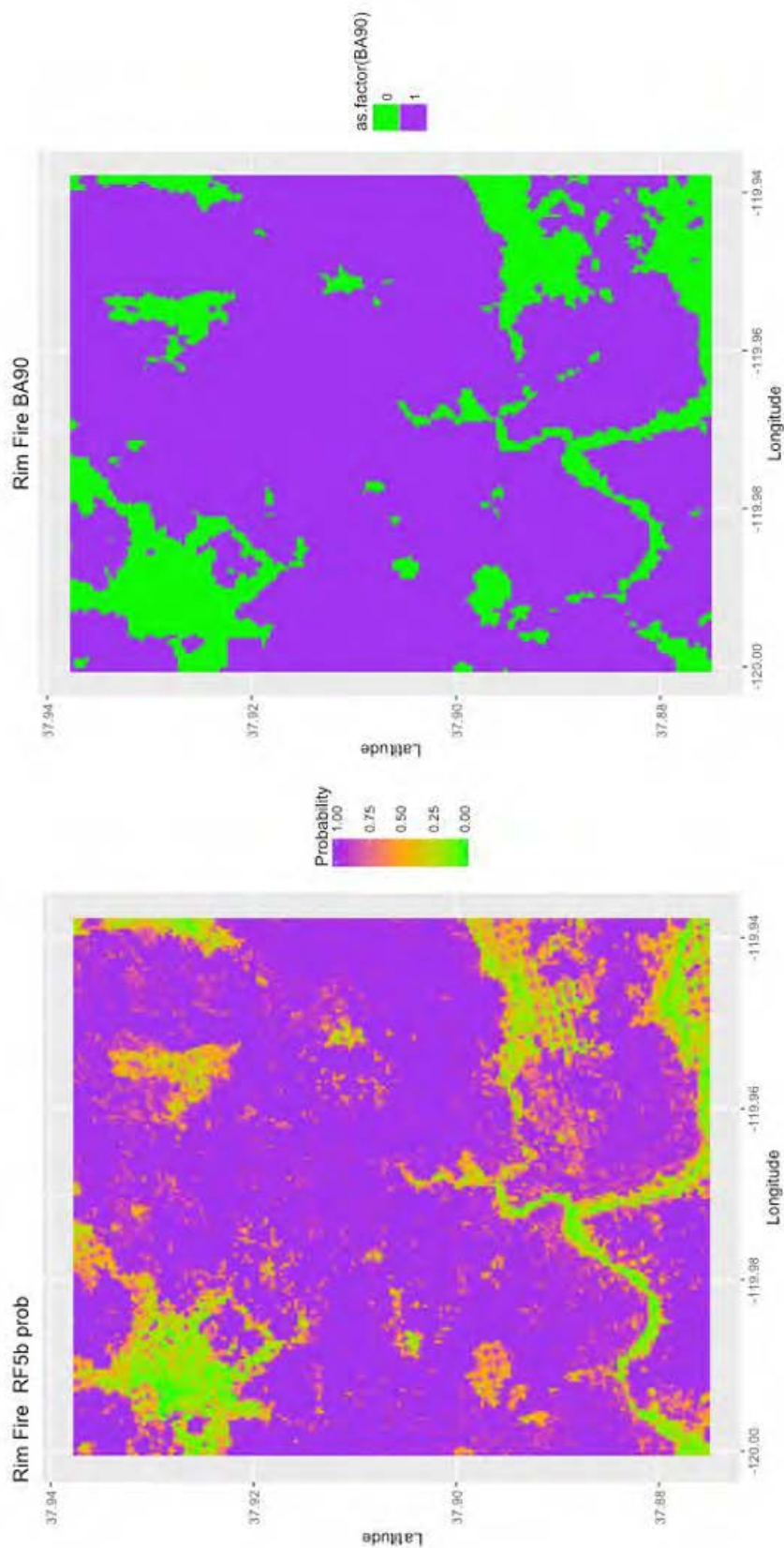


Fig. S17. The predicted probability of BA90 presence (left) produced with the Random Forest fine-scale fire model is paired with observed BA90 presence (right) for area containing the 2013 Rim Fire. These plots demonstrate the performance of the FS model relative to observations. This predicted probability uses the actual fire size; for our FS probability surfaces, we created seven surfaces similar to this for the entire Sierra Nevada bioregion, each with a different pattern of probability according to the fire size bin. These probabilities are drawn from to assign pixel values in the allocation algorithm.

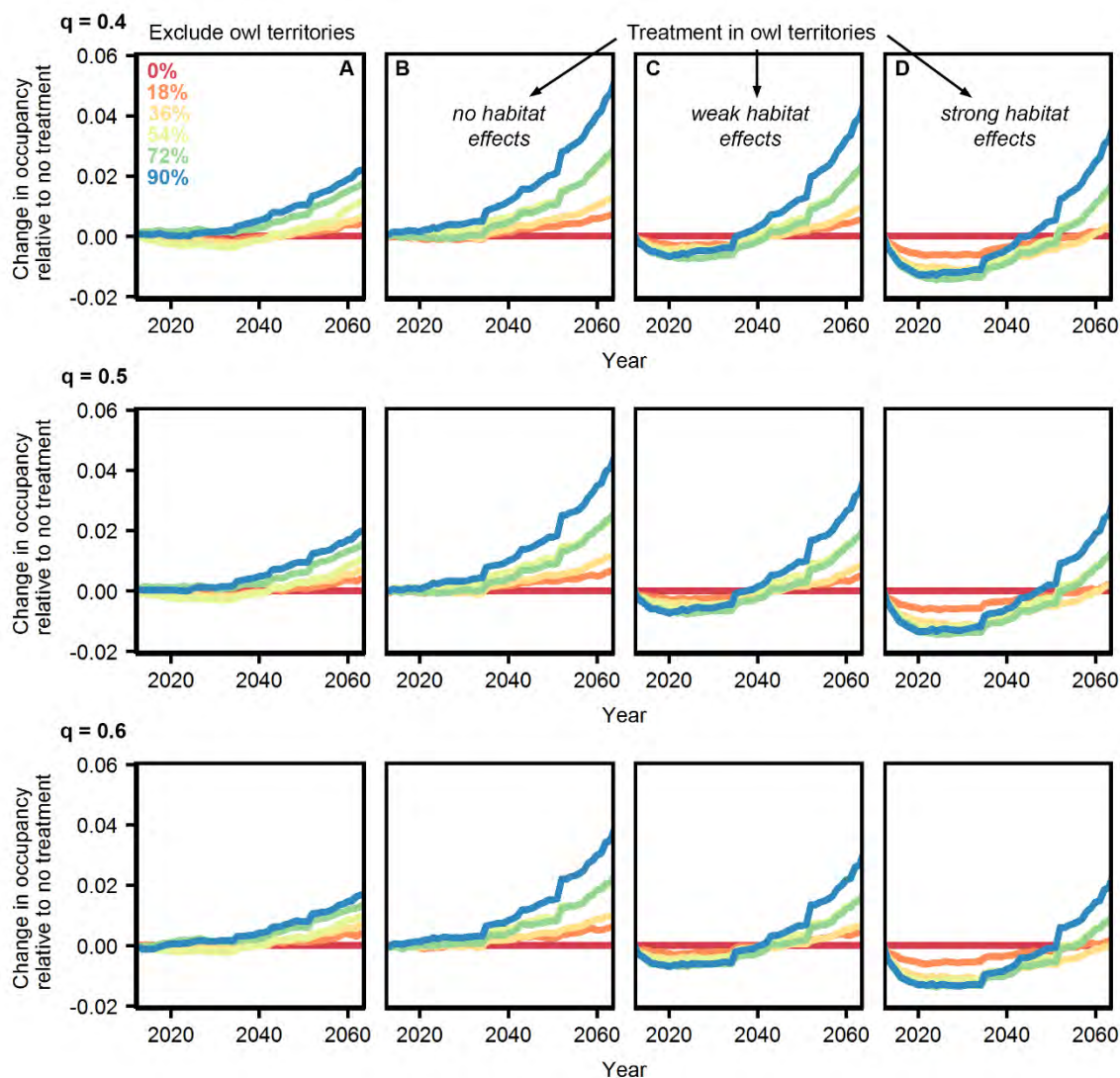


Fig. S18. Summary effects of treatment on spotted owls in the Sierra Nevada showing annual range-wide occupancy for each treatment scenario relative to the baseline no-treatment scenario (red line). This is a repeat of Figure 2 from main text, but showing the effects of different assumptions about the proportion of severe fire in an owl territory that will induce a semi-permanent extinction event ($q=0.4, 0.5, 0.6$). The middle row is equivalent to Figure 2 from the main text, included here for comparison. Results are shown from the CNRM-CM5 GCM only.

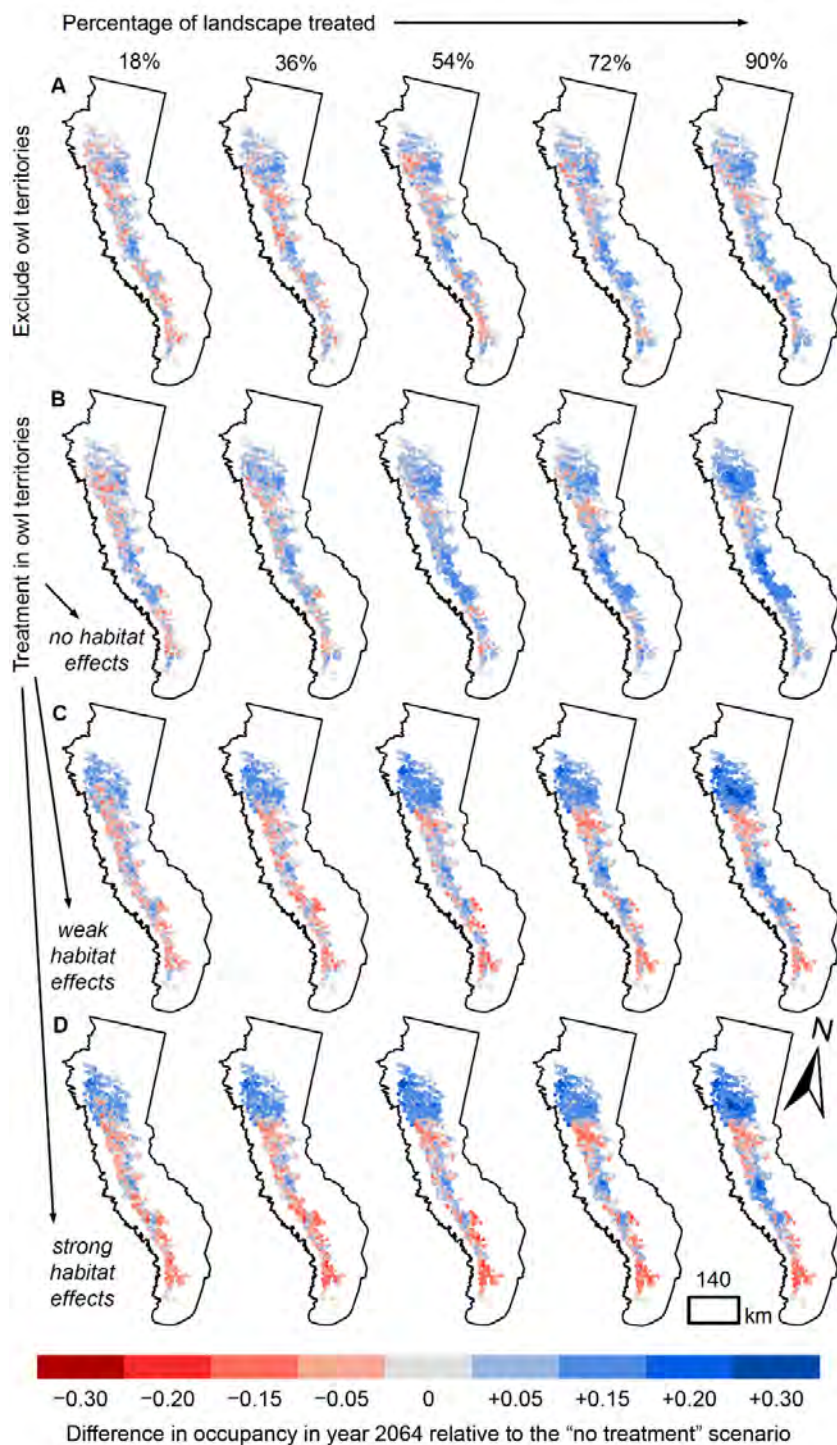


Fig. S19. Spatial effects of the location and extent of fuel treatments on spotted owl territory occupancy. Map shows the mean change in mid-century occupancy (at year 2064) across all 1844 spotted owl territories in the Sierra Nevada, relative to a no-treatment scenario. This is a repeat of Figure 3 from main text showing $q=0.4$ (CNRM-CM5 only).

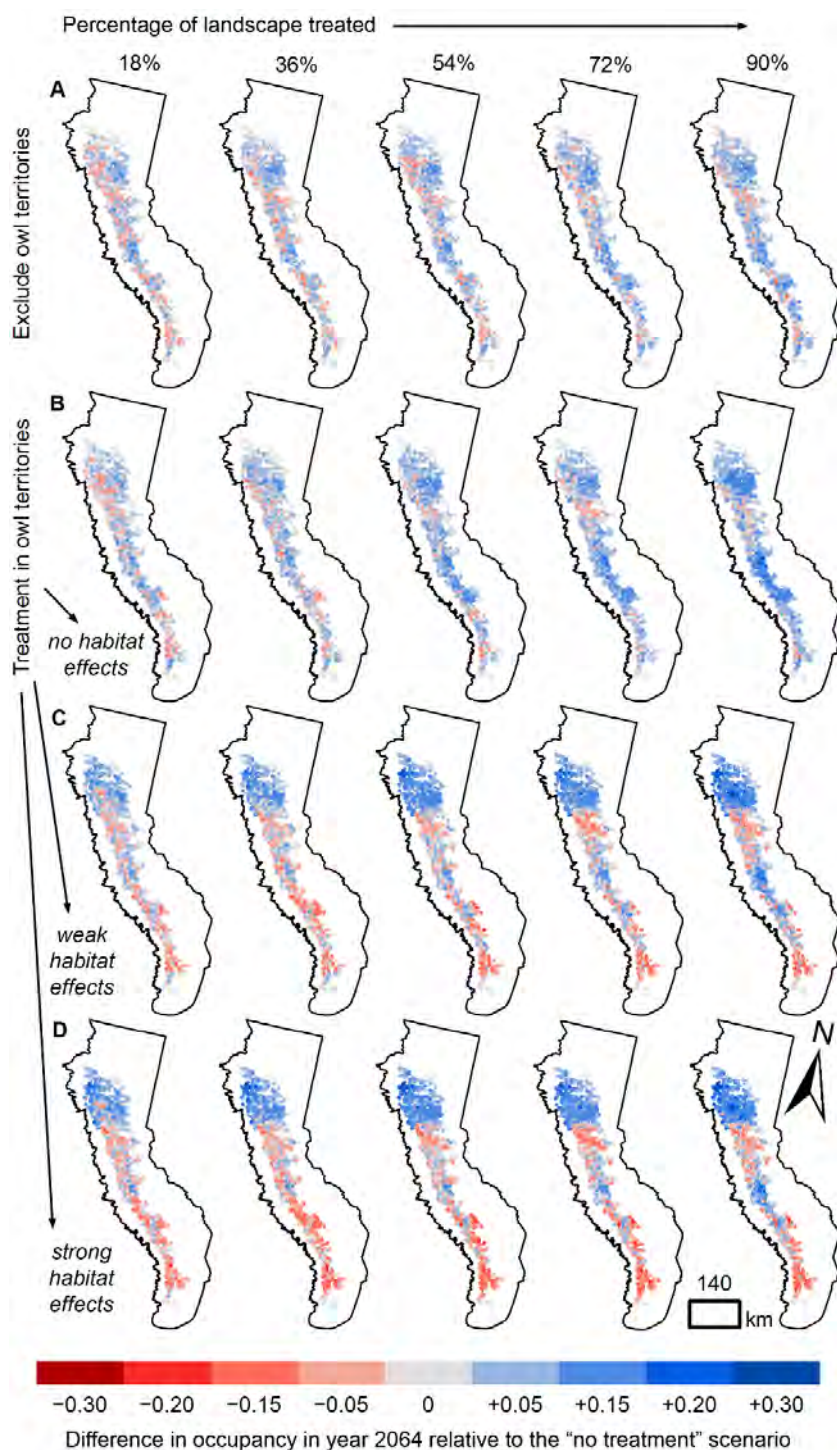


Fig. S20. Spatial effects of the location and extent of fuel treatments on spotted owl territory occupancy. Map shows the mean change in mid-century occupancy (at year 2064) across all 1844 spotted owl territories in the Sierra Nevada, relative to a no-treatment scenario. This is a repeat of Figure 3 from main text showing $q=0.6$ (CNRM-CM5 only).

Table S1. Change in predicted BA90 area compared to the baseline (no treatment) scenario for the LS fire model.

	CNRM-CM5	Percentage of landscape treated				
		18%	36%	54%	72%	90%
Annual change in BA90 hectares (2035-2064)						
Treatment in owl territories		-1668.5	-2568.9	-4240.3	-4892.9	-7150.1
Exclude owl territories		-1551.6	-1927.9	-3099.2	-3845.2	-5021.4
Total change in BA90 hectares (2035-2064)						
Treatment in owl territories		-48386	-74498	-122970	-141895	-207353
Exclude owl territories		-44996	-55909	-89876	-111511	-145619
Percent reduction in BA90 (2035-2064) compared to no-treatment						
Treatment in owl territories		7.1%	11.0%	18.1%	20.9%	30.5%
Exclude owl territories		6.6%	8.2%	13.2%	16.4%	21.4%
CanESM2						
Annual change in BA90 hectares (2035-2064)						
Treatment in owl territories		-665.8	-871.8	-1334.3	-2049.6	-3048.4
Exclude owl territories		-386.2	-836.7	-1149.0	-1534.3	-1786.3
Total change in BA90 hectares (2035-2064)						
Treatment in owl territories		-19308	-25283	-38694	-59438	-88403
Exclude owl territories		-11200	-24264	-33320	-44495	-51803
Percent reduction in BA90 (2035-2064) compared to no-treatment						
Treatment in owl territories		2.8%	3.7%	5.7%	8.7%	13.0%
Exclude owl territories		1.6%	3.6%	4.9%	6.5%	7.6%

Table S2. Parameter estimates from the spatial occupancy model (point estimates and Bayesian credible intervals).

parameter	description	mean	SD	2.50%	97.50%	$\hat{R}$
extinction						
β_0	intercept for north (reference) bioregion	-1.537	0.177	-1.931	-1.223	1.013
β_1	difference in intercept from β_0 for central bioregion	0.427	0.303	-0.133	1.055	1.040
β_2	difference in intercept from β_0 for south bioregion	0.316	0.238	-0.142	0.814	1.008
β_3	slope of lgTree.hiCanopy for north (reference) bioregion	-3.577	2.236	-7.82	0.950	1.005
β_4	slope of lgTree.medCanopy for north (reference) bioregion	-11.18	2.899	-14.837	-4.005	1.017
β_5	difference in slope of lgTree.hiCanopy from β_3 for central bioregion	-2.737	3.371	-9.408	3.629	1.017
β_6	difference in slope of lgTree.hiCanopy from β_3 for south bioregion	-4.408	2.816	-9.995	1.116	1.006
β_7	difference in slope of lgTree.medCanopy from β_4 for central bioregion	6.231	5.063	-5.129	14.352	1.019
β_8	difference in slope of lgTree.medCanopy from β_4 for south bioregion	8.207	3.475	0.026	13.753	1.020
ρ_0	baseline colonization probability for coincident sites ($d=0$)	0.009	0.001	0.007	0.012	1.001
σ	scale parameter describing decay rate in colonization function	13.291	1.380	10.878	16.247	1.002
detection						
α_0	intercept	0.923	0.026	0.871	0.975	1.000
α_1	slope for detection effect of lgTree.hiCanopy	1.062	0.200	0.666	1.461	1.001
α_2	slope for detection effect of lgTree.medCanopy	-0.754	0.293	-1.325	-0.184	1.001
occupancy in 2011						
ψ_{2011}	proportion of sites occupied in 2011; input data for year 0 of projection	0.757	0.016	0.725	0.787	1.002
derived parameters						
β_{0+1}	intercept for central bioregion	-1.111	0.259	-1.596	-0.6	1.024
β_{0+2}	intercept for south bioregion	-1.222	0.165	-1.553	-0.904	1.001
β_{3+5}	slope of lgTree.hiCanopy for central bioregion	-6.315	2.648	-11.567	-1.109	1.011
β_{3+6}	slope of lgTree.hiCanopy for south bioregion	-7.985	1.829	-11.834	-4.656	1.006
β_{4+7}	slope of lgTree.medCanopy for central bioregion	-4.948	4.183	-13.702	2.110	1.012
β_{4+8}	slope of lgTree.medCanopy for south bioregion	-2.973	2.075	-7.397	0.747	1.005

Table S3. Logistic regression model specification for large fire presence (LS fire model).

for $q_m(X_{mij})$ terms:	variable	description
$q_m(X_{mij}) =$	$q(CWD_{ij})$	basis spline of cumulative monthly climate water deficit
	$q(T_{ij})$	basis spline of average temperature
	$q(VFR_{ij})$	basis spline of vegetation fraction
	$q(POP_{ij})$	basis spline of population
	$CWD0_{ij}$	cumulative water year climate water deficit
	$CWD1_{ij}$	lagged cumulative water year climate water deficit
	AET_{ij}	cumulative monthly actual evapotranspiration
	Emu_i	mean elevation
	$M_{78} * TRjja_{ij}$	Regional JJA temperature interacted with a factor for month = July or August
	M	factor for month of the year
for $\sum \beta_m \times X_{mij}$ terms:	variable	description
$X_{mij} =$	$CWD_{ij} * AET_{ij}$	interaction between cumulative monthly climate water deficit and cumulative monthly actual evapotranspiration
	FSR_i	standardized fraction of grid cell in federal or state protection responsibility areas
	$Tmam_{ij}$	average March-April-May (MAM) temperature

Table S4. The distribution of fires within each fire size bin.

Fire size range (ha)	Total number of fires	Number after year 2000	Years spanned	Size midpoint (ha)
3291-6300	93	58	1985-2015	4500
6301-10,000	54	26	1987-2015	8000
10,001-15,000	34	28	1987-2015	12,500
15,001-20,000	21	11	1987-2014	17,500
20,001-30,000	21	11	1985-2015	25,000
30,001-60,000	30	11	1985-2015	45,000
60,001-199,555	11	11	2002-2013	60,000

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Megafires: an emerging threat to old-forest species

Gavin M Jones¹, RJ Gutiérrez², Douglas J Tempel¹, Sheila A Whitmore¹, William J Berigan¹, and M Zachariah Peery^{1*}

Increasingly frequent “megafires” in North America’s dry forests have prompted proposals to restore historical fire regimes and ecosystem resilience. Restoration efforts that reduce tree densities (eg via logging) could have collateral impacts on declining old-forest species, but whether these risks outweigh the potential effects of large, severe fires remains uncertain. We demonstrate the effects of a 2014 California megafire on an iconic old-forest species, the spotted owl (*Strix occidentalis*). The probability of owl site extirpation was seven times higher after the fire (0.88) than before the fire (0.12) at severely burned sites, contributing to the greatest annual population decline observed during our 23-year study. The fire also rendered large areas of forest unsuitable for owl foraging one year post-fire. Our study suggests that megafires pose a threat to old-forest species, and we conclude that restoring historical fire regimes could benefit both old-forest species and the dry forest ecosystems they inhabit in this era of climate change.

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The frequency and severity of “megafires” (ie large wildfires >10,000 ha in extent [Stephens *et al.* 2014b]) in the dry forests of North America has increased after a century of fire suppression and climate warming (Westerling *et al.* 2006; Miller *et al.* 2009b), incurring considerable societal and economic costs by destroying homes, human infrastructure, and timber resources, in addition to necessitating increased taxpayer-funded support for fire-fighting (Stephens *et al.* 2013, 2014b). In the western US, major reforms in forest fire management have been proposed to restore low- and moderate-severity fire regimes through forest tree thinning (North *et al.* 2015). However, the vision of restoring “pre-European” fire regimes, as well as forest structure and composition, is constrained by concerns over fuels-reduction treatments that simplify the structurally and floristically diverse forests inhabited by old-forest species (ie species that inhabit forests characterized by large, old trees, closed over-story canopy, and complex vertical structure) (Pilliod *et al.* 2006). Potential short-term consequences of fuels-reduction and restoration treatments may be outweighed by long-term benefits of forest restoration if large, high-severity fires negatively affect old-forest species (Sweitzer *et al.* 2015; Tempel *et al.* 2015). However, research suggests that severe fires may have neutral or beneficial effects on biodiversity, including old-forest species (Hutto 2008; Swanson *et al.* 2011; DellaSala and Hanson 2015; Lee and Bond 2015), which seemingly increases the perceived divide between forest restoration and species conservation

objectives. Nevertheless, the ecological effects of high-severity fire likely depend in part on the size, distribution, and configuration of burned patches (Fontaine and Kennedy 2012), and the impacts of large, severe fires on old-forest species remain a source of considerable uncertainty.

Here, we demonstrate the negative short-term impacts of a California megafire on a model old-forest species, the spotted owl (*Strix occidentalis*; Figure 1), by taking advantage of a natural before–after control–impact (BACI) experimental design on our long-term (23-year) demographic study area. In September and October 2014, the human-ignited “King Fire” burned 39,545 ha and was one of the largest and most severe forest fires recorded in California history (Figure 2), with high-severity fire (75–100% canopy mortality) occurring on 19,854 ha (50% of the area burned), with one continuous 13,683-ha high-severity burned patch. The King Fire affected 15,594 ha (44%) of our 35,500 ha study area and overlapped 30 of 45 spotted owl sites we have monitored continuously since 1993 (Tempel *et al.* 2014b). Of the 15,594 ha that burned within our study area, 64% burned at high-severity (WebTable 1). The extreme nature of the fire, more than two decades of pre-fire site occupancy data, and location information on owls – outfitted with Global Positioning System (GPS) receivers and tagged with colored leg bands for identification of individual birds – allowed us to draw strong inferences regarding the effect of severe fire on a species considered to be a barometer of old-forest wildlife community health (Simberloff 1998). Our results suggest that (1) reducing the frequency of large, severe fires could benefit spotted owls and, by extension, other old-forest species, and (2) forest restoration and old-forest species conservation objectives may be more compatible than previously believed.

¹Department of Forest and Wildlife Ecology, University of Wisconsin–Madison, Madison, WI * (mpeery@wisc.edu);

²Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St Paul, MN



Figure 1. A female California spotted owl (*Strix occidentalis occidentalis*) within the Eldorado Density Study Area in the central Sierra Nevada, California.

Methods

Study area and spotted owl surveys

We conducted our study on the contiguous 35,500-ha Eldorado Density Study Area (EDSA) within the Eldorado National Forest in the central Sierra Nevada, California. The EDSA has been the site of a long-term mark-recapture demographic study of California spotted owls (Tempel and Gutiérrez 2013), and forms the primary part of a larger study area containing a greater number of owl sites (Tempel *et al.* 2014a). We used data from owl sites only within the EDSA because some sites outside of this area experienced a complex history of fire and post-fire management that could have confounded the natural BACI design within the EDSA. Moreover, sites outside of the EDSA were added at various times during the study, potentially complicating our evaluation of the effect of the King Fire on long-term spotted owl population trends.

Approximately 60% of the EDSA was public lands managed by the US Forest Service (USFS) and 40% was private land managed by timber companies. The primary vegetation type within the EDSA was mixed-conifer

forest dominated by Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), and California black oak (*Quercus kelloggii*). Forests within the EDSA have a complex history of management, logging, and fire suppression dating back at least 100 years. Early timber harvesting generally involved the selective removal of large, commercially valuable trees, with a more recent emphasis on clear-cutting on private lands and “diameter-limited thinning from below” on public lands. Prior to fire suppression, the ingrowth of shade-tolerant trees, and the removal of large trees, historical fire regimes consisted mainly of frequent low- to moderate-severity fire occurring in 5–15-year intervals (Stephens and Collins 2004). Elevation within the EDSA ranged from 360 to 2400 m, and the climate was characterized by cool, wet winters and warm, dry summers.

We surveyed the entire area each year for territorial spotted owls during the breeding season (1 Apr to 31 Aug) without regard to land cover, topography, access, or land ownership, and for this analysis we used survey data from 1993–2015. Spotted owls (usually mated pairs, but sometimes single birds) occupy and defend sites (ie “territories”), the locations of which remain reasonably stable across years. We considered a site to be occupied in a given year when at least one owl was detected. Additional survey details can be found elsewhere (Tempel and Gutiérrez 2013; Tempel *et al.* 2014b).

BACI analysis

We evaluated the potential impact of high-severity fire on spotted owls using a BACI design with multi-season site occupancy data (MacKenzie *et al.* 2003; Popescu *et al.* 2012). We carried out parallel continuous and categorical BACI analyses, where the proportion of a spotted owl site (a circle with radius equal to one-half the mean nearest-neighbor distance across years = ~1100 m; Tempel *et al.* 2014a) affected by high-severity fire was the impact covariate (ie “treatment”). We defined “high-severity” as forests that experienced 75–100% canopy mortality (Lee and Bond 2015), corresponding to a relative differenced Normalized Burn Ratio (RdNBR) threshold of >572 (Miller *et al.* 2009a). The continuous BACI analysis contained two groups: sites that were unburned ($n = 15$) and sites that overlapped with the King Fire and thus experienced some degree of burn ($n = 30$). The categorical BACI analysis contained three groups: sites that were unburned ($n = 15$), sites that experienced <50% high-severity fire ($n = 16$), and sites that experienced >50% high-severity fire ($n = 14$). For both continuous and categorical BACI analyses, we followed a hierarchical modeling procedure by first modeling within-season detection probability as a function of covariates (WebTable 2). We then modeled the potential effects of high-severity fire on colonization (γ) and

extinction (ϵ) rates separately using Akaike's information criterion (AIC) to select between competing models (WebTable 3), while allowing the non-focal parameter to vary by year (Tempel *et al.* 2014a).

Previous attempts to test for the effects of wildfire on spotted owls have been hindered by the potential confounding effect of post-fire salvage logging (Lee *et al.* 2012; Clark *et al.* 2013). However, in our study, all surveys used to estimate occupancy metrics were completed before the implementation of proposed post-fire salvage logging on public lands (USFS 2015), which comprised a median of 89% of the area that occurred within burned owl sites (versus ~11% on private lands). We also evaluated the potential effects of post-fire salvage logging on private lands in the continuous site occupancy analysis. Specifically, when fire effects were supported, we introduced a covariate representing the proportion of spotted owl sites that experienced salvage logging. The continuous variables – high-severity fire and salvage logging – were not strongly associated at fire-affected sites ($R^2 = 0.10$).

Population trend analysis

We fit a fully time-varying dynamic occupancy model to our 23-year detection/non-detection data to obtain unconstrained annual estimates of occupancy (ψ_t) and rate of change in occupancy (λ_t) for the study area (MacKenzie *et al.* 2003). Our statistical model directly estimated initial occupancy (ψ_1), annual estimates of extinction (ϵ_t), and annual estimates of colonization (γ_t), so we used the recursive equation

$$\psi_t = \psi_{t-1}(1 - \epsilon_{t-1}) + (1 - \psi_{t-1})\gamma_{t-1} \quad (\text{Eq 1})$$

to estimate occupancy (ψ_t) for each year of the study period. Then, using the estimates of ψ_t , we calculated λ_t for each year using the equation:

$$\lambda_t = \frac{\psi_{t+1}}{\psi_t} \quad (\text{Eq 2}).$$

This analysis allowed us to consider occupancy and rate of change in occupancy after the King Fire within the context of a long-term decline in our study population (Tempel and Gutiérrez 2013). We fit several linear

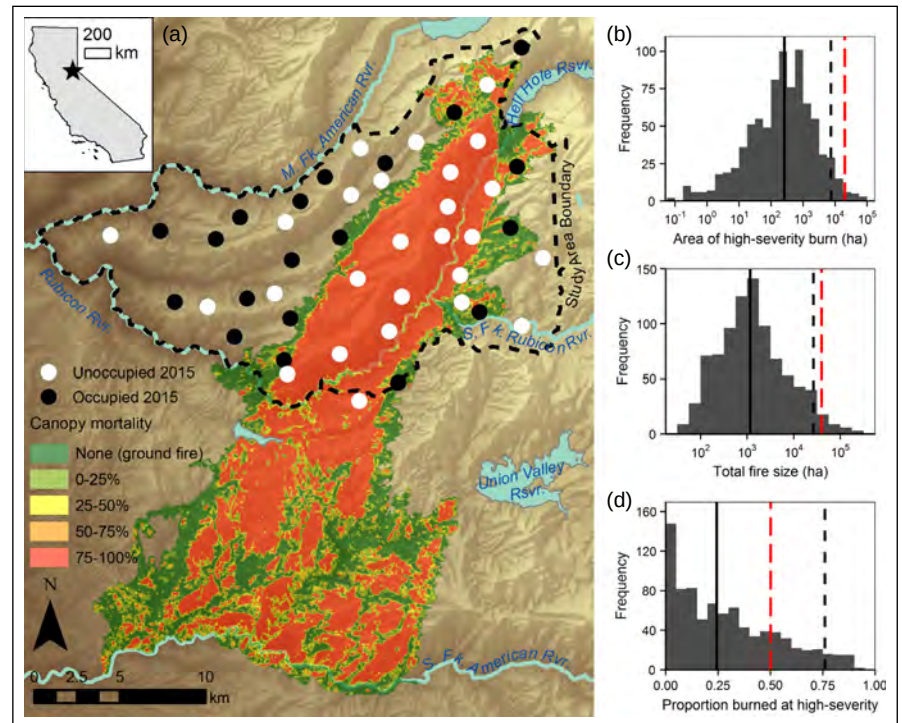


Figure 2. The geography and historical context of the 2014 King megafire. (a) The distribution of occupied and unoccupied spotted owl sites in 2015 within our 23-year demographic study area, which was located ~20 km west of Lake Tahoe, California. Elevation is represented by brown shading (darker brown = low elevation, lighter brown = high elevation) and ranges from approximately 150 to 3000 m. (b–d) A comparison of the King Fire to all California fires since 1984 in terms of area of high-severity burn (b), total fire size (c), and proportion burned at high-severity (d); the solid black lines represent the 50th percentile, the dashed black lines represent the 95th percentile, and the dashed red lines represent the 2014 King Fire.

models to annual estimates of occupancy ψ_t and used AIC to evaluate relative support for different time trends (linear, log-linear, quadratic) and a segmented (ie “break-point”) model over the pre-fire years 1993–2014 (WebTable 4). We used the segmented model to evaluate support for an initial decline followed by a period of apparent population stability prior to the King Fire.

Habitat use and selection analysis

We collected post-fire foraging locations from nine spotted owls during the 2015 breeding season using backpacks equipped with a Lotek Pinpoint 100 mini-GPS archival tag and a VHF radio transmitter. GPS tags recorded 1–2 locations at random times between dusk and dawn each night, May–August, to characterize nocturnal habitat use during the breeding season. We collected 1085 locations but discarded ~11 locations per owl with suboptimal measures of precision (dilution of precision [DOP] ≥ 5). Using burn severity maps produced by the USFS, we performed a compositional analysis of habitat use (Aebischer *et al.* 1993) and derived Manly's selection ratios (ω ; Manly *et al.* 2002)

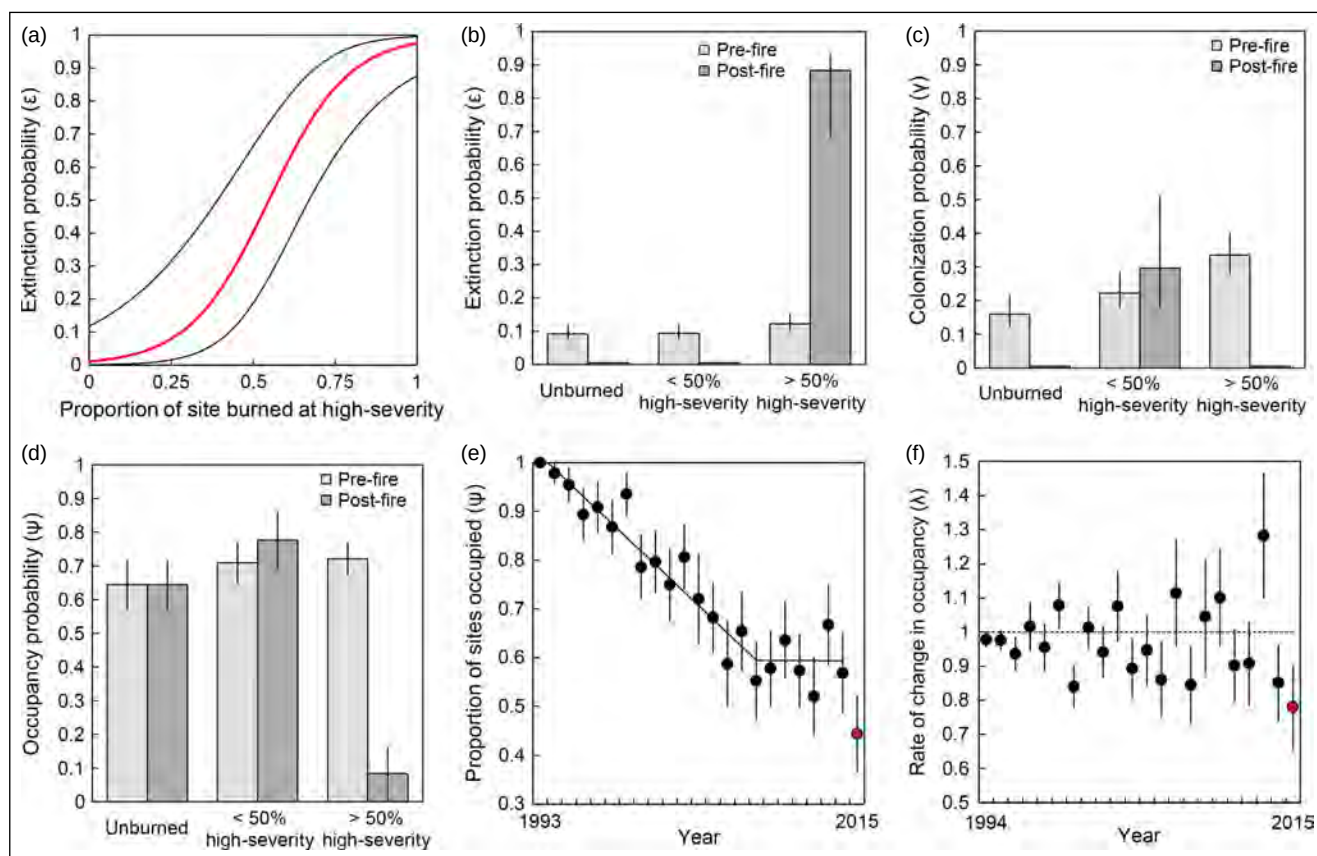


Figure 3. Before–after control–impact and population analyses. (a) The continuous relationship between the proportion of an owl site that burned at high-severity and the probability of site extinction. (b–d) Colonization (b), extinction (c), and occupancy (d) probabilities for owl sites that experienced different degrees of high-severity burn both pre- and post-fire. (e) Annual estimates of occupancy (ψ) over the study period, where the black line represents a segmented regression function fitted to the mean occupancy for years 1993–2014 (WebTable 4) demonstrating the periods of decline and subsequent stability before the 2014 King Fire (solid red circle). (f) Annual estimates of rate of change in occupancy (λ) over the study period, where the dashed black line at $y = 1$ indicates a stable rate of change, and the solid red circle indicates the rate of change after the 2014 King Fire. The black curved lines in (a) and all error bars in (b–f) represent ± 1 SE of the mean.

for third-order habitat selection to assess selection or avoidance of forests in different burn classes (unburned, low-severity, high-severity).

We defined available habitat area for each owl using a circle with the center equal to the geometric mean of 2015 nest tree, roosts, and daytime capture locations (ie “activity center”) and a radius equal to the 95th percentile of linear foraging distances from the activity center (similar to Bond *et al.* 2009). We used the 95th (not 100th) percentile so that distant areas rarely visited by owls in foraging bouts (Bond *et al.* 2009) were not counted as “available” habitat. As a result, the analysis consisted of GPS locations that occurred within distance ranges used at relatively high frequencies (WebFigure 2). We used a circle instead of a minimum convex polygon (MCP) to define available habitat because MCPs often failed to include the large, high-severity patch as “available” although it was generally within the foraging radius of owls (WebFigure 3). We performed habitat selection analyses using the R package “adehabitatHS” (Calenge 2006).

Results and discussion

The BACI analysis indicated that high-severity fire had a strong negative impact on spotted owls. The probability of site extinction (ϵ) increased from 0.01 to 0.98 as the proportion of high-severity fire at a spotted owl site increased from 0 to 1 (Figure 3a). Moreover, extinction rates at severely burned sites (>50% of site area burned at high-severity) increased sevenfold following the King Fire ($\hat{\epsilon}_{1993-2014} = 0.12$, 95% confidence interval [CI] = 0.08–0.18; $\hat{\epsilon}_{2015} = 0.88$, CI = 0.49–0.98), whereas post-fire extinction rates were estimated to be zero at less severely burned and unburned sites (Figure 3b). Sites that burned <50% at high-severity were more likely to be colonized after the fire ($\hat{\gamma}_{<50\% \text{ High-severity}} = 0.30$, 95% CI = 0.07–0.72) than unburned sites and sites that burned >50% at high-severity ($\hat{\gamma}_{\text{Unburned}}$ and $\hat{\gamma}_{>50\% \text{ High-severity}} = 0$; Figure 3c). Colonization of sites after the fire was largely the result of individuals moving to less burned sites

after abandoning their original sites that burned at >50% high-severity (WebFigure 4). Predicted occupancy rates ($\hat{\psi}$) at sites that burned >50% at high-severity declined by almost ninefold from their pre-fire value ($\hat{\psi}_{\text{Pre-fire}} = 0.72$, 95% CI = 0.62–0.82; $\hat{\psi}_{\text{Post-fire}} = 0.08$, 95% CI = 0.00–0.24), based on a model that combined top colonization and extinction covariate structures in the categorical analysis (Figure 3d).

Using spatially explicit data obtained from privately owned natural resource companies (Sierra Pacific Industries and Mason, Bruce & Girard Inc) that managed timberlands in our study area, we estimated that post-fire salvage logging on private lands constituted a median of only 2% of the area within owl sites. The extent of high-severity fire was large relative to the extent of salvage logging within owl territories (WebFigure 1), strengthening potential inferences because this ratio reduced the confounding effects of high-severity fire and post-fire salvage logging on spotted owls. In addition, the term for salvage logging appeared as an uninformative parameter in the modeling procedure (Arnold 2010), also suggesting that post-fire salvage logging operations did not confound associations between occupancy metrics and high-severity fire (WebTable 3; WebFigures 1 and 5).

The King Fire exacerbated a longer-term decline in spotted owl occupancy within our study area. The proportion of occupied spotted owl sites declined by 43% over a 22-year period leading up to the 2014 King Fire ($\hat{\psi}_{1993} = 1.0$, standard error of the mean [SE] = 0.0; $\hat{\psi}_{2014} = 0.57$, 95% CI = 0.41–0.73) (Figure 3e). After the King Fire, occupancy dropped from 0.57 to 0.44 ($\hat{\psi}_{2014} = 0.57$, 95% CI = 0.41–0.73; $\hat{\psi}_{2015} = 0.44$, 95% CI = 0.29–0.60) following ~7 years of relatively stable occupancy (Figure 3e). The 22% decline in site occupancy after the fire ($\hat{\lambda}_{2015} = 0.78$, 95% CI = 0.53–1.03) was the greatest single-year decline recorded over our 23-year study period (Figure 3f).

Analyses of spotted owl foraging locations along the perimeter of the King Fire (no owls were present in the interior of the large patch that burned at high-severity; Figure 3, a–d) indicated that spotted owls foraged non-randomly (Wilks's lambda $\Lambda = 0.40$, $P = 0.017$) by avoiding foraging in areas that burned at high-severity ($\hat{\omega}_{\text{High-severity}} = 0.31$, 95% CI = 0.10–0.51) (Figure 4, e and f). Forests that burned at low-severity and unburned forests were used in proportion to their availability on the

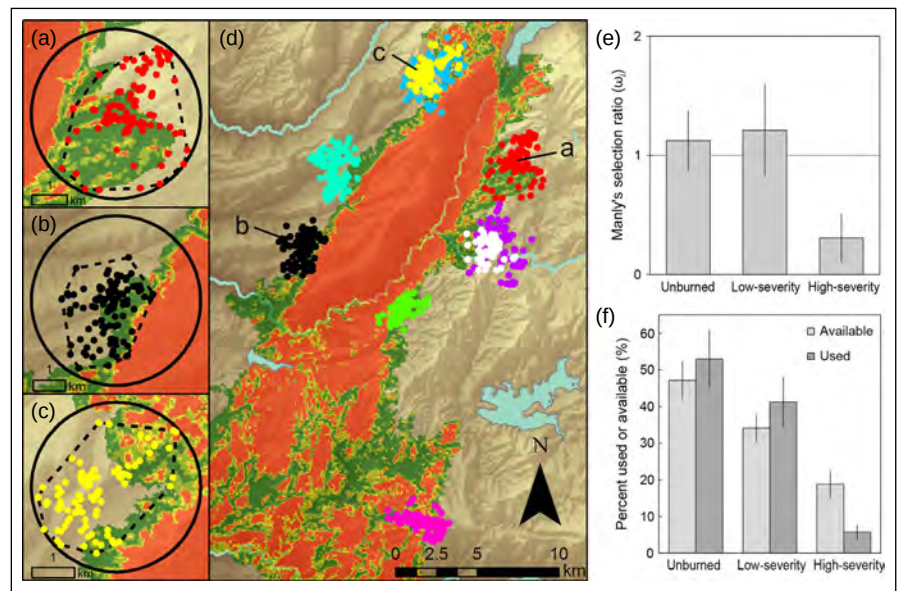


Figure 4. Distribution of spotted owl foraging locations following a megafire developed from 985 GPS locations from nine owls (individuals represented by different colors) during the 2015 breeding season in relation to the 2014 King Fire (d). Inset examples (a–c) of foraging locations for three owls (small solid-colored circles) and the area defined as available habitat (large open black circles) compared to a minimum convex polygon (black dashed polygon) demonstrate the owls' apparent avoidance of the high-severity burned area. Burn severity for the King Fire is displayed in 25% classes as in Figure 2a. (e) Manly's selection ratios ($\hat{\omega} \pm 1.96 \times \text{SE}$, where a selection ratio $\hat{\omega} > 1$ indicates habitat preference, $\hat{\omega} < 1$ indicates habitat avoidance, and $\hat{\omega} = 1$ indicates neither preference nor avoidance). (f) Mean ($\pm$ SE) availability and use among nine owls for unburned forests, forests that experienced 0–75% canopy mortality (low-severity), and forests that experienced 75–100% canopy mortality (high-severity).

landscape ($\hat{\omega}_{\text{Low-severity}} = 1.21$, 95% CI = 0.82–1.60; $\hat{\omega}_{\text{Unburned}} = 1.12$, 95% CI = 0.87–1.38) (Figure 4, e and f).

The observation that lower-severity fire is benign, and perhaps even moderately beneficial, to spotted owls is consistent with previous studies (Roberts *et al.* 2011; Lee *et al.* 2012) and is not surprising given that, within dry mixed-conifer forests, the spotted owl and other old-forest species evolved in association with such fire regimes (Noss *et al.* 2006; North *et al.* 2009). However, we provide the first definitive evidence that a large, high-severity fire (ie a megafire) had strong negative population impacts on an old-forest species and that areas burned at high-severity were avoided by individuals of that species. These findings contrast with a recent spotted owl population study that reported high site occupancy after another megafire (the "Rim Fire"; Lee and Bond 2015). The Rim and King fires could have affected owls differently because of differences in the patterns of patches that burned at high-severity and the resulting distribution of remnant habitat. The largest high-severity patch in the Rim Fire (21,426 ha) was 1.5 times larger than the largest high-severity patch in the King Fire (13,683 ha), but made up a smaller percentage of the total area burned (21% versus 36% for the Rim and King fires, respectively) and, despite its larger area, had an

edge-to-area ratio 1.5 times greater than that of the King Fire. The relatively high spatial complexity and heterogeneity in high-severity burn patterns in the Rim Fire may have resulted in a wider range of vegetation conditions and more remnant live trees suitable for owls (Lee and Bond 2015) as compared with the King Fire, where the largest patch of high-severity fire was more homogeneously severe and overlapped a greater density of owl sites (Figure 2; see WebFigure 6). Alternatively, because owls were not individually marked in the Rim Fire study, some detections at “occupied” sites may have involved individuals from neighboring territories or non-territorial “floaters” (Lee and Bond 2015), both of which may have contributed to inflated estimates of territory occupancy. Regardless, our study demonstrates that megafires can have strong negative effects on spotted owls, particularly when severely burned areas occur as large homogenous patches that leave little or no interspersed remnant habitat.

While we used only one year of post-fire data, the substantial decline in occupancy at severely burned sites is unlikely to reflect a temporary loss of individuals that will soon be replaced by colonization, but rather represents a direct loss of suitable nesting and roosting habitat that will likely not be replaced for many decades. Moreover, we found the scorched remains of one adult spotted owl from a severely burned site (WebFigure 7), indicating that, in some instances, this highly vagile species was unable to avoid the rapidly moving fire. It is not unreasonable to suspect that less mobile old-forest specialists will be equally – and perhaps more – affected by megafires like the King Fire. Collectively, these findings suggest that megafires constitute an additional mechanism by which climate change will threaten old-forest species, along with previously recognized climate-associated stressors such as habitat shifts, physiological impacts, and changes in community interactions (Dawson *et al.* 2011).

■ Conclusions

Our study demonstrates that increasingly frequent megafires pose a threat to spotted owls and likely other old-forest species and, as a result, suggests that forest ecosystem restoration and old-forest species conservation may be more compatible than previously believed. Restoration practices that can demonstrably reduce the frequency of large, high-severity fires and reintroduce low- to moderate-severity fire as the dominant disturbance regime will likely benefit both dry-forest ecosystems and old-forest species such as spotted owls. Yet forest restoration efforts that remove key habitat elements and areas of currently suitable habitat could exacerbate the risk of extirpation in the short term before the long-term benefits of restored fire regimes are realized, particularly in light of the present deficit in large and old trees in natural landscapes (Tempel *et al.* 2015). Rather, implementing fuels and restoration treatments outside

of key habitats (eg nesting and denning areas) is more likely to minimize short-term impacts and ensure that old-forest species persist until forest resiliency objectives are achieved (Stephens *et al.* 2014a). However, the calculus behind these trade-offs is complex and depends on several considerations that merit additional research, such as the magnitude of short-term impacts that treatments impose on old-forest species, the relative increase in the frequency of severe fire as a function of climate change, and the efficacy of forest restoration for reducing both severe fires and tree mortality from drought and insects (Asner *et al.* 2015). Managers and policy makers will be faced with challenging decisions regarding the pace and scale of forest restoration efforts in light of scientific uncertainty and conflict among stakeholders (Redpath *et al.* 2013). We suggest, however, that old-forest species should not be viewed as an impediment to forest restoration objectives; rather, ensuring the persistence of old-forest species including the spotted owl, northern goshawk (*Accipiter gentilis*), pileated woodpecker (*Dryocopus pileatus*), Pacific fisher (*Pekania pennanti*), and American marten (*Martes americana*) can serve as a barometer for the successful restoration of the ecosystems they inhabit.

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■ Supporting Information

Additional, web-only material may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/fee.1298/supinfo>

Declining old-forest species as a legacy of large trees lost

Gavin M. Jones¹  | John J. Keane² | R. J. Gutiérrez^{1,3} | M. Zachariah Peery¹

¹Department of Forest & Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA

²U.S.D.A. Forest Service, Pacific Southwest Research Station, Davis, CA, USA

³Department of Fisheries, Wildlife and Conservation Biology, University of Minnesota, St. Paul, MN, USA

Correspondence

Gavin M. Jones, Department of Forest & Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA.
Email: gavin.jones@wisc.edu

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Abstract

Aim: Global declines in large old trees from selective logging have degraded old-forest ecosystems, which could lead to delayed declines or losses of old-forest-associated wildlife populations (i.e., extinction debt). We applied the declining population paradigm and explored potential evidence for extinction debt in an old-forest dependent species across landscapes with different histories of large tree logging.

Location: Montane forests of the Sierra Nevada, California, USA.

Methods: We tested hypotheses about the influence of forest structure on territory extinction dynamics of the spotted owl (*Strix occidentalis*) using detection/non-detection data from 1993 to 2011 across two land tenures: national forests, which experienced extensive large tree logging over the past century, and national parks, which did not.

Results: Large tree/high canopy cover forest was the best predictor of extinction rates and explained 26%–77% of model deviance. Owl territories with more large tree/high canopy cover forest had lower extinction rates, and this forest type was ~4 times more prevalent within owl territories in national parks ($\bar{x}$ = 19% of territory) than national forests ($\bar{x}$ = 4% of territory). As such, predicted extinction probability for an average owl territory was ~2.5 times greater in national forests than national parks, where occupancy was declining ($\hat{\lambda} < 1$) and stable ($\hat{\lambda} = 1$), respectively. Large tree/high canopy cover forest remained consistently low, but did not decline, during the study period on national forests while owl declines were ongoing—an observation consistent with an extinction debt.

Main conclusions: In identifying a linkage between large trees and spotted owl dynamics at a regional scale, we provide evidence suggesting past logging of large old trees may have contributed to contemporary declines in an old-forest species. Strengthening protections for remaining large old trees and promoting their recruitment in the future will be critical for biodiversity conservation in the world's forests.

KEYWORDS

declining population paradigm, forest management, forest restoration, logging, occupancy modelling, spotted owl

1 | INTRODUCTION

Large old trees have declined across nearly all global ecosystems, in part because their high commercial value has led to logging pressure that outpaces sometimes centuries-long recruitment and development

(Lindenmayer, Laurance, & Franklin, 2012). Agriculture (Laurance, Sayer, & Cassman, 2014), fire (Jones, Gutiérrez, Tempel, Whitmore et al., 2016; Westerling, 2016) and disproportionate drought susceptibility (Bennett, McDowell, Allen, & Anderson-Teixeira, 2015) also increasingly threaten large old trees and conservation of old-forest

ecosystems (Lindenmayer & Laurance, 2017). Loss of large old trees is a major contributor to habitat loss for many globally endangered old-forest-dependent (hereafter “old-forest”) species such as the orangutan (*Pongo spp.*) in South-East Asia (Wich et al., 2003), the marbled murrelet (*Brachyramphus marmoratus*) and northern spotted owl (*Strix occidentalis caurina*) in western North America (Noon & Blakesley, 2006; Raphael, 2006), the Leadbeater's possum (*Gymnobelideus leadbeateri*) in south-east Australia (Lindenmayer et al., 2013) and the Blakiston's fish owl (*Bubo blakistoni*) in the Russian Far East and Japan (Slaght, Surmach, & Gutiérrez, 2013).

Like large old trees, many old-forest species have “slow” life histories with long generation times and high adult survival, which increases vulnerability when environments change rapidly (Webb, Brook, & Shine, 2002). Long-lived individuals may persist for many years in marginal or degraded forests long after critical breeding habitat elements such as large old trees are lost or substantially reduced, but gradually these individuals die off and may not be replaced. Delayed population declines or local extinctions resulting from prior habitat loss or degradation is termed “extinction debt,” which can be assessed across different levels of organization (e.g., individual species vs. community) and may be evaluated at spatial scales ranging from local extirpation within a habitat patch to regional or global extinction of a species. Extinction debt challenges the ability of scientists to establish causal links between habitat loss and population declines of individual species (Kuussaari et al., 2009). Uncertainty about population status or causes of decline, then, could delay implementing conservation measures for old-forest species and the restoration of degraded old-forest ecosystems. Moreover, this uncertainty creates political opportunities to undermine governmental or social responses to make corrective changes (Oreskes & Conway, 2010).

Global challenges facing the conservation of large old trees and old-forest-associated species (Lindenmayer & Laurance, 2016) have led some to propose new and more rigorous policies for ensuring their protection and improving conservation outcomes (Lindenmayer et al., 2014). Nevertheless, if an extinction debt has already been created, population declines of old-forest species may continue to occur long after policies protecting large old trees are put into place. Here, we studied the potential long-term (multi-generational) impacts of large tree loss on an old-forest species, the spotted owl (*S. occidentalis*), across a large mountain ecosystem by comparing forest conditions and population dynamics between national parks (long-established protected areas) and national forests (areas that experienced widespread large tree logging but more recent protections). Following a century of extensive, intensive and selective logging of very large trees on national forests (Laudenslayer & Darr, 1990; Stephens, Lydersen, Collins, Fry, & Meyer, 2015), forest policy was enacted immediately prior to our study to conserve remaining old-forest elements such as large trees and multi-layered canopy around spotted owl activity centres (Verner et al., 1992).

Despite these recent protections, we hypothesized that this historical loss of large trees on national forests could be associated with contemporary population declines, or an extinction debt, for spotted owls. In testing this hypothesis, we treated protected areas (national parks) as “contemporary reference landscapes” (Collins et al., 2016;

Meyer, 2015; Miller et al., 2016), because prohibition of logging within national park boundaries over the past century has largely preserved historical forest structure and prevalence of very large and old trees (Beesley, 1996; Lydersen & North, 2012). Thus, in principle, contemporary forests characteristics in spotted owl territories on national parks (e.g., large trees) might more closely represent forests characteristics that might have existed on national forests if protections for large trees had been established long ago.

Comparing spotted owl populations on national forests and national parks, then, allowed us to diagnose causes of decline (Caughley, 1994; Green, 1995; Peery, Beissinger, Newman, Burkett, & Williams, 2004) for a species considered to be a barometer of old-forest wildlife community health in western North America (Simberloff, 1998). Despite the fact that the spotted owl is one of the most intensively studied species in the world with 40 years of demographic and ecological research across its range, no definitive causal link between ongoing owl declines and changes in habitat has been established. Here, we offer insight into this elusive question by applying the concept of extinction debt and provide an unprecedented case study about the potential ecological legacies of large tree loss on increasingly rare global old-forest species and ecosystems (Lindenmayer et al., 2012, 2014).

2 | METHODS

2.1 | Study areas and logging histories

Four spotted owl study areas—Lassen (LAS), Eldorado (ELD), Sierra (SIE) and Sequoia-Kings Canyon (SKC)—span nearly the entire latitudinal range of California's Sierra Nevada (Figure 1). Elevations range

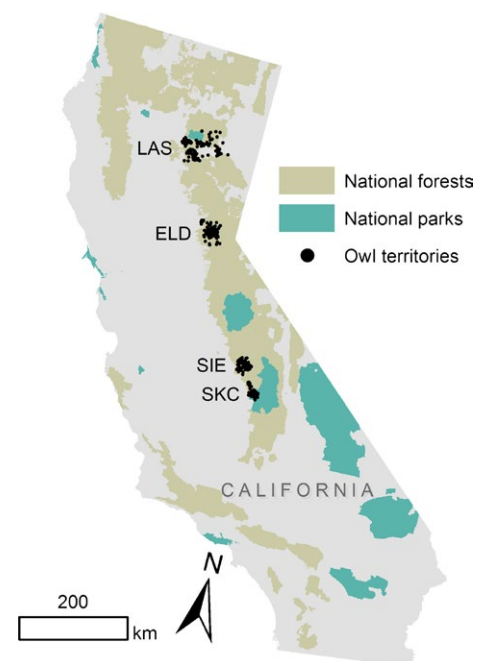


FIGURE 1 Locations of owl territories across the four spotted owl study areas in the Sierra Nevada, California, USA. [Colour figure can be viewed at wileyonlinelibrary.com]

from 300 to 3,050 m across the four study areas, and the climate is Mediterranean (Tempel et al., 2016). LAS, ELD and SIE study areas are primarily located within national forests (with intermixed private land), whereas SKC occurs within two national parks of the same name. While Sierran mixed-conifer montane forest is the primary vegetation type within owl territories across all study areas (Tempel et al., 2016), contemporary structure of these forests has been strongly affected by different management legacies across the two land tenures (i.e., national forests vs. national parks).

Very large (e.g., >125 cm dbh) old trees were not uncommon throughout the Sierra Nevada at the turn of the twentieth century (McKelvey & Johnston, 1992; Safford & Stevens, 2016). Several national parks including Sequoia (of SKC) were established in 1890 (Kings Canyon National Park adjoined in 1940), and the prohibition of logging within park boundaries over the following century largely acted to preserve historical forest structure and prevalence of very large and old trees (Beesley, 1996; Lydersen & North, 2012). In contrast, logging activities on what would eventually become Sierra Nevada national forest lands were well underway by 1900 (Beesley, 1996; Thomas, 2008). Commercial logging (i.e., selective removal of very large trees) on Sierra Nevada national forests increased from ~470,000 cubic metres (m^3) year^{-1} in the 1870s to its peak during the 1940s when timber production reached 4.5 million m^3 year^{-1} . Timber production remained reasonably high thereafter (generally between 2.8 and 3.8 million m^3 year^{-1}) for several decades before a near-historic peak in timber production in 1990 when production again neared 4.5 million m^3 year^{-1} (McKelvey & Johnston, 1992).

Concern about the continued and cumulative loss of large trees required by spotted owls reached a highpoint around the same time and as a result, in 1992, logging of ≥ 76 cm dbh trees on national forests was restricted (with some allowable exceptions for equipment operability), as was almost all logging within 121 ha areas around known owl nest and roost sites (USFS, 2004; Verner et al., 1992). Our study on spotted owls began in 1993, immediately following near-peak logging activity and subsequent restrictions. Recent work has established that national forest lands indeed contain greater prevalence of younger trees that are smaller in diameter and height (Laudenslayer & Darr, 1990; Stephens et al., 2015) and significantly fewer trees in the largest size classes compared to historical baselines (Collins, Fry, Lydersen, Everett, & Stephens, in press; McIntyre et al., 2015; Safford & Stevens, 2016; Stephens et al., 2015). Given that SKC did not experience the same history of selective logging and forest structural change as the three study areas on national forests, we treated it as a contemporary reference landscape for evaluating differences in forest structure and owl population dynamics between land tenures.

2.2 | Owl surveys

As part of prior work, we have established that temporal changes in occupancy rates of spotted owl territories (i.e., based on detection/non-detection data) can provide inferences regarding overall population trends that are comparably reliable to estimates of overall population trends based on changes in abundance (Conner, Keane, Gallagher,

Munton, & Shaklee, 2016; Tempel & Gutiérrez, 2013; Tempel, Peery, & Gutiérrez, 2014). As such, we conducted detection/non-detection surveys for spotted owls at 275 owl territories located during breeding seasons (Apr–Aug on LAS and ELD; Mar–Sept on SIE and SKC) across the four study areas over a 19-year period (1993–2011). All study areas consisted of a core study area that we surveyed completely in each year of the study (i.e., both the areas containing owl territories and all areas not containing known owl territories within the core area were surveyed every year). In addition, we added some owl territories over time, either as an expansion of the core area (LAS) or as individual “satellite” territories (i.e., adjacent to, but not part of, the core area) to increase owl sample sizes for demographic analysis (LAS and ELD), and we dropped a portion of SKC in 2006 (Tempel et al., 2016). We surveyed all satellite territories used in our occupancy analyses for a minimum of 3 years; most territories in the core areas were surveyed for ≥ 15 years.

We located spotted owls by imitating their vocalizations (vocal lure) for 10 min at a survey station or used vocal lures while walking along a survey route. We then considered sites to be a territory where owls responded to vocal lures and were subsequently observed either roosting or nesting during diurnal hours. Some surveys occurred prior to 1993 but previous analyses have determined that survey coverage and effort required for population analyses (such as ours presented here) became adequate beginning in 1993 (Tempel & Gutiérrez, 2013; Tempel et al., 2016). We did not survey all territories in all years of the study. However, of the 275 owl territories used in the study, ≥ 205 were surveyed in all but the first year of the study (in 1993, 187 owl territories were surveyed). The average number of owl territories surveyed annually was 239 (87% of all known territories; standard error = 21 territories), with a maximum of 263 territories surveyed in 2008 (95.6% of all known territories). Moreover, while most intervening area between territories was intensively surveyed each year, spotted owls on our study areas rarely established new territories outside of territories located in the early stages of the study. For example, the most recently located territory on the ELD was found in 1997. We included all surveys in our analyses but excluded nocturnal detections of unknown owls (i.e., owls that were not re-sighted by unique colour leg-bands as part of a concomitant mark-recapture study) that occurred outside of a delineated territory boundary (see below for information on owl territories) using a Geographic Information System (GIS) to eliminate potential spurious positive detections of owls not occupying the nominal territories. A survey in which no owls were detected needed a total duration of ≥ 30 min to be included as an absence record. Extensive details about each study area and additional survey details can be found in Tempel et al. (2016).

2.3 | Sampling units and vegetation covariates

We treated owl territories as sampling units, where a territory had at least one owl detection during diurnal hours in ≥ 3 years. For quantifying habitat covariates within spotted owl territories, we first calculated the geometric centre of each territory as the average spatial coordinates of all nest and roost locations across all years in the territory.

We then calculated the mean nearest neighbour distance among territory centres for each study area as the average distance between each territory centre and the centre of its nearest neighbouring territory. Thus, the location of owl territories was assumed to remain the same throughout the study period, and territories in each study area were assumed to be of equal size based on the nearest neighbour distance. In a recent meta-analysis (Tempel et al., 2016), we defined the spatial extent of a territory as a circle around each territory centre with a radius equal to half of the mean nearest neighbour distance. The resulting territory size for each study area decreased along a north–south gradient: Lassen = 639.4 ha (1,427-m radius), Eldorado = 399.5 ha (1,128-m radius), Sierra = 301.6 ha (980-m radius) and Sequoia–Kings Canyon = 254.3 ha (900-m radius). This process nearly eliminated spatial overlap among adjacent territory circles. In the present study, we defined territories as hexagons instead of circles with areas and geometric centres equal to those determined by Tempel et al. (2016) to facilitate integration into concurrent projects using spatial population models (e.g., HexSim; Schumaker, 2015).

We defined site-specific covariates based on two vegetation variables within owl territories using the “GNN” (Gradient Nearest Neighbour) forest structural maps produced by the Landscape Ecology, Modeling, Mapping & Analysis (LEMMA) research group (Oregon State University, Corvallis, OR, USA). GNN is an imputation method used by LEMMA that integrates regional forest inventory plots with Landsat imagery to produce fine-scale (30-m resolution) and large-domain (currently the entire land area for the U.S. states of Washington, Oregon and California) vegetation structure and species composition maps. The GNN approach is one variation of nearest neighbour imputation methods that use (1) a neighbourhood value of

$k = 1$ as the number of neighbours imputed to each cell and (2) direct gradient analysis as the “distance” metric (see <https://lemma.forestry.oregonstate.edu/methods>). The first variable was the quadratic mean diameter of dominant and codominant trees in each 30×30 m pixel (“QMD_DOM”). Quadratic mean diameter (QMD) is a commonly used metric in forestry that more strongly reflects the influence of large trees on stand tree size classifications than arithmetic mean (Curtis & Marshall, 2000). The second variable was the per cent canopy cover of live trees in each pixel (“CANCOV”).

Large trees are a key feature of spotted owl nest sites (Gutiérrez et al., 1992), and owl site occupancy has been positively correlated with large trees (>61 cm dbh) and high canopy cover (>70%) at nest areas (Blakesley, Noon, & Anderson, 2005). However, forests with intermediate canopy cover (40%–70%) can constitute spotted owl nesting or roosting habitat if large, remnant trees are present (Hunter & Bond, 2001; Moen & Gutiérrez, 1997), and recent work found that both medium and high canopy cover were associated with spotted owl occupancy in the Sierra Nevada (Jones, Gutiérrez, Tempel, Zuckerberg, & Peery, 2016; Tempel, Gutiérrez, et al., 2014; Tempel et al., 2016). Thus, we estimated the proportion of each owl territory containing the following five covariates: large trees (QMD > 61 cm) regardless of canopy cover class; high canopy cover (>70% cover) regardless of tree size class; as well as the spatial intersection ($\cap$; see Figure 2) of large trees and high canopy cover, large trees and medium canopy cover (40%–70% cover), and medium trees (QMD = 30–61 cm) and high canopy cover. These proportions were calculated by dividing the number of 30×30 m pixels in the territory for a particular variable by the total number of 30×30 m pixels in the territory. Several of the predictor variables were highly collinear (e.g., $r = .7-.9$), so we developed

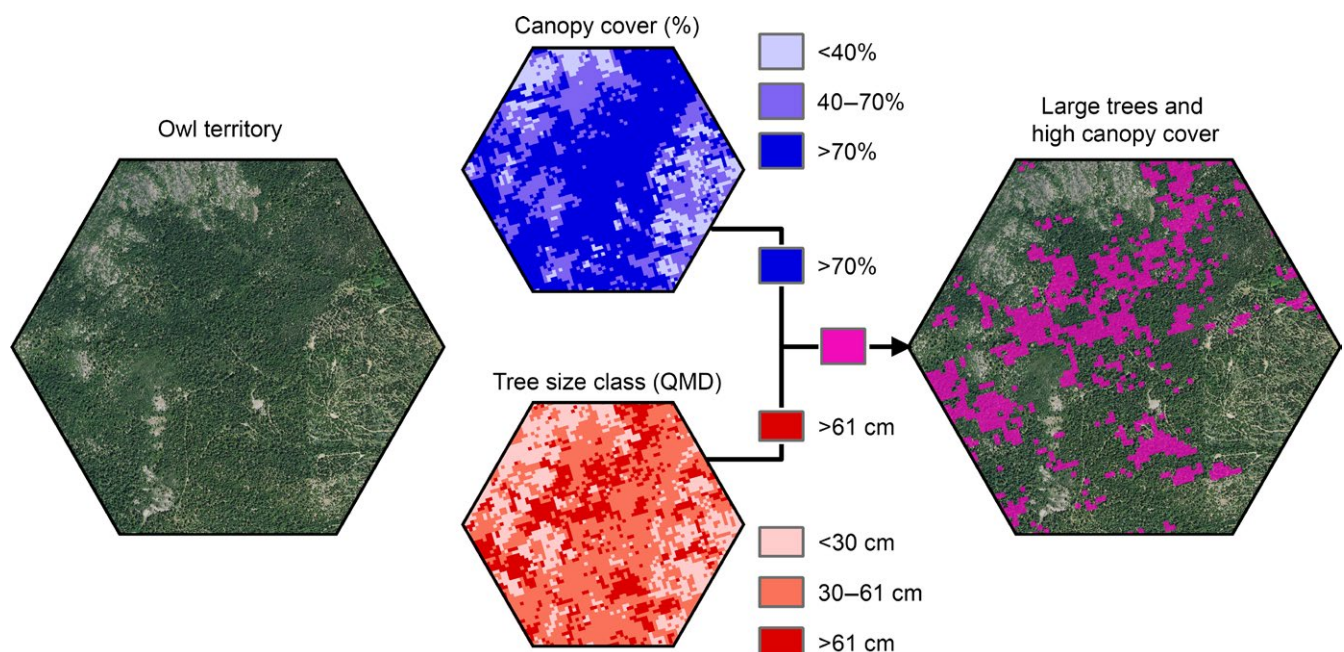


FIGURE 2 An example showing how we produced covariates representing spatial intersections between GNN-derived canopy cover and tree size classes by overlaying classified pixels using a GIS. Here, we see the high canopy cover class (>70% canopy cover) and the large tree size class (>61 cm dbh) combining in a spatial intersection ($\cap$) to produce a covariate called “large trees and high canopy cover” for an example spotted owl territory. [Colour figure can be viewed at wileyonlinelibrary.com]

models that contained a single predictor variable and used AIC to identify which predictor variables best explained owl extinction dynamics (see below).

We adopted the above tree size classes because they are commonly used by foresters (Blakesley et al., 2005; Verner et al., 1992), although the large old trees used by owls for nesting are typically larger than 61 cm dbh (e.g., mean 157 cm dbh; North et al., 2000). Median QMD in the >61 cm dbh size class was 75.5 cm and reached a maximum of 279 cm (Fig. S1). Finally, for each forest structure variable listed above, we averaged the within-territory covariate values across all years (1993–2011) to produce a single, static territory-level covariate that varied across space (but was averaged over time), because nearly all variation in the covariates was spatial rather than temporal (large among-territory differences). Ranges of covariate values for each study area are provided in Table 1.

2.4 | Statistical analysis and model selection

We used multi-season occupancy models to assess territory occupancy dynamics on each study area separately (Tempel et al., 2016) using program PRESENCE 11.5. The models contained parameters for initial occupancy (ψ_1), local extinction (ϵ_t), local colonization (γ_t) and detection probability ($p_{t,j}$) (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). Our primary sampling periods (t) were breeding seasons (i.e., years), and our secondary sampling periods (j) were bimonthly periods within each breeding season (April 1–15, April 16–30, etc.). No surveys were conducted on SKC in 2005 so we fixed p , ϵ and γ for that year to zero. We allowed colonization to vary as a year-specific effect rather than a function of covariates because (1) colonization may be related more to site availability than site conditions, and (2) we were interested in factors associated with elevated extinction rates.

We used multi-stage modelling (Tempel et al., 2016). At each stage, we ranked models using AIC (Burnham & Anderson, 2002) to select the base model for the next stage. We first modelled p as a function of the above forest structure covariates and within- and among-year

temporal trends (i.e., linear, log-linear or quadratic trends in p) while γ and ϵ varied by year. We then examined linear, logarithmic and quadratic forms of covariates on ψ_1 while γ and ϵ varied by year. Finally, we examined the potential effects of covariates on ϵ while γ varied by year, again considering linear, logarithmic and quadratic covariate forms because previous owl studies showed evidence of non-linear relationships (Dugger, Wagner, Anthony, & Olson, 2005; Forsman et al., 2011). We used analysis of deviance to assess the amount of variation explained by model covariates. This approach compares deviance explained by the covariates in a model with the amount of deviance not explained by these covariates, thus providing an estimate of r^2 for the model (Skalski, Hoffman, & Smith, 1993). The global model for the analysis of deviance consisted of the top-ranked model for the given study area with additional annual effects for ϵ , and the constant model consisted of the best detection structure with only and intercept for ϵ (Tempel et al., 2016).

We used the best p model from the first stage with year-specific γ and ϵ to obtain derived estimates of ψ_t which we used to calculate the geometric mean of the rate of change in occupancy ($\hat{\lambda}$) and estimated the realized change in occupancy (Δ_k) for each study area. We calculated variance for $\hat{\lambda}$ and Δ_k using the delta method (Powell, 2007).

3 | RESULTS

We found that local extinction rates were higher when owl territories contained less forest characterized by large trees (>61 cm dbh) and high canopy cover (>70%), and extinction rates declined as this forest type increased (Figure 3). Indeed, local extinction was best explained by the proportion of an owl territory containing large tree/high canopy cover forest, as evidenced by the presence of this covariate in the top models on three of the four study areas (ELD, SIE, SKC) having nearly all (88%–97%) of AIC weight (Table S1). The top three models for the fourth study area (LAS) were closely competing (within 1 AIC), containing parameters for large trees only, large trees and high canopy

TABLE 1 Median (SD) proportion of a spotted owl territory^a containing GNN structure variables used to assess local extinction dynamics on four study areas^b in the Sierra Nevada, CA, USA. The number of spotted owl territories identified on each study area is shown in the bottom row of the table

Variable	Study area			
	LAS	ELD	SIE	SKC
Large trees ^c	0.07 (0.05)	0.11 (0.06)	0.13 (0.11)	0.33 (0.19)
High canopy cover ^d	0.46 (0.16)	0.54 (0.14)	0.25 (0.16)	0.48 (0.16)
Large trees and high canopy cover	0.03 (0.05)	0.06 (0.05)	0.04 (0.08)	0.19 (0.14)
Large trees and medium canopy cover	0.02 (0.02)	0.02 (0.03)	0.05 (0.06)	0.10 (0.08)
Medium trees and high canopy cover	0.28 (0.12)	0.32 (0.09)	0.15 (0.10)	0.18 (0.12)
	<i>n</i> = 90	<i>n</i> = 74	<i>n</i> = 66	<i>n</i> = 45

^aTerritory areas (ha) for each study area were as follows: LAS (639.4), ELD (399.5), SIE (301.6) and SKC (254.3) (Tempel et al., 2016).

^bStudy area abbreviations: LAS = Lassen, ELD = Eldorado, SIE = Sierra, SKC = Sequoia-Kings Canyon.

^cSummed across all canopy cover classes.

^dSummed across all tree size classes.

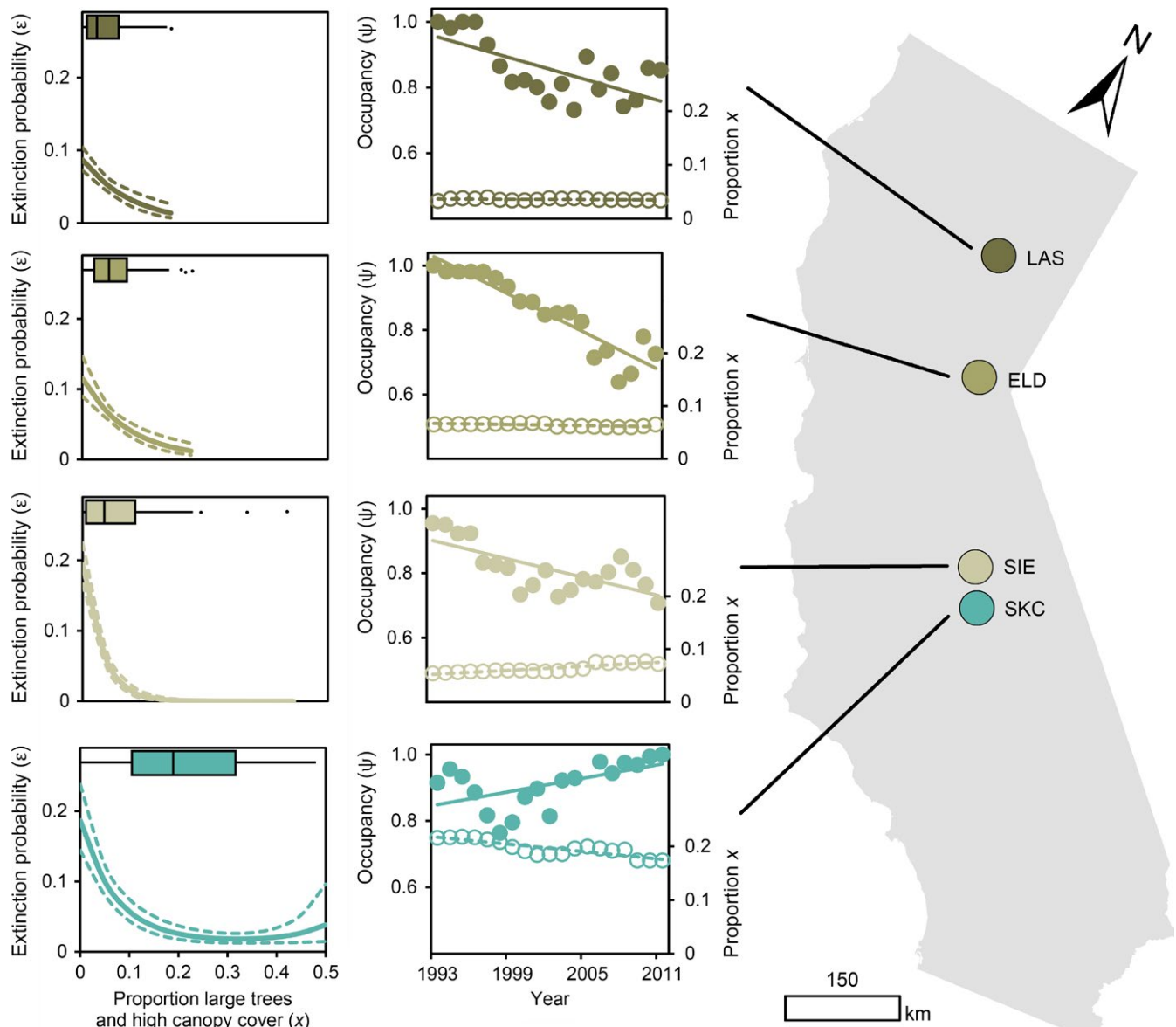


FIGURE 3 The relationship between large tree/high canopy cover forest and spotted owl occupancy dynamics. The left column of panels shows (1) the modelled relationship between spotted owl territory extinction probability and the proportion of an owl territory containing forests with large trees and high canopy cover (x), where the solid coloured lines represent the modelled relationship and the dashed lines represent ± 1 SE, plotted over the range of observed values, and (2) the distribution of values for x present on each study area, which are represented by horizontal boxplots (corresponding to the x -axis). The right column of panels shows (1) annual estimates of derived occupancy (solid circles) from a fully time-varying model (see Methods) on the primary (left) axis, where the solid line represents a linear trend to emphasize population trajectories (see Table 2) over the 19-year study period, and (2) the median annual proportion of large tree/high canopy cover forest (x ; open circles) on the secondary (right) axis, where the dashed line represents a linear trend to emphasize that this variable did not decline on national forests (three northernmost study areas, colored brown) over the 1993–2011 study period (also see Fig. S2). [Colour figure can be viewed at wileyonlinelibrary.com]

cover, and high canopy cover only, respectively (Table S1), although the coefficient estimate for the high canopy cover only model was imprecise (Table S2).

No other models were competitive with the large tree/high canopy cover model for any study area (all >5 AIC from top model; Tables S1 and S3). However, models containing other forest structural covariates such as high canopy cover, medium trees and high canopy cover, and large trees and medium canopy cover sometimes outperformed the null model and yielded coefficient estimates with 95% confidence

intervals that did not overlap zero (Table S2), suggesting they may be biologically meaningful. Analysis of deviance showed that the covariate for large tree/high canopy cover forest explained 28%, 26%, 77% and 53% of the variation in local extinction rates on LAS, ELD, SIE and SKC, respectively.

The median proportion of an owl site containing large tree/high canopy cover forest on national forests (LAS, ELD, SIE) was similar, ranging from 0.03 to 0.06 (Table 1). These values corresponded with higher predicted rates of local extinction ($\epsilon = 0.06$ – 0.074) and ongoing

TABLE 2 Estimates^a of model parameters^b and occupancy trends^c for California spotted owls on four study areas in the Sierra Nevada, CA, USA

Study area	α	β_x	β_x^2	$\hat{\lambda}$	Δ_k
LAS	-2.35 [-2.74, -1.96]	-10.58 [-18.68, -2.48]	—	0.991 [0.9827, 0.9997]	0.853 [0.720, 0.987] [†]
ELD	-2.04 [-2.58, -1.50]	-11.84 [-20.25, -3.43] ^d	—	0.983 [0.9733, 0.9918]	0.728 [0.601, 0.855] [†]
SIE	-1.45 [-1.82, -1.08]	-26.24 [-36.28, -16.19]	—	0.981 [0.9717, 0.9904]	0.709 [0.583, 0.834] [†]
SKC	-1.47 [-2.08, -0.87]	-15.66 [-24.85, -6.47]	24.30 [1.86, 46.74]	1.005 [0.9997, 1.0105]	1.096 [0.990, 1.202] [*]

^aNumbers in square brackets represent the lower and upper boundaries of 95% confidence intervals for the point estimate, which precedes the square brackets.

^b α = intercept, β_x = model coefficients for the variable (x) representing the proportion of a spotted owl territory containing large trees and high canopy cover.

^c $\hat{\lambda}$ = geometric mean of the annual rate of change in occupancy, Δ_k = realized change in occupancy (ψ_k/ψ_1) where k is the number of years in the study. Symbols († and *) following estimates and confidence intervals for Δ_k indicate groups resulting from pairwise comparisons where estimates that share the same symbol had Δ_k estimates that were not statistically different from one another at the $\alpha = 0.05$ level.

^d $\beta_{\ln(x)}$

occupancy declines according to estimates of the geometric mean rate of change in occupancy ($\hat{\lambda} < 1$) and realized change in occupancy ($\Delta_k < 1$) over the period 1993–2011 (Table 2). By contrast, the median proportion of large tree/high canopy cover forest within owl territories on national parks (SKC) was 0.19 (Table 1), which was associated with much lower predicted extinction rates ($\varepsilon = 0.027$) and stable occupancy ($\hat{\lambda} = 1$, $\Delta_k = 1$) (Figure 3, Table 2). Thus, extinction probability at a “typical” owl territory was ~2.5 higher on average in national forests (LAS, ELD, SIE) than national parks (SKC). A post-hoc comparison showed that estimates of realized change in occupancy (Δ_k) for LAS, ELD and SIE were not statistically different from one another, but all were significantly lower than SKC (Table 2).

The extent of large trees/high canopy cover forest within owl territories differed among study areas ($F_{3,271} = 38.3$, $p < .01$) and was ~4 times greater in national parks than in national forests on average (Table 1). Furthermore, this forest type did not appear to decline within owl territories on national forests over the study period (Figures 3 and S2), suggesting the considerable deficit of large tree/high canopy cover forest on national forests may have resulted from historical (as opposed to more recent) logging activities that selectively removed very large old trees (Collins et al., in press; Laudenslayer & Darr, 1990; McKelvey & Johnston, 1992; Stephens et al., 2015).

4 | DISCUSSION

4.1 | Extinction debt and restoration opportunities

Our work presents several key inferences suggesting ongoing declines in spotted owl populations on national forests are consistent with an extinction debt, or a legacy effect, resulting from logging of large trees prior to the initiation of our study. First, we found that local extinction rates were consistently higher across a large bioregion (the Sierra Nevada) when large tree/high canopy cover forest was less common in owl territories. Second, large tree/high canopy cover forest was far more common in owl territories on national parks (SKC), where large trees have not been logged. Third, owl populations are declining on

all national forest study areas, which contain far less large tree/high canopy cover forest in owl territories than national parks where the owl population is stable. Fourth, although logging activities prior to our study led to a deficit of large tree/high canopy forest on national forests, no further declines in this forest type were observed from 1993 to 2011 (Fig. S2) while owl populations experienced long-term declines over the same period. Together, these inferences suggest that past large tree logging on national forests, which removed key habitat elements for spotted owls, may have created an extinction debt that led to contemporary owl declines long after policies were enacted to protect large trees (Figure 3).

We note that other emerging threats to the spotted owl, such as large, severe wildfires (Jones, Gutiérrez, Tempel, Whitmore et al., 2016) and invasive barred owls (*S. varia*) (Wiens, Anthony, & Forsman, 2014) did not contribute to observed declines given that our study areas did not experience significant severe fire or appreciable numbers of barred owls during the study period (Keane, 2017). Secondary ingestion of anticoagulant rodenticides used to kill rodents on illegal marijuana (*Cannabis* sp.) cultivations has been documented in fishers (*Pekania pennanti*) and barred owls in the Sierra Nevada and north-western California (Gabriel et al., 2012; Keane, 2017). However, we know of no documented cases of exposure in spotted owls, and it is currently unknown to what extent this stressor has contributed to observed changes in spotted owl populations.

The concept of extinction debt is defined by the idea that individuals, populations or species can initially survive habitat change but later become locally extirpated or experience declines without any further habitat modification (Kuussaari et al., 2009). As such, it is important to note that by identifying the potential presence of an extinction debt in owl populations on national forests, our inferences do not suggest that total population extinction is a foregone conclusion. On the contrary, it is possible (or even likely) that spotted owl occupancy on national forests will eventually reach a new, lower equilibrium once the extinction debt is paid (Hylander & Ehrlén, 2013). In the present study, we did not explore when the extinction debt might be paid off (i.e., when the population will stop declining and persist at its new

lower equilibrium level), nor did we attempt to identify an empirical extinction threshold (i.e., the minimum amount of habitat required in a territory for individuals to persist). Rather, we focused on identifying potential mechanisms of extinction debt to guide more targeted conservation action (Hylander & Ehrlén, 2013).

An emerging conservation paradigm for degraded old-forest ecosystems, and the many endangered species that inhabit them, centres on restoring forest structure and function (Chazdon, 2008) thereby increasing forest resilience to disturbance from fire, disease, and drought (Millar & Stephenson, 2015) and conserving wildlife habitat over the long term (Tempel et al., 2015). The consistent relationship we identified between spotted owl extinction rates and large tree/high canopy cover forest across the latitudinal range of the Sierra Nevada has significant implications for developing meaningful ecosystem restoration targets at bioregional scales (Peery et al., 2017). In particular, high canopy cover is thought to increase severe fire risk and spread by creating fuel continuity, yet appears to be relatively more prevalent (when co-occurring with large trees) within owl territories in national parks (SKC) that have been subjected to restored, lower-severity frequent-fire regimes for nearly half a century (van Wagtenonk, 2007). This indicates the potential that increased prevalence of large tree/high canopy cover forest types within owl territories in national forests may not be incompatible with fire resistance/resilience while at the same time providing conservation benefits to spotted owls.

The potential direct benefits to owls of increasing this forest type may be considerable. Employing our models, increasing large tree/high canopy cover forest from the median within-territory value of 0.03–0.06 to 0.10 (30–64 ha) on national forests reduced predicted local extinction rates by 36%–79%. Increasing the median within-territory value further to 0.20 (60–127 ha), similar to the median value at SKC (0.19), reduced predicted extinction rates by 80%–98%. Furthermore, because they are cornerstones of old-forest ecosystem stability, greater prevalence of large trees within owl territories and across the broader landscape probably would provide direct benefits to both spotted owls and increase resilience of old-forest ecosystems to emerging stressors.

Forests in national parks representing contemporary reference landscapes generally contain less canopy cover and lower tree densities than fire-suppressed forests on average (Lydersen & North, 2012). Why then do owl territories on national parks appear to contain considerably more large tree/high canopy cover forest than their counterparts on national forests? First, although national forests may contain higher densities of trees of all sizes, they contain significantly lower densities of trees in the largest diameter (i.e., >91 cm dbh) (Collins et al., in press) and height classes (>48 m) (North et al., 2017). Second, forest patches characterized by both large trees and higher canopy cover are not a product of fire suppression, but occurred historically throughout Sierra Nevada forests within a diverse mosaic of forest types in systems maintained by mixed-severity fire regimes (Hessburg et al., 2016). Spotted owl territories likely contained disproportionately more large trees and higher canopy cover than the broader forested landscape because owls are known to select for these specific

features (Lahaye, Gutiérrez, & Call, 1997; Moen & Gutiérrez, 1997; North et al., 2017).

While areas managed for multiple uses including resource extraction (i.e., national forests) and protected areas serve different societal purposes and, for this reason and others, are unlikely to have convergent forest structure and function, we can still learn important lessons when protected areas contain stable populations of species of conservation concern. For example, protected areas often form refuges for ecosystems containing distinctive biological features such as large old trees (Miller et al., 2016) and, therefore, they can act as blueprints for ecological restoration (Boisramé, Thompson, Collins, & Stephens, 2017). Furthermore, protected areas may contain tree sizes, age structure and intact disturbance regimes (Lydersen & North, 2012) characteristic of ecologically resilient landscapes (i.e., landscapes that have the capacity to recover their ecological functioning following a disturbance) and that more closely reflect species' evolutionary environments (Moore, Covington, & Fulé, 1999). Thus, in certain cases, protected areas might act as contemporary reference landscapes (Collins et al., 2016; Meyer, 2015) to provide a frame of reference for the goals of ecological restoration (White & Walker, 1997) for large old trees and recovery of old-forest-associated species across different land tenures.

Care should be taken, however, to acknowledge the potential limitations of using national parks and other protected areas as contemporary reference landscapes to inform conservation action at broader spatial scales. For example, protected areas do not necessarily represent a random sampling of area on the landscape, but instead are often biased towards places that are less likely to face land conversion pressures—areas characterized by higher elevations, steeper slopes and greater distances to roads and cities (Joppa & Pfaff, 2009). In our study, we treat Sequoia and Kings Canyon national parks (SKC) as a contemporary reference landscape, yet it is also most southerly of all study areas examined (Figure 3). This raises the question of whether SKC can truly act as a reference, or if other fundamental differences related to differences in latitude (e.g., climate or vegetation types) could play a stronger role than past forest management on observed dynamics of spotted owls.

While this is a possibility, we present several lines of evidence to support our use of SKC as a contemporary reference landscape. First, average temperatures and annual precipitation in SKC fell within the range experienced by the other three more northerly studies (Franklin et al., 2004). Second, mixed-conifer forests characterized primarily by sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*) and incense cedar (*Calocedrus decurrens*) were the dominant vegetation type on all four study areas. While SKC did contain ten groves of giant sequoia (*Sequoiadendron giganteum*), these covered only 7% of the study area (Tempel et al., 2016). Third, the two most southerly study areas, SIE and SKC, occur immediately adjacent to one another in the southern Sierra Nevada in a paired study design. Yet these two study areas exhibit the largest differences in population trends according to estimates of $\hat{\lambda}$ and Δ_k (Table 2), suggesting differences in trajectory may be unrelated to underlying differences in climate or potential vegetation type.

4.2 | Global conservation of large trees and forest policy

The case study presented here demonstrates globally informative principles for old-forest species and large tree conservation. Notably, our results are consistent with an extinction debt resulting from historical logging of large trees that yielded long-term declines in old-forest species populations even after policies protecting large trees were enacted, highlighting an urgent need to protect existing old-forest habitat and potential large tree refugia (Lindenmayer et al., 2014). Indeed, national and international environmental legislation often do not emphasize the protection of large trees and old-forest ecosystems (e.g., the European Union Habitats Directive; EU, 1992).

Regional-scale plans to protect and restore old-forest ecosystems allow exceptions to rules limiting removal of large old trees to meet needs for equipment operability in forest restoration projects (e.g., USFS, 2004), and the sale of larger trees is necessary to offset operational costs of ecological restoration activities in heavily managed or degraded forests ecosystems (North et al., 2015). Therefore, alternative approaches for funding restoration may be required to prevent further large tree loss, which may lead to ecosystem collapse in landscapes with significant legacies of exploitive land use (Burns et al., 2015; Lindenmayer, Messier, & Sato, 2016). Despite these global challenges and conservation gaps, an emerging paradigm is to emphasize highly targeted and fine-scale conservation of large old trees as small (or sometimes individual) natural features (Lindenmayer, 2017). Policies that emphasize the protection as well as the social and ecological value of individual large old trees will offer a new hope for the perpetuity of old-forest ecosystems and the increasingly rare biodiversity that depends on them.

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ORCID

Gavin M. Jones  <http://orcid.org/0000-0002-5102-1229>

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BIOSKETCH

Gavin M. Jones is a graduate student in the Department of Forest & Wildlife Ecology at the University of Wisconsin-Madison. His research broadly focuses on developing ecological models that inform management decisions and improve conservation outcomes.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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RESEARCH ARTICLE

Habitat selection by spotted owls after a megafire reflects their adaptation to historical frequent-fire regimes

Gavin M. Jones · H. Anu Kramer · Sheila A. Whitmore · William J. Berigan · Douglas J. Tempel · Connor M. Wood · Brendan K. Hobart · Tedward Erker · Fidelis A. Atuo · Nicole F. Pietrunti · Rodd Kelsey · R. J. Gutiérrez · M. Zachariah Peery

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Abstract

Context Climate and land-use change have led to disturbance regimes in many ecosystems without a historical analog, leading to uncertainty about how species adapted to past conditions will respond to novel post-disturbance landscapes.

Objectives We examined habitat selection by spotted owls in a post-fire landscape. We tested whether selection or avoidance of severely burned areas could be explained by patch size or configuration, and whether variation in selection among individuals could be explained by differences in habitat availability.

Methods We applied mixed-effects models to GPS data from 20 spotted owls in the Sierra Nevada, California, USA, with individual owls occupying home ranges spanning a broad range of post-fire conditions after the 2014 King Fire.

Results Individual spotted owls whose home ranges experienced less severe fire (< 5% of home range severely burned) tended to select severely burned forest, but owls avoided severely burned forest when more of their home range was affected (~ 5–40%). Owls also tended to select severe fire patches that were smaller in size and more complex in shape, and rarely traveled > 100-m into severe fire patches. Spotted owls avoided areas that had experienced post-fire salvage logging but the interpretation of this effect was nuanced. Owls also avoided areas that were classified as open and/or young forest prior to the fire.

Conclusions Our results support the hypothesis that spotted owls are adapted to historical fire regimes characterized by small severe fire patches in this region. Shifts in disturbance regimes that produce novel landscape patterns characterized by large, homogeneous patches of high-severity fire may negatively affect this species.

G. M. Jones (✉) · H. A. Kramer · S. A. Whitmore · W. J. Berigan · D. J. Tempel · C. M. Wood · B. K. Hobart · T. Erker · F. A. Atuo · N. F. Pietrunti · R. J. Gutiérrez · M. Z. Peery
Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI, USA
e-mail: gavinjones@ufl.edu

G. M. Jones
Department of Wildlife Ecology and Conservation,
University of Florida, Gainesville, FL, USA

R. Kelsey
The Nature Conservancy, Sacramento,
CA, USA

R. J. Gutiérrez
Department of Fisheries, Wildlife, and Conservation
Biology, University of Minnesota, St. Paul,
MN, USA

Keywords California spotted owl · Disturbance · Functional response · Individual variation · Resource selection · Salvage logging · *Strix occidentalis* · Wildfire

Introduction

Disturbance regimes create and maintain the characteristic vegetation patterns and dynamics to which animals are adapted in ecological systems (Lytle 2001; Betts et al. 2019). Climate and human land use change have led to modern disturbance regimes in many ecosystems that do not have a historical analog (Seidl et al. 2016), giving rise to novel post-disturbance landscape mosaics and altered regeneration pathways (Johnstone et al. 2016). Landscapes experiencing novel disturbance regimes are often characterized by changes in vegetation composition, patch size, and configuration that are expected to change selection pressures, which can affect the behavior and fitness of individual organisms (Karr and Freemark 1985). Responses to changing disturbance regimes vary among taxa (Elmqvist et al. 2003), but are likely to depend on the species' degree of habitat specialization as well as the extent to which these novel disturbances affect resources that limit individuals and populations (e.g., nesting or denning sites, primary prey/food) (Clavero et al. 2011). Therefore, the way in which individuals and populations select or avoid conditions in novel post-disturbance landscapes may offer insights into the ability of species to persist in landscapes experiencing changing disturbance regimes.

Wildfire is an important disturbance regime that is changing worldwide (Turner 2010; Seidl et al. 2017), and is considered to be a significant evolutionary force (Bond and Keeley 2005; Pausas and Parr 2018; Foster et al. 2020). The dry forests of western North America appear to be experiencing changes from a historically frequent-fire regime that consisted of predominately lower-severity fire with a relatively small component of high-severity fire by comparison (Stephens and Collins 2004; Steel et al. 2015; Safford and Stevens 2017), to one where fires have become larger and more severe (Steel et al. 2015; Abatzoglou and Williams 2016; Westerling 2016). More frequent 'megafires' in western dry forests are generally thought to be the consequence of a century of fire suppression, which increased landscape fuels (Stephens et al. 2014; Collins et al. 2017a), and anthropogenic climate change, which produced conditions enhancing fire risk (Diffenbaugh et al. 2015). As a consequence, the patch structure in post-fire landscapes is increasingly characterized by homogeneous large patches of

severely burned areas (Collins et al. 2017b; Stevens et al. 2017). Decreased heterogeneity in post-fire conditions (i.e., more homogeneously severe burned areas) may influence the behavior and space use of species that have evolved to exploit more heterogeneous environments and ultimately reduce individual fitness and population abundance.

Forest-dependent species inhabiting dry forests in western North America evolved under a frequent-fire regime that created diverse mosaics of post-fire conditions and thus have developed life history strategies to accommodate the structural and landscape heterogeneity created by fire. One of the more well-known of these species is the spotted owl (*Strix occidentalis*), an older-forest associated raptor that inhabits dry forests in portions of its geographical range that has been the focus of forest management conflict in the western United States for several decades (Simberloff 1987; Redpath et al. 2013; Gutiérrez et al. 2015). Recently, this conflict has shifted from "owls versus jobs" to "owls versus forest restoration"—a seemingly intractable conflict between efforts to increase resilience of seasonal dry forests and the conservation of spotted owl habitat (Peery et al. 2019; Stephens et al. 2019). A key feature of the current conflict involves the potential effects of large, severe wildfires on spotted owls. If such fires render forests unusable by spotted owls and thereby adversely affect owl populations, then fuels reduction activities (e.g., mechanical removal of small and medium trees, prescribed fire, and managed fire) might benefit this species by reducing severe fire impacts, if fuels reduction activities have minimal negative effects to owls (Peery et al. 2017). However, there is considerable disagreement in the literature regarding these tradeoffs and this has led to uncertainty about how to manage forests (Ganey et al. 2017; Lee 2018).

Uncertainties about how spotted owls respond to severe fire may be resolved, in part, by (i) distinguishing between the mean, population-level response and variation in responses by individual owls that experience a range of post-fire conditions, and (ii) explicitly incorporating the role of the spatial configuration of severe fire (e.g., patch size and shape), which has not been the focus of previous studies (Ganey et al. 2017). Resource selection functions (RSFs) offer an analytical method for characterizing selection or avoidance of resources (hereafter 'habitat'; i.e., cover types) that are available to individuals or populations

(Manly et al. 2002). It is often assumed when using RSFs that individuals will select (or avoid) habitats in the same way (i.e., habitat selection is a constant function of habitat availability; Mysterud and Ims 1998). However, the strength of habitat selection or avoidance can vary strongly in both direction and magnitude among individuals within a population, so accounting for individual variation in selection patterns is important for statistically rigorous testing of population-level selection (Duchesne et al. 2010). Individual-specific habitat selection may vary as a function of habitat availability, a phenomenon known as a “functional response” in habitat selection (Mysterud and Ims 1998; Hebblewhite and Merrill 2008; Matthiopoulos et al. 2011; Aarts et al. 2013). Testing for functional responses may give insights into how individuals respond across a gradient of habitat conditions—including novel landscape conditions and configurations—and allow explicit testing of hypotheses about the effects of increasing novelty caused by either climate change or human impacts on habitat selection.

We used mixed-effects RSFs to examine both individual- and population-level habitat selection (Muff et al. 2020) in GPS-tagged California spotted owls (*S. o. occidentalis*) occupying home ranges containing a wide range of high-severity fire effects following a recent California megafire (2014 King Fire; Jones et al. 2016). We examined the potential effects of fire characteristics (fire severity, pyrodiversity, and severe fire patch size and configuration) on owls while controlling for potential confounding factors (pre-fire forest cover), post-fire salvage logging, and the central-place foraging behavior exhibited by spotted owls (Carey and Peeler 1995; Rosenberg and McKelvey 1999). Because spotted owls have presumably adapted to frequent-fire regimes dominated by lower-severity effects (Ganey et al. 2017; Rockweit et al. 2017), we predicted that individual owls would avoid severely burned forests when these areas comprised a large portion of the home range or occurred in large patches. We also predicted that spotted owls would select burned areas with greater pyrodiversity, which would be expected to create structural and landscape heterogeneity preferred by owls (Gutiérrez et al. 1995; Franklin et al. 2000). In addition, we tested for the potential effects of salvage logging in burned forests on habitat use because previous studies have found that spotted owls

tend to avoid foraging in logged, post-fire landscapes (Comfort et al. 2016). We tested whether spotted owls exhibited functional responses to novel habitat conditions by assessing support for interaction terms within the RSF.

Methods

Study area

The study was conducted in the central Sierra Nevada, California, USA, as part of a longer-term spotted owl demographic study on the Eldorado and Tahoe national forests (Tempel et al. 2016; Jones et al. 2018). The study area was ~ 50,000-ha in size and consisted of mixed-use publicly-owned lands (~ 54%) managed by the U.S. Forest Service and privately-owned lands (~ 46%) managed primarily for timber resources. Elevations ranged from 590 to 2200 m, the climate was Mediterranean with warm, dry summers and cool, wet winters, and the dominant vegetation type was Sierran mixed-conifer montane forest. The elevational range, climate, and species composition of these forests historically resulted in frequent fires (mean return interval = 11 years; range = 5–50 years) of generally lower severity (5–15% area burned at high-severity), with some inclusion of smaller (< 10–100 ha) patches of high-severity fire (Stephens and Collins 2004; Safford and Stevens 2017).

In September and October 2014, the King Fire burned ~ 40,000 ha of primarily forested land in the central Sierra Nevada (Jones et al. 2016). Approximately half (~ 20,000 ha) of the King Fire burned at high-severity (> 75% canopy mortality), including very large contiguous patches, making the King Fire one of the largest and most uniformly severe fires in recent California history (Stevens et al. 2017). Areas along the fire boundary and in the southern portion of the King Fire experienced greater “mixed-severity” fire effects, characterized by a mosaic of low, moderate, and high-severity fire. Post-fire salvage logging occurred in portions of the burned area (Fig. 1) and the majority of salvage-logged areas (89%) occurred on private lands.

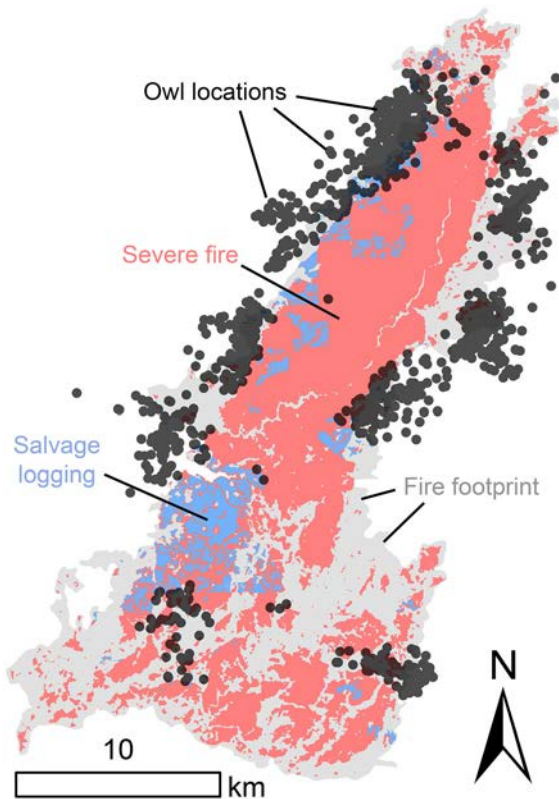


Fig. 1 King fire study area, showing the extent of the fire, severe fire, salvage logging, and locations used by owls

Global positioning system (GPS) data

In 2015–2017, we captured adult spotted owls occupying forests within and near the King Fire perimeter (Fig. 1) and fitted them with 7–10 g backpack-mounted dual GPS/VHF units (hereafter “GPS tags”) (Biotrack Ltd., Wareham, UK). We exhaustively searched the study area to locate owls during daytime and nocturnal walk-in surveys, and once located we captured owls using snare poles, hand-grabs, or bal-chatri traps. All relevant state and federal permits were obtained prior to capture and handling. In 2015, 2016, and 2017, we deployed 12, 10, and 4 GPS tags, respectively (total $n = 26$). There were no owls available for GPS tagging within the large, severely burned patch in the center of the study area (Fig. 1) because owl territories in that patch went extinct immediately after the fire (Jones et al. 2016) and were not re-colonized during the course of the study (G.M. Jones, unpublished data). Three individual spotted owls with GPS tags dispersed before data could be

retrieved (two in 2015, one in 2016), so our final sample size was 23. Of the 23 owls sampled, three individuals were sampled in consecutive years, which we accounted for by specifying a random effect for individual owl. GPS tags were deployed each year in May and early June and recorded 100–150 locations during nocturnal hours (1–3 per night; mean = 1.33/night/owl), and were retrieved in July and August. When multiple locations were recorded in a single night, they were pre-programmed to be separated by at least two hours to reduce spatial autocorrelation. GPS tags had a median location error of approximately ± 20 -m when data were filtered to include only those points recorded with ≥ 5 satellites and a dilution of precision (DOP) ≤ 3 (HA Kramer, unpublished data), so we used only these data in analyses.

Habitat selection analysis

We analyzed our data using mixed-effects RSFs (logistic regression) with intercepts and slopes that varied by individual (Duchesne et al. 2010; Muff et al. 2020). Including coefficients that vary by individual enables explicit modeling of functional responses (Mysterud and Ims 1998) and reduces biases in estimated population-level (fixed) effects (Duchesne et al. 2010; Harrison et al. 2018). Available points were assigned weight $W = 1000$ to facilitate approximate convergence to the inhomogeneous Poisson process likelihood, and we fixed the variance term for individual-specific intercepts to a large value ($\sigma^2 = 1000$) to avoid shrinkage toward zero (Muff et al. 2020). Available area for each individual owl was defined as a circle with radius equal to the furthest Euclidean GPS distance from the activity center (minimum radius = 1654.8 m; maximum = 5165.5 m; mean = 3437.6 m), where the activity center was the geometric mean of annual daytime nest and roost locations obtained from walk-in surveys. We generated 10 times as many available points as used points for each owl (Hooten et al. 2017). Available points were distributed uniformly with respect to distance to the activity center (i.e., all distances had equivalent point densities).

There were three types of inferences we were interested in drawing from mixed-effects RSF models. First, we were interested in understanding how spotted owl habitat selection was explained by a suite of environmental predictor variables including pre-fire

forest conditions, fire conditions including whether or not areas burned at high-severity and the diversity of fire effects (pyrodiversity), and post-fire management (salvage logging). Second, we were interested in whether spotted owl use (or non-use) of areas that burned at high-severity could be explained by spatial characteristics of those areas, such as severe fire patch size and configuration. Finally, we wanted to examine whether there was evidence for functional responses in habitat selection. With respect to severe fire effects, these inferences can be viewed as a set of three sequential or hierarchical questions: do owls select or avoid severely burned areas; is that selection (or avoidance) mediated by spatial characteristics of severely burned areas; are these patterns driven by variation in the availability of severe fire within individual home ranges? We therefore examined these questions in three stages, constructing models in each stage that allowed us to test the underlying hypothesis related to each question in sequence.

In the first stage, we fitted a single model containing covariate effects for distance to activity center, pre-fire forest cover (sparse/open forest and young forest), and disturbance-related covariates (severe fire,

pyrodiversity, and post-fire salvage logging) (Table 1). Each covariate effect was specified as having a fixed component (population-level coefficient that was constant across individuals) and a random component (coefficient varying by individual) following Muff et al. (2020). The model intercept varied by individual owl. We expected distance to activity center and pre-fire forest cover covariates to be important in explaining space use patterns in spotted owls, but they were not the central focus of this analysis; we included them to control for their potential effects. Distance to activity center was the Euclidean distance (m) between a given GPS location and the individual's geographic activity center. Including distance to activity center as a model covariate in RSFs of central place foragers reduces the potential for a positive bias of selection for habitat types near the central place as well as a negative bias for habitat types more distant from the central place (Rosenberg and McKelvey 1999). Preliminary analyses supported the use of a quadratic (distance + distance²) form, which we used in all subsequent models. Pre-fire sparse/open forest cover was defined as 30 × 30-m pixels with < 40% canopy cover in the year prior to the King Fire (2014)

Table 1 Model covariates for habitat selection function (RSF) analysis including the variable description, group, type and range of values

Variable	Description	Group	Type	Range of used values
Distance to activity center	The Euclidean distance between a point and the annual activity center	–	Continuous	0–5165 m
Pre-fire sparse/open forest	Areas with < 40% canopy cover prior to the King Fire	Pre-fire	Categorical	0 or 1
Pre-fire young forest	Areas with > 40% canopy cover but smaller (< 25 cm QMD) average tree size	Pre-fire	Categorical	0 or 1
Severe fire	Areas that experienced > 75% canopy mortality following the King Fire and were <i>not</i> salvage-logged	Disturbance	Categorical	0 or 1
Pyrodiversity	Shannon Diversity Index of burn severity classes	Disturbance	Continuous	0–1.38 unitless
Salvage logging	Areas that experienced post-fire management that removed standing and downed trees	Disturbance	Categorical	0 or 1
Patch size	The area of a contiguous grouping of severely burned forest	Patch-based	Continuous	0–88.2 km ²
Patch complexity	The perimeter-to-area ratio of a severe fire patch	Patch-based	Continuous	0–0.066 m/m ²
Permeation distance	The distance traveled into a severely burned patch	Patch-based	Continuous	0–356.3 m

All continuous variables were scaled to a range of 0–1 for model fitting

as determined using the VEGCLASS variable classes 1 and 2 in the Gradient Nearest Neighbor (GNN) forest structure dataset for our study area (LEMMA Lab, Oregon State University, Corvallis, OR; lemma-forestry.oregonstate.edu) (Ohmann and Gregory 2002). Pre-fire young forest was also calculated using the VEGCLASS category of the GNN dataset (classes 3, 5, and 8), defined as 30×30 -m pixels with $> 40\%$ canopy cover but with smaller trees (quadratic mean diameter < 25 cm). Including pre-fire sparse/open/young forest vegetation covariates controlled for potential bias toward avoidance of these forest types, independent of the post-fire vegetation patterns created by the King Fire. We assigned the pre-fire sparse/open or young forest class to used/available points when these cover types were the majority class within a 100-m buffer around a given point location.

Disturbance covariates were severe fire, pyrodiversity, and post-fire salvage logging (Table 1). We defined severe fire as areas that experienced $> 75\%$ overstory mortality resulting from the King Fire. We used the 75% overstory mortality threshold to define high-severity because it increases our capacity to compare our results to previous studies (Bond et al. 2009, 2016; Eyes et al. 2017), while acknowledging that more notable ecological effects may correspond with a higher (e.g. 90%) threshold (Miller and Quayle 2015; Jones 2019). We treated this covariate as a categorical effect, such that $x_{ij} = 1$ if the GPS location for individual $i = 1, \dots, I$ at location $j = 1, \dots, J_i$ occurred in severely burned forest and $x_{ij} = 0$ otherwise. If a point fell within a severely burned area that was also salvage-logged (see below), we set the categorical effect for severe fire to $x_{ij} = 0$ and the effect for salvage logging to $x_{ij} = 1$. Thus, within our model the ‘severe fire’ effect can be interpreted as the selection coefficient for ‘unlogged snag forest’. We obtained burn severity data from the Monitoring Trends in Burn Severity (MTBS) project (www.mtbs.gov). We did not investigate potential selection patterns related to forests that burned at low- and moderate-severity because (i) we wanted to limit the number of candidate variables to reflect key hypotheses of interest and (ii) previous work has shown that either they do not affect spotted owls or owls generally use these types of burned forest in proportion to their availability during nocturnal hours (Bond et al. 2009, 2016; Jones et al. 2016; Eyes et al.

2017). Thus, low and moderate burn severities, as well as unburned forests, were effectively grouped together in the reference class of our models. However, we did more explicitly consider low and moderate fire severity in the context of pyrodiversity, which was defined as the Shannon Diversity Index of unburned or unchanged (under 5% site area burned), low severity (up to 25% overstory mortality), moderate severity (25–75% overstory mortality), and high-severity (over 75% overstory mortality) classes within a 100-m buffer of point locations. Based on Google Earth aerial imagery, we determined that the majority of salvage operations that occurred within owl home ranges were completed in late 2014 and early 2015 prior to the initiation of this study (2015), so we hand-digitized areas that had been post-fire salvage logged from the National Agriculture Imagery Program (NAIP) aerial imagery from July 2016. We delineated polygons containing visible heavy disturbance (including areas where logging roads had been created, presumably in preparation for salvage logging) in areas that burned in the King Fire, and that had forest present before the fire. While our delineation of salvage logging was limited to areas visibly discernable on NAIP imagery, territory-scale estimates of salvage were highly correlated ($r = 0.88$) with estimates obtained from timber companies conducting salvage operations within our study area (HA Kramer, unpublished data). We erased pre-fire sparse/open forest (GNN) and areas classified as unburned or outside the fire perimeter so that the salvage layer only included areas that were forested pre-fire and disturbed by dense road networks or logging post-fire. Approximately 80% of salvage logging occurred in areas that experienced high-severity fire.

In the second stage, we explored whether severe fire patch characteristics affected spotted owl habitat selection: patch size, patch complexity, and permeation distance (distance an owl traveled into a severely burned patch) (Table 1). We did so adding covariate effects for each of the above variables to the stage one model, and likewise allowed coefficients to vary by individual owl. Stage two variables were moderately- to highly-collinear with each other and therefore were not included in the same model; thus stage two consisted of three separate RSF models. Patch size was the total area (m^2) of a severe fire patch delineated with the four-neighbor rule (Turner et al. 2001). Patch complexity was calculated as the perimeter-to-area ratio of a severe fire patch. Permeation distance was

the minimum Euclidean distance (m) from a used or available point occurring within a severe fire patch to the patch edge (all points outside of severe fire patches were assigned $x = 0$). We transformed stage two variables using the natural logarithm (ln).

In the third stage, we tested for evidence of functional responses by including an interaction term between habitat availability at the level of the individual owl (the mean covariate value in an individual's home range for available points) and the corresponding habitat covariate (*sensu* Matthiopoulos et al. 2011; Aarts et al. 2013). For example, to test for a functional response related to high-severity fire, we included: (i) a covariate for whether a used/available point occurred in severely burned forest (0/1; Table 1), (ii) a covariate that represented the proportion of an owl's home range that burned severely (i.e., this covariate had a constant value for each individual), and (iii) an interaction between these two covariates. If the interaction term (slope) was statistically different from zero, we interpreted this as evidence in support of a functional response in habitat selection. We transformed habitat availability using the natural logarithm because functional responses are assumed to be non-linear (Mysterud and Ims 1998; Hebblewhite and Merrill 2008; Beyer et al. 2010). We conducted tests for functional responses among disturbance and patch-level covariates when individual coefficients (i.e. random slope variance) improved model fit according to likelihood ratio tests (see below) from stages one and two to minimize the potential for spurious inferences. We note that while using the mean habitat value within an individual's home range is commonplace in the literature when computing functional response (Gillies et al. 2006; Hebblewhite and Merrill 2008; Aarts et al. 2013), the underlying assumption is that the average value sufficiently describes availability. Such an assumption could mask differences among individuals if the average availability does not reflect the encounter rate of different habitats across the landscape (Beyer et al. 2010).

We made inferences about the statistical importance of fixed effects from their direction (positive/negative), effect size (magnitude), and uncertainty (95% confidence intervals), but avoided interpreting the "significance" of estimates using arbitrary p-value thresholds when possible (Amrhein et al. 2019). We determined whether the variance terms for the random slopes improved model fit (test of $H_0: \sigma^2 = 0$) by

performing likelihood ratio tests (LRT) using restricted maximum likelihood (REML) estimation, correcting for the 'testing on the boundary' problem using $p = 0.5 \times (\chi_1^2 + \chi_2^2)$ (Zuur et al. 2009). All mixed-effects models were fitted using REML (Zuur et al. 2009). We rescaled all continuous covariates to range from 0 to 1. We used the R packages glmmTMB v. 0.2.3 to fit models. All analyses were conducted in program R version 3.6.0.

Results

Variables describing the central place foraging behavior of owls, pre-fire forest cover, and disturbance effects were all associated with spotted owl habitat selection. Population-level (fixed) effects from the stage one model indicated overall selection for areas closer to the activity center ($\beta_{\text{distance}} = 1.6$, 95% confidence interval $[-0.19, 3.43]$; $\beta_{\text{distance}}^2 = -8.25 [-11.44, -5.06]$). The model also indicated avoidance of pre-fire sparse/open forest ($\beta_{\text{sparse/open}} = -1.00 [-1.41, -0.59]$), young forest ($\beta_{\text{young}} = -0.32 [-0.63, -0.001]$), and salvage-logged areas ($\beta_{\text{salvage}} = -1.07 [-1.88, -0.26]$) (Fig. 2a). The estimated coefficient for pyrodiversity was in the hypothesized direction (positive) but slightly overlapped zero ($\beta_{\text{pyrodiversity}} = 0.49 [-0.12, 1.09]$) (Fig. 2a). Similarly, the coefficient for the effect of severe fire (binary effect disregarding patch characteristics) was in the hypothesized direction (negative) but with confidence intervals that overlapped zero ($\beta_{\text{severe}} = -0.35 [-1.07, 0.37]$) (Fig. 2a). While estimated coefficients for pyrodiversity and severe fire overlapped zero when considered at the population-level (i.e., effect fixed across individuals), individual-specific coefficients showed a high degree of variability (Fig. 2b) that improved model fit (likelihood ratio tests; $p < 0.001$). Thus, while the mean effect of pyrodiversity at the population level was 0.49, the deviation from that effect varied significantly across individuals with an estimated variance of $\sigma^2 = 1.92$ (individual coefficients ranged from -1.2 to 2.9) (Fig. 2b). Likewise, while the mean effect of severe fire at the population-level was -0.35 , individual-specific deviations from that effect were considerable ($\sigma^2 = 2.49$; individual coefficients ranged from -3.4 to 2.8) (Fig. 2b).

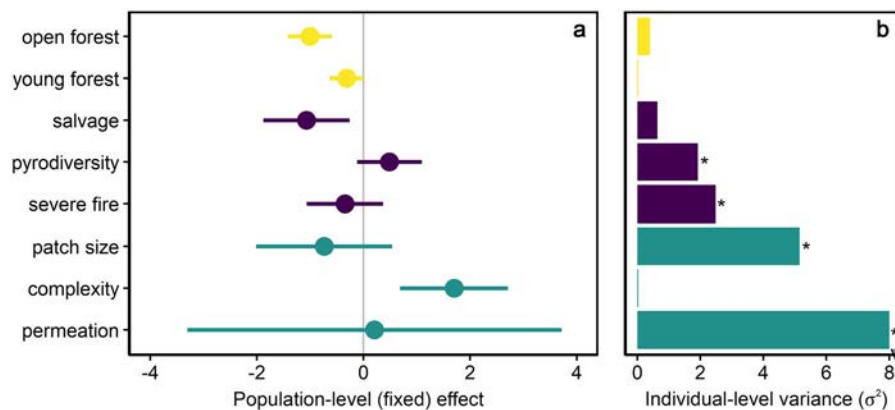


Fig. 2 Coefficient estimates from mixed-effects habitat selection functions. **a** Mean fixed-effects coefficients and their associated 95% confidence intervals. **b** The variance estimates for the individual slope coefficients (random effects), with effects that improved model fit (using likelihood ratio tests) indicated with an asterisk (*). the x-axis of b is truncated to a

Selection/avoidance of severely-burned areas by spotted owls appeared to be mediated by spatial characteristics of severe fire patches (stage two). Population-level (fixed) effects for patch size was negative ($\beta_{\text{patchSize}} = -0.74 [-2.01, 0.54]$) indicating spotted owls selected smaller patches of severely-burned forest, but the 95% confidence interval overlapped zero (Fig. 2a). Spotted owls selected severe fire patches with greater spatial complexity (higher perimeter-area ratio; $\beta_{\text{complexity}} = 1.70 [0.69, 2.71]$) (Fig. 2a). The population-level effect of permeation distance was slightly positive ($\beta_{\text{permeation}} = 0.21 [-3.30, 3.72]$) but confidence intervals widely overlapped zero (Fig. 2a). While their population-level coefficient estimates overlapped zero, both patch size and permeation distance showed significant variation among individuals; individual-specific coefficients improved model fit (likelihood ratio tests; $p < 0.001$). While the mean effect of severe fire patch size at the population level was -0.74 , the deviation from that effect varied significantly across individuals with an estimated variance of $\sigma^2 = 5.15$ (individual coefficients ranged from -4.22 to 5.4) (Fig. 2b). Likewise, while the mean effect of permeation distance (distance traveled into severe fire patch) at the population-level was 0.21 , individual-specific deviations from that effect were considerable ($\sigma^2 = 8.0$; individual coefficients ranged from -5.3 to 28) (Fig. 2b).

smaller range (0–8) for visualization, but note that the variance term for permeation distance was 58.9 . Colors correspond with different covariate groups (see Table 1); yellow = pre-fire forest cover, dark blue = disturbance variables, turquoise = severe fire patch variables. (Color figure online)

The large variation in habitat selection coefficients among individual owls for severe fire (stage one), severe fire patch size (stage two), and permeation distance (stage two) was partially explained by differences in individual-level habitat availability, indicating an apparent functional response (FR). Habitat $\times$ availability interaction coefficients and 95% confidence intervals for these three variables did not overlap zero in stage three models testing for functional responses. Moreover, functional response curves identified thresholds in habitat availability at which point predicted individual coefficients changed sign from positive to negative (the point at which the fitted curve crosses zero; Fig. 3a–c). Individual spotted owls tended to select severely burned forest only when it represented a small proportion of their home range (< 0.05), but avoided severely burned forest when it was more prevalent ($\beta_{\text{severe-FR}} = -0.76 [-1.33, -0.19]$) (Fig. 3a). Individual owls tended to select larger patches of severe fire when the area-weighted average patch size in their home range was smaller than ~ 115 ha, but selected smaller patches of severe fire when their home ranges were characterized by larger patches ($\beta_{\text{patch-FR}} = -9.39 [-13.78, -5.00]$) (Fig. 3b). Owls also avoided making deep forays into severe fire patches when the average permeation distance in their home range exceeded 47 m, corresponding with larger patches on average ($\beta_{\text{permeation-FR}} = -28.17 [-43.67, -12.68]$) (Fig. 3c). Figure 4 provides examples of spotted owls

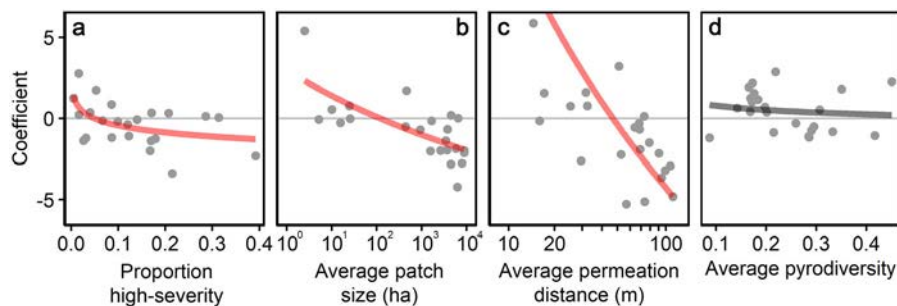


Fig. 3 Functional responses in habitat selection. **a** Severe fire, **b** patch size, **c** permeation distance, **d** pyrodiversity. The y-axes represent slope coefficient estimates for individual owls, and the x-axis represents average covariate conditions within an individual owl's home range (**b**, **c** represent area-weighted

means for patch-based covariates). Functional responses with 95% confidence intervals that did not overlap zero are depicted in red (**a–c**). Note that the y-axis is truncated in panel **c** for better visualization; there is one additional data point located at $x = 11.1$, $y = 27.98$. (Color figure online)

selecting smaller patches of severe fire (Fig. 4a, b), avoiding larger patches of severe fire (Fig. 4b, c), and using a large severe fire patch (unlogged snag forest) but only making short forays into it (Fig. 4c). There was no evidence for a functional response in habitat selection for pyrodiversity ($\beta_{\text{permeation-FR}} = -0.48$ [$-2.15, 1.20$]) (Fig. 3d).

Discussion

There is a natural hierarchical response by species that can be estimated following disturbance: a primary response and a secondary response. The *primary response* is whether an individual either survives or is able to remain (i.e., occupy) in the affected area following a disturbance event. The *secondary response* is conditional on the primary response (i.e., continued occupancy) and may represent shifts in movement, foraging, or reproductive behavior by persisting individuals that are induced by the disturbance. Key uncertainties exist regarding both primary and secondary responses by spotted owls to fire. With respect to primary responses, the 2014 King Fire displaced a significant portion of the population that experienced extensive severe fire and at least one apparent direct mortality (Jones et al. 2016), but other researchers reported no negative effects in a different population of owls that experienced a large, severe fire (Lee and Bond 2015, but see Berigan et al. 2019). With respect to secondary responses, different studies have revealed that GPS- or VHF-tagged owls avoided (Jones et al. 2016; Eyes et al. 2017), preferentially selected (Bond et al. 2009), or used severely burned

forests in proportion to their availability (Bond et al. 2016) when foraging. The analytical approaches used in these studies were similar, raising the question of why owls apparently responded in different ways. We posit one of the reasons may be that these studies have lacked an explicit landscape perspective (i.e., role of spatial patterns of severe fire), which precluded the ability to disentangle different factors that might have led to these conflicting results. While previous work has advanced our understanding of the importance of edges between fire severity classes as a predictor of spotted owl habitat selection (Bond et al. 2009, 2016; Eyes et al. 2017) and the role of these edges across scales (Comfort et al. 2016), they did not explicitly consider the role of severe fire patch size, configuration, permeation distance, or how responses may be conditional on individual variation in habitat availability (i.e., functional response).

Owl response to high-severity fire

Landscape structure and composition following fires appear to affect habitat selection by spotted owls in a more nuanced way than previously reported. Although severe fire was not clearly avoided nor selected at the population level, individuals showed avoidance of severely burned forests (i.e., expected individual coefficients became negative) when $> 5\%$ of their home range burned at high-severity (Fig. 3a). Thus, for those owls not displaced or killed, severe fire appeared to be, on average, benign or beneficial below this threshold, yet appeared to affect owl movements above this threshold. Therefore, spotted owls continued to occupy home ranges in the short term when

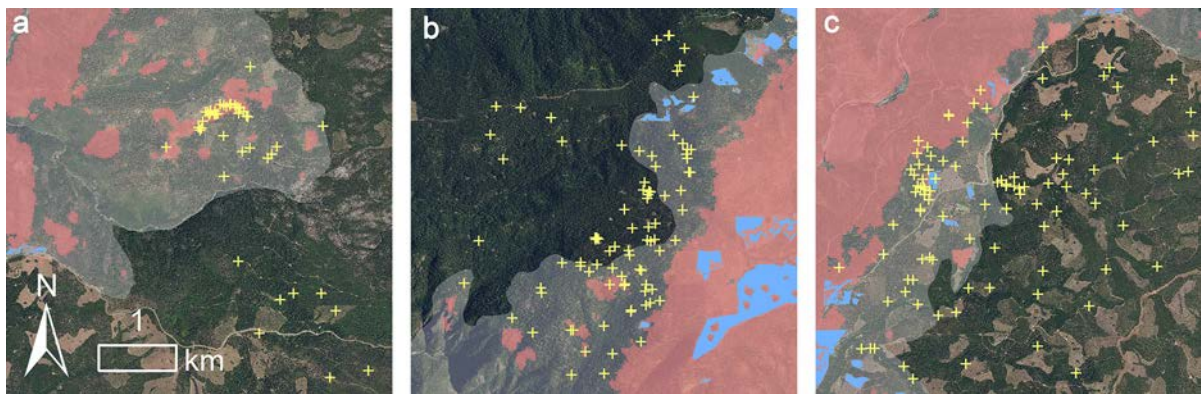


Fig. 4 Examples of owl locations that show selection preferences across different availabilities of severe fire and patch sizes. **a** Selection for a small patch of severe fire; **b**, **c** avoidance of a large patch of severe fire; **c** also shows short (< 100 m)

forays into a large severe fire patch. The fire area is shown in semitransparent white, high-severity fire with no salvage logging in red, salvage logging in blue, and owl locations as yellow “+” signs. (Color figure online)

their home ranges were burned by up to 40% severe fire (the maximum extent experienced by GPS-tagged owls in this study), perhaps via behavioral plasticity including the shifting of foraging sites. However, previous work has shown that habitat loss related to severe fire occurring over > 50% of an owl territory led to territory abandonment and mortality (Jones et al. 2016). These thresholds could serve as benchmarks for understanding severe fire effects on spotted owls when detailed site occupancy and tagging information are not available, but we hypothesize that wildfires with different severe fire spatial patterns may result in different responses by owls than we report here. We observed similar functional responses for severe fire patch size and permeation distance; owls avoided using larger patches of severe fire and avoided making deeper forays into severely burned areas when their home ranges were characterized by a larger severe fire component. Had we used a more traditional analysis that did not account for individual variation and spatial configuration, and simply made inference about population-level effects, we would likely have concluded that owls use severely burned forests in proportion to its availability (i.e., the model from stage one). Instead, we gained a more nuanced understanding that patch size and the spatial extent and configuration of severely burned forests within individual spotted owl home ranges strongly mediated the effect of severe fire.

The specific thresholds at which we observed that spotted owls began to avoid severely burned forest appear to align closely with the best available

estimates of historical severe fire extent and patch sizes within dry mixed-conifer forests (Safford and Stevens 2017). Specifically, fires that historically burned in yellow pine mixed-conifer forests in the Sierra Nevada contained 5–15% severe fire effects (Safford and Stevens 2017); our study suggested owls tended to avoid severely burned forest when more than 5% of their home range was affected. Moreover, historical severe fire patch sizes in yellow pine mixed-conifer forests in the Sierra Nevada typically ranged from 10 to 100 ha in size (Safford and Stevens 2017); we showed that spotted owls tended to avoid larger severe fire patches when the average patch size in their home range exceeded ~ 115 ha in size. In addition, the spatial complexity of severe fire patches has been decreasing in recent decades (Stevens et al. 2017); we showed that owls select more complex severe fire patches. We suggest these results provide evidence that owls are responding to severe fire in a way that reflects adaptation to historical fire regimes under which this species evolved. Our work suggests that increasingly novel fire conditions within this system—i.e., more severe fire characterized by patches that are larger and less complex—will negatively affect spotted owls.

There are several possible reasons why spotted owls avoided large patches of unlogged, severely burned forest. First, severe fire in the King Fire likely altered spotted owls’ prey communities either (i) indirectly by eliminating the understory and coarse woody debris important for key small mammal prey species such as woodrats (*Neotoma* spp.; Roberts 2017) in the

short term, or (ii) directly through fire-related mortality. Although some dense brush cover regenerated within many severely burned patches 1–2 years post-fire that could potentially provide prey habitat, owls appeared to avoid large, severely burned patches throughout the three-year study, suggesting prey populations had not yet recovered. Second, perching structures in large tracts of severely burned forest may not provide adequate concealment for this “sit and wait” predator relative to forests with live trees and foliage structure (Gutiérrez et al. 1995; Ganey et al. 2017). Third, and related to the second reason, large fires create extensive open areas that provide habitat for avian predators of spotted owls such as great-horned owls (*Bubo virginianus*; Gutiérrez et al. 1995), which increases predation risk (Johnson 1992). Discriminating among these hypotheses will be challenging and require both small mammal and predator sampling. There is a fourth explanation for why spotted owls avoided large tracts of severely burned forest: severely burned forest contains a limiting resource (e.g., food) that is preferentially selected when it is scarce, but is relatively less important (and its use/availability ratio decreases) when it is abundant (Beyer et al. 2010; Aarts et al. 2013). Given our three above hypothesized mechanisms for avoidance of large severely burned areas we think this is relatively unlikely because rather than containing abundant resources, large severe fire patches appear to contain fewer food resources and more risks to owls.

Owl response to salvage logging

Salvage logging is a management practice that removes fire-killed or fire-affected trees with the primary intention of recouping economic value and reducing safety hazards in multi-use forests (Lindenmayer and Noss 2006). Salvage logging can affect post-fire forest conditions and ecosystem processes by altering post-fire biological communities (Thorn et al. 2018), increasing fire risk by leaving behind fine and coarse woody fuels (Donato et al. 2006), and reducing natural vegetative recovery (Lindenmayer et al. 2008). However, salvage logging is also being used as a tool for improving post-fire reforestation success in dry forest types of the western US (North et al. 2019) that face an increased risk of natural regeneration failure and conversion to non-forest ecosystems following large, high-severity fires (Welch et al. 2016; Shive

et al. 2018; Wood and Jones 2019). Thus, there is strong practical interest among land managers to understand ways to reduce negative effects of salvage logging on species and communities of conservation concern, particularly the spotted owl (Peery et al. 2017).

Our results suggest that spotted owls tended to avoid areas that experienced salvage logging. However, interpreting the significant negative statistical effect of salvage was challenged by several considerations. First, 95% confidence intervals for the population-level severe fire effect (i.e., unlogged snag forest) overlapped the 95% confidence intervals for the salvage effect (Fig. 2)—suggesting that salvage and severe fire effects at the population level may have been similar. Second, salvage logging was often embedded within the very large patch of severely burned forest in the northern part of the King Fire that owls strongly avoided (e.g., Figs. 1, 4b, c) such that owls may have been predisposed to avoiding some salvage-logged areas. Third, salvage-logged areas were relatively rare within owl home ranges (average 3.4% of owl home range) compared to severely burned areas (14.5%), and rare cover types are subject to false negative error (Frair et al. 2010).

Nevertheless, our study may provide some important insights into the relative effects of salvage logging and severe fire on spotted owl habitat selection. While the population-level (fixed) effect of salvage logging was negative and numerically more negative than population-level effect of severe fire, the variance among individual-level effects for salvage logging was narrow ($\sigma^2 = 0.64$) and not statistically different from zero, compared to the significant variance among individual-level effects for severe fire ($\sigma^2 = 2.49$). These variances resulted in a narrow range of individual coefficients (ranging from -1.6 to -0.2) for salvage logging, compared to a wider range for severe fire individual coefficients (ranging from -3.4 to 2.8) (Fig. 5). Thus, it appears that individual owls with relatively large high-severity burned areas within their home range tended to avoid these areas more strongly than any owls avoided salvage-logged areas (Fig. 3a). Conversely, owls with smaller areas of high-severity burned areas in their home ranges tended to select severely burned areas but still tended to avoid salvaged areas, notwithstanding the considerations discussed above.

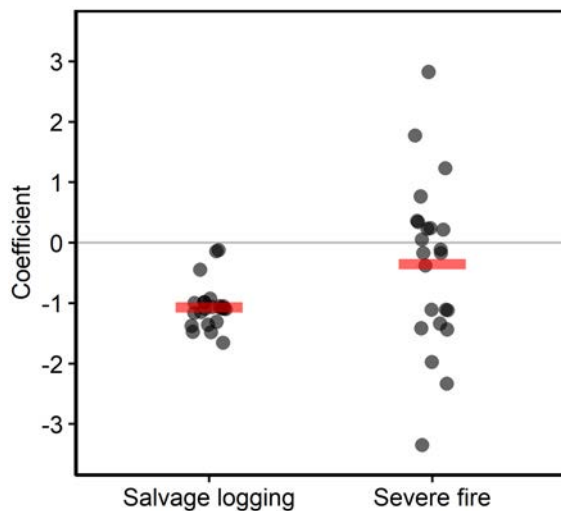


Fig. 5 Comparison of the population-level (red line) and individual-level (black dots) coefficients for salvage logging and severe fire (unlogged snag forest). (Color figure online)

Despite these uncertainties, our findings also have novel implications for post-fire forest management as it relates to species conservation. Specifically, the owls' tendency to avoid large, but not necessarily small patches of severely burned forest and also avoid traversing into interior portions of larger patches (Figs. 3, 4) suggests that salvage logging within interior portions of larger patches may be less likely to affect spotted owls than salvage logging within small patches of severely burned forest. For example, of all spotted owl GPS locations, only 0.6% occurred further than 100 m into a severe fire patch. Stillman et al. (2019) showed that black-backed woodpeckers (*Picoides arcticus*), another focal management species in post-fire landscapes in the Sierra Nevada, tended to use areas of severely burned forest that were closer to patch edges and rarely traveled further than > 500-m into severe fire patches. Thus, salvage operations within the interior of large patches of severely burned patches may be less likely to impact both of these focal species. However, most (89%) of salvage logging within the King Fire perimeter occurred on private lands that often involved higher proportions of harvesting than is typical on national forests (i.e., patches of unlogged snag forest were often left intact within salvage-logged areas on national forests). This limited the inferences we could make about the effects of salvage logging on public lands. Nevertheless, retaining perch sites and snags, and/or creating

habitats that promote the preferred prey species of spotted owls in areas that are salvage-logged (e.g., slash piles for woodrats; Innes et al. 2007), might encourage use of these areas by owls in the future.

Implications for dry forest restoration

The tendency of spotted owls to avoid large areas within their home ranges that burned at high-severity has implications for the management of seasonal dry forests within the range of this species. Our findings of avoidance by spotted owls of forests extensively modified by severe fire suggests that the reduction of large, severe fires ("megafires"; Stephens et al. 2014) such as the King Fire by restoring frequent fire regimes characterized by small patches of severe fire is likely to benefit both spotted owl populations and increase forest resilience. This comes with the caveat also supported by our results that salvage logging be judiciously applied particularly in areas where fires burn heterogeneously within occupied spotted owl home ranges, because owls tend to use smaller patches of severely burned forests and forage along edges of larger patches. Our study (i) supports the general premise that species conservation and forest ecosystem restoration objectives in the Sierra Nevada can be compatible (Scheller et al. 2011; Tempel et al. 2015; Jones et al. 2016; Jones 2019) and (ii) could help reconcile a conservation conflict pitting those promoting restoration of seasonal dry forests in parts of western North America against those interested in preserving old-growth trees and habitat for spotted owls (Redpath et al. 2013; Gutiérrez et al. 2017).

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Megafire causes persistent loss of an old-forest species

G. M. Jones¹ , H. A. Kramer², W. J. Berigan², S. A. Whitmore², R. J. Gutiérrez² & M. Z. Peery²

¹ USDA Forest Service Rocky Mountain Research Station, Albuquerque, NM, USA

² Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA

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Correspondence

Gavin M. Jones, USDA Forest Service Rocky Mountain Research Station, Albuquerque, NM, USA.

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Abstract

Climate change and a long legacy of fire suppression are leading to an increased prevalence of ‘mega-disturbances’ such as drought and wildfire in terrestrial ecosystems. Evidence for the immediate effects of these novel disturbances on wildlife is accumulating, but little information exists on longer term impacts to species and ecosystems. We studied the occurrence dynamics of an iconic old-forest species, the spotted owl (*Strix occidentalis*), on a long-term study area in the Sierra Nevada, CA, USA from 1989 to 2020 to evaluate their multi-scale population response following a 2014 megafire (the ‘King’ Fire) that affected a portion of our study area. We found that extensive severe fire within spotted owl sites resulted in both immediate site abandonment and prolonged lack of re-colonization by owls six years post-fire. Sites that experienced high pyrodiversity – a mosaic of burn severities – were more likely to persist after the fire, but this effect was only apparent at finer spatial scales. A potentially confounding factor, post-fire salvage logging, did not explain variability in the probability of either owls persisting at sites or sites becoming re-colonized; effects could be attributed only to severe fire extent and pyrodiversity. Our study demonstrates the prolonged effects of severe fire on the occupancy of this forest-dependent species, suggesting that forest restoration that reduces megafires could benefit spotted owls. Our work emphasizes that long-term monitoring can offer surprising learning opportunities and provide unparalleled value for understanding and addressing emerging environmental concerns.

Introduction

Disturbance regimes are changing across global forest ecosystems because of past land use (e.g., fire suppression) and climate change (Seidl et al., 2017). A new era of mega-disturbances catalyzed by a changing climate may lead to large-scale transformation of ecosystems as we know them (Millar & Stephenson, 2015; Westerling et al., 2011). Large-scale droughts and ‘megafires’ not only threaten the persistence of forest ecosystems, they also threaten the species that inhabit them and the services those ecosystems provide to people (Hurteau et al., 2014; Wood & Jones, 2019). Consequently, in some forest ecosystems, forest managers and policymakers are faced with either the challenges of managing these vital forests for restoration and persistence or allowing their transition to novel non-forest ecosystems (Rissman et al., 2018) with resulting implications for biodiversity and ecosystem services.

Recent extreme global fire years (e.g., 2019–2020) have hastened efforts to quantify potential impacts of megafires on biodiversity. For example, the 2019–2020 Australia bushfires likely resulted in significant (>30%) habitat loss to 70 taxa

including 21 already threatened with extinction (Ward et al., 2020). An analysis of the 2019 Amazon fires suggested that most species experienced habitat losses across 20–30% of their range (Mortara et al., 2020). Rapidly changing fire regimes, especially when considered alongside synergies from other pressures (e.g., land-use change, invasive species) threaten the habitat and persistence of at least 4400 taxa globally (Kelly et al., 2020). Forest-dependent taxa, in particular, can experience rapid habitat loss following severe, stand-replacing fires (e.g., bats: Ancillotto et al., 2020; Bosso et al., 2018), but less is understood about longer term dynamics. The emergence of the era of megafires has led scientists and managers to consider what can be done to avoid repeat events of large-scale loss of habitat (Wintle, Legge, & Woinarski, 2020).

Can proactive land management prevent or mitigate large-scale fire events that threaten biodiversity? The answer likely varies across ecosystem types (Halofsky et al., 2018; Krawchuk & Moritz, 2011). In seasonally dry forest ecosystems, notably those in western North America, wildfires are now burning larger, longer and at higher severity than they did historically (Singleton et al., 2018; Steel, Safford, & Viers,

2015; Westerling, 2016). In these forests, large-scale restoration approaches such as prescribed fire, managed wildfire and tree thinning have been proposed to enhance ecosystem resilience to wildfire and drought (Stephens *et al.*, 2020). Abundant empirical observations now demonstrate that these restoration activities alter fire behavior in dry forests by reducing tree densities and fuel loads (Tubbesing *et al.*, 2019), reduce drought-related tree mortality (Bradford & Bell, 2016) and promote structural variability that is expected to increase forest resilience to disturbance (Koontz *et al.*, 2020).

Yet large-scale restoration may also result in short-term negative effects to sensitive wildlife populations by removing or altering key habitat elements (e.g., complex understory and horizontal canopy cover). Recent research has sought to understand trade-offs between these potential short-term negative effects of restoration and longer term benefits of mitigating habitat loss from large, stand-replacing fires (e.g., Scheller *et al.*, 2011; Tempel *et al.*, 2015). Whether short-term negative effects of forest restoration are outweighed by longer term benefits of reducing habitat loss to mega-disturbances hinges on the degree to which restoration alters habitat as well as the magnitude of megafire effects on wildlife. So, for example, if large, severe fires are clearly detrimental to sensitive wildlife populations, then the potential short-term impacts of forest restoration to these species' habitats are likely to be outweighed by longer term benefits – assuming some retention of key elements of the species' habitat can be maintained to support landscape scale occupancy while benefits accrue (e.g., Jones *et al.* 2018). The potential benefits of restoration further increase if habitat loss from large, severe fires is persistent (i.e., will not regenerate for long time periods).

We studied the empirical short- and longer term effects of a large megafire on a declining population of spotted owls (*Strix occidentalis*) that has been monitored annually since the late 1980s. The King Fire, which burned 97 717 acres of predominately forested land in the central Sierra Nevada, CA, USA in September and October 2014, impacted approximately one half of our study area while leaving the remaining portion unburned (Fig. 1). This event, therefore, allowed the use of a natural Before–After Control–Impact experimental design to examine the effects of this fire on our study population. Whereas we have previously reported the immediate impact of the fire on owls (Jones *et al.*, 2016), here we sought to characterize the population response to the King Fire over a 6-year post-fire period. As a result, this study answers a criticism of such short-term studies that owls and other old-forest species may simply return after a brief displacement by a fire event. In addition, we (i) conducted our population analysis at multiple spatial scales to assess whether and to what extent fire effects are scale-dependent (McGarigal *et al.*, 2016; Wan, Cushman, & Ganey, 2020), (ii) included survey data from additional spotted owl territories in our study area to strengthen inferences about fire effects, (iii) applied a novel data filtering approach of detection/non-detection data to improve biological meaning of effects (Berigan *et al.*, 2019) and (iv) explored the potential role of pyrodiversity (variation in burn severity) in

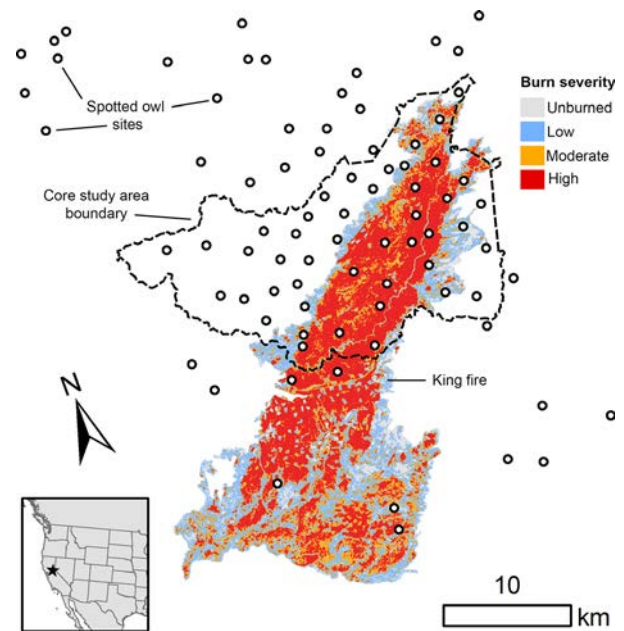


Figure 1 Study area map showing the distribution of spotted owl sites in relation to the 2014 King Fire. The Before–After Control–Impact natural experiment was made possible because a portion of sites was unburned (those outside the King Fire) while other sites experienced a gradient of burn severity. The core study area is outlined with a dashed line; sites outside this boundary were “satellite” territories that were added after initiation of the study (see Methods) [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

mediating population response to fire (Jones and Tingley, in press).

We hypothesized that because spotted owls evolved in a frequent, low-severity fire regime, they are poorly adapted to persist in novel conditions after a large, severe fire (Jones *et al.*, 2020). We developed two predictions that would indicate support for this hypothesis. We predicted that (i) post-fire persistence and colonization rates would decrease in areas with extensive severe fire via loss of larger trees that provide suitable nest sites (e.g., Jones *et al.*, 2016) and (ii) post-fire persistence and colonization would increase in areas with higher pyrodiversity, which may more closely reflect historical post-fire conditions, as well as maintain nest structures and produce diverse prey habitat and hunting cover (e.g., Hobart *et al.*, 2021). We also hypothesized that post-fire owl dynamics were driven by the fire itself, rather than post-fire management. Therefore, we predicted that variation in post-fire persistence and colonization would be associated with high-severity fire and pyrodiversity, rather than post-fire salvage logging.

Materials and methods

Study area and data collection

Our study area encompassed ~800 km² of the Eldorado and Tahoe National Forests in the central Sierra Nevada,

California, USA. The study area consisted primarily (~63%) of public land managed by the USDA Forest Service, but contained inholdings of private land (~37%). Elevation on the study area ranged between 300 and 2500 m. Summers were hot and dry, and most precipitation fell as rain or snow during the winter and early spring (Franklin *et al.*, 2004). The primary vegetation type was mixed-conifer forest dominated by ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*) and Douglas-fir (*Pseudotsuga menziesii*). Common understory species were California black oak (*Quercus kelloggii*), tanoak (*Notholithocarpus densiflorus*), canyon live oak (*Q. chrysolepis*) and bigleaf maple (*Acer macrophyllum*). At higher elevations, vegetation transitioned to red fir (*A. magnifica*) and lodgepole pine (*P. contorta*). Barred owls (*S. varia*) were not present on our study area until the last decade but have remained extremely rare once they invaded this area (Keane, 2017). Thus, we remain confident that our inferences about the effects of severe fire on spotted owls were not influenced by the presence of barred owls.

In the midst of a significant multi-year drought (Asner *et al.*, 2015), the King Fire burned across ~39 545 ha (97 717 acres) of predominately forested land in the central Sierra Nevada in September and October of 2014 (Coen, Stavros, & Fites-Kaufman, 2018). Nearly half of the total area burned experienced stand-replacing fire (>75% canopy mortality), making the King Fire one of the most uniformly severe and homogenous megafires in recent California history (Stevens *et al.*, 2017). The King Fire burned ~44% of our core study area and affected 34 of 83 owl sites (at the 1500-m scale; Table 1), most of which have been consistently monitored since the early 1990s (Fig. 1). Of the portion of our study area that burned, most (64%) of that area burned at high severity (Jones *et al.*, 2016). Because the King Fire affected a contiguous portion of our study area and we had over two decades of pre-fire monitoring data (see below), we were afforded an opportunity to study the effects of fire on spotted owls within a natural Before–After Control–Impact (BACI) experimental design framework (Popescu *et al.*, 2012). Since 2014, California has experienced numerous fires that have matched or exceeded the size and severity of the King Fire (e.g., 2020 Creek Fire and 2020 North Complex). Thus, understanding King Fire effects may foreshadow potential effects of more recent megafires on spotted owls.

We conducted spotted owl surveys annually across the study area from 1989 to 2020. We conducted detection/non-detection surveys from April through August each year, which corresponds with the breeding season for spotted owls. Our study area consisted of a core area that was completely surveyed annually, and additional “satellite” survey areas, approximating the size of a spotted owl home range, surrounding the core area that were added over time to increase sample sizes for demographic analyses. Most satellite survey areas were added to annual survey efforts in 1996 and 1997, and thus have been consistently surveyed for close to 25 years. Several additional satellite survey areas were added to annual surveys in 2005 and 2006. Sampling protocols at satellite survey areas were identical to those conducted in the core area and different only in their start year. The original analyses presented in Jones *et al.* (2016) used owl data only from the core area, but here we expand the analysis to include these satellite survey areas as well (Fig. 1), which includes several additional unburned sites, sites burned by the King Fire and sites burned by other smaller fires earlier in the study period. For the purposes of this analysis, we considered fire effects attributable to the King Fire only, and thus our estimates of fire effects may be conservative because potential variation explained by other fires on the study area was absorbed into other controlling variables in the statistical model (see below). Three smaller fires (2001 Star Fire, 2006 Ralston Fire, 2013 American Fire) occurred on the study area since the year 2000 and resulted in predominately low-severity effects. The 2001 Star Fire likely resulted in reduced post-fire colonization rates at 1–2 territories that experienced moderate amounts of high-severity fire (Tempel *et al.*, 2014). The 2006 Ralston and 2013 American Fires burned ~5 owl territories, but only one territory occurred adjacent to a larger severely burned patch.

We surveyed for spotted owl presence by imitating owl vocalizations at designated survey stations or while walking along routes through historical owl territories or between survey stations (Franklin *et al.*, 1996). When owls were detected through a response vocalization, we determined the sex of the owl by the call pitch, because females have a higher pitched call than males (Forsman, Meslow, & Wight, 1984). Owl surveys were primarily conducted at night, and when owls were detected at night, we conducted follow-up crepuscular and daytime surveys to locate roost and nest locations, assess reproductive status and to capture and band

Table 1 Summary of model covariates for burned sites as calculated across the four selected spatial scales of analysis: nest site scale (300 m), protected activity center (PAC) scale (700 m), territory scale (1100 m) and home-range scale (1500 m)

Variable	Spatial scale			
	Nest site 300 m	PAC 700 m	Territory 1100 m	Home range 1500 m
Sites affected by King Fire (<i>n</i>)	27	29	32	34
Proportion burned at high severity	0.53 (0.44)	0.49 (0.39)	0.41 (0.35)	0.38 (0.33)
Pyrodiversity	0.56 (0.47)	0.71 (0.41)	0.77 (0.39)	0.81 (0.37)
Proportion salvage logged	0.03 (0.10)	0.06 (0.10)	0.07 (0.10)	0.08 (0.10)

Values represent covariate means with standard deviation in parentheses evaluated at *n* burned sites.

unmarked owls (Franklin *et al.*, 1996). Recent work has shown that including detections from nocturnal surveys when colored leg bands (used to identify individuals) were not able to be observed likely results in an overestimation of territorial occupancy owing to wide-ranging, extraterritorial movements by owls (Berigan *et al.*, 2019). Therefore, in this present analysis, we included in our detection history only detections recorded during daytime and twilight, or otherwise detections of individuals within their ‘home’ territories as determined by resighting of uniquely colored leg bands.

Statistical analysis

We used a Bayesian formulation of a dynamic occupancy model (MacKenzie *et al.*, 2003; Royle & Kéry, 2007; Siegel *et al.*, 2019) to assess patterns and correlates of site occupancy on our study area. The model contained parameters for initial occupancy ($\psi_{i,1}$), colonization ($\gamma_{i,t}$), persistence ($\phi_{i,t}$, which is the complement of extinction, $\epsilon_{i,t}$) and detection probability ($p_{i,j,t}$). The primary sampling periods (t) were breeding seasons (i.e., April–August) and the secondary sampling periods (j) were 2-week periods within each breeding season (April 1–15, April 16–30, May 1–15, etc.). Sometimes, multiple surveys within a given site (i) were conducted within a secondary sampling period, in which case a “1” was assigned if owls were detected in any survey during that period, and “0” otherwise. We considered sites where at least one owl was detected during diurnal hours in at least 2 survey years to constitute a bona fide owl territory. Previous research reported one-half the average nearest-neighbor distance between territory centers on our study area to be 1128 m, resulting in ~400-ha circular territories, which approximates an area predicted to be defended by owls (Berigan *et al.*, 2019; Jones *et al.*, 2018; Tempel *et al.*, 2014, 2016).

We calculated a suite of covariates to model the potential effects of the King Fire on local colonization and persistence dynamics of spotted owl territories. We used four spatial scales (varying radii extending from a mapped activity center) to approximate ecologically and/or administratively relevant scales for spotted owls: nest site scale (300 m), protected activity center (PAC) scale (700 m), territory scale (1100 m) and home-range scale (1500 m) (Berigan, Gutiérrez, & Tempel, 2012; Peery *et al.*, 2017; Tempel *et al.*, 2014). We took a multi-scale approach to examine whether and to what extent fire effects were scale dependent (Jackson & Fahrig, 2015; McGarigal *et al.*, 2016; Wan, Cushman, & Ganey, 2020). At each scale, we calculated (i) the proportion of the area that experienced stand-replacing fire (>75% canopy mortality), (ii) the variation in burn severity classes, or pyrodiversity and (iii) the proportion of the area that experienced post-fire salvage logging (Table 1). Fire boundary and severity data were obtained from the Monitoring Trends in Burn Severity project (<http://www.mtbs.gov>). Pyrodiversity was calculated as the Shannon diversity index of five burn categories: unburned (outside fire perimeter), burned but unchanged canopy structure (within fire perimeter), low severity (<25% canopy mortality), moderate severity (25–75% canopy mortality) and high severity (>75%

canopy mortality) (Kramer *et al.*, 2021). Salvage logging was inferred from annual post-fire imagery from the National Agricultural Imagery Program (NAIP) and spatial layers were hand-digitized by one of the authors (HAK) and verified by a second author (WJB). Only areas that had forest cover prior to the fire were considered in salvage digitization; we ensured pre-fire clear-cuts and other non-forested areas were not included in our salvage estimation. Hand-digitized layers were combined with layers indicating that post-fire salvage had occurred in the USDA Forest Service’s Forest Activity Tracking System (FACTS) database.

We constructed a model to describe territory occupancy dynamics and the King Fire’s effects to the spotted owl population. We modeled detection probability p as a logit-linear function of the following covariates:

$$\text{logit}(p_{i,t}) = a_0 + a_1 \text{repro}_{i,t} + a_t$$

where a_0 was the intercept, a_1 was the effect of reproductive status on detection probability where $\text{repro}_{i,t}$ took the value of 0 for non-reproductive territories and 1 for territories that produced young observed on the nest, and a_t was a random year effect to control for unmodeled temporal heterogeneity in p .

We modeled initial occupancy during the first year of our study (1989) at each territory $\psi_{i,1}$ using the following logit-linear function:

$$\text{logit}(\psi_{i,1}) = b_0 + b_1 kf_i$$

where kf_i was an indicator variable for territories that intersected with the King Fire footprint. The kf_i covariate helped control for background differences in occupancy rates at owl sites that were affected by the King Fire and those that were not. For the subsequent years ($t > 1$), we modeled annual occupancy as a process dependent on the true occupancy status ($z_{i,t}$) and affected by the probability that a vacant territory would become colonized ($\gamma_{i,t}$) or that an occupied territory would persist ($\phi_{i,t}$):

$$\psi_{i,t} = \gamma_{i,t-1}(1 - z_{i,t-1}) + \phi_{i,t-1}z_{i,t-1}$$

where colonization and persistence patterns were altered through the effects of site- and time-varying covariates constructed to detect pre- and post-fire effects on site occupancy

$$\text{logit}(\gamma_{i,t-1}) = c_0 + c_1 kf_i + c_2 \text{after}_t + c_3 kf_i \text{after}_t + c_4 kf_i \text{after}_t pSev_i + c_5 kf_i \text{after}_t \text{pyro}_i + c_6 kf_i \text{after}_t pSalvage_{i,t} + c_7 \text{year}_t$$

and

$$\text{logit}(\phi_{i,t-1}) = d_0 + d_1 kf_i + d_2 \text{after}_t + d_3 kf_i \text{after}_t + d_4 kf_i \text{after}_t pSev_i + d_5 kf_i \text{after}_t \text{pyro}_i + d_6 kf_i \text{after}_t pSalvage_{i,t} + d_7 \text{year}_t$$

where kf_i was an indicator variable for fire-affected territories as described above, after_t was an indicator variable for post-fire survey years, $pSev_i$ was a continuous variable representing the proportion of the territory that was affected by stand-replacing fire, pyro_i was a continuous variable describing pyrodiversity and $pSalvage_{i,t}$ was a time-varying site covariate

describing the cumulative proportion of the owl site that had experienced post-fire salvage logging. We modeled salvage logging as a time-varying covariate because most salvage logging within owl sites occurred immediately after the fire (in 2015), but some additional logging occurred in subsequent years. The terms $c.year_t$ and $d.year_t$ were annual, normally distributed random effects that allowed annual unmodeled heterogeneity in colonization and extinction parameters.

We fit the above model at each of the four covariate scales (300, 700, 1100 and 1500 m) to the data using JAGS (Plummer, 2003) in the R statistical programming environment. All coefficients were assigned uninformative Gaussian priors with $\mu = 0$ and $\sigma = 2$ as recommended by Northrup & Gerber (2018). Although on the logit scale this prior appears informative, it is approximately flat when back-transformed to the probability scale (Northrup & Gerber, 2018). We ran three chains of 10 000 iterations, an adaptation phase of 1500 and a thin rate of 10 yielding 3000 posterior samples for each parameter across all chains. We assessed convergence using the Gelman–Rubin statistic (all values <1.1). We made inference about parameters by examining the direction and magnitude of mean effects, the extent to which posterior distributions overlapped zero, computation of odds ratios following Jones & Peery (2019), and by graphical visualization of derived annual rates of occupancy, colonization and persistence.

Results

Following the King Fire, spotted owl sites were less likely to persist when they experienced more stand-replacing fire ($>75\%$ canopy mortality) across all spatial scales examined (Fig. 2a). The strongest effect of severe fire on persistence was found at the 1100 m (territory) scale, where the mean odds of persistence decreased by 7.8% for every 10-ha increase in severely burned area (logit coefficient $d_4 = -3.12$, 95% Bayesian credible interval $[-5.05, -1.23]$). In contrast, the effect of pyrodiversity on spotted owl site persistence was scale-dependent (Fig. 2a). At the nest area (300 m) and PAC (700 m) scales, increased pyrodiversity led to increased persistence probability ($d_5 = 1.30$ $[-0.35, 2.94]$ and $d_5 = 1.19$ $[-0.25, 2.73]$), respectively (posterior densities were 93 and 94% positive; Table S1 in Appendix). Whereas at the territory (1100 m) and home-range (1500 m) scales, the pyrodiversity effect weakened and the CRIs widely overlapped zero. Salvage logging had no effect on persistence probability; posterior means were near zero and credible intervals widely overlapped zero across all scales (Fig. 2a). Thus, we considered salvage logging to be an uninformative parameter for spotted owl site persistence.

Like site persistence, more extensive severe fire reduced the probability of site colonization at all spatial scales examined (Fig. 2b). The effect of severe fire was strongest at the territory (1100 m) scale, where the mean odds of colonization decreased by 8.3% for every 10-ha increase in severely burned area ($c_4 = -3.28$ $[-5.26, -1.52]$). Unlike site persistence, pyrodiversity did not appear to influence site colonization probability, regardless of spatial scale (Fig. 2b). Neither

pyrodiversity nor salvage logging had any apparent effects on site colonization probability; posterior means were near zero and credible intervals widely overlapped zero (Fig. 2b). Posterior distributions for all model coefficients for persistence and colonization sub-models, as well as detection and initial occupancy, are available in the Table S1 in Appendix.

Derived estimates of annual occupancy showed a gradual decline in occupancy over a 25-year pre-fire period for all owl sites, followed by the largest single-year occupancy decline over the study period (-0.08 ; declining from 0.54 to 0.46) in the year following the King Fire. However, when sites were grouped by broad classes of exposure to severe fire at the home-range (1500 m) scale (unburned, $<50\%$ high-severity, $>50\%$ high-severity), a distinctive “hockey stick” post-fire trajectory for the most severely burned sites was apparent (Fig. 3). The probability that sites that experienced $>50\%$ severe fire (at the 1500-m scale) remained occupied dropped sharply from 0.62 in the year prior to the fire (2014) to 0.23 following the fire (2015). Then in 2016, the probability of site occupancy for this severely burned group dropped to 0.039 and remained near zero through the remainder of the study period. Sites that burned less severely ($<50\%$ high severity) experienced a relatively smaller apparent decline in occupancy probability after the fire (from 0.59 in 2014 to 0.40 in 2015), but then remained between 0.42 and 0.55 over the period 2016–2020 (Fig. 3). The probability of occupancy for unburned sites appeared to remain stable or slightly increase following the King Fire (Fig. 3).

Discussion

We have shown that a large, severe “megafire” of a type that is becoming more frequent in some forest ecosystems can lead to dramatic and persistent local population declines. Following the 2014 King Fire in the central Sierra Nevada, CA, spotted owls at severely burned sites went locally extinct and did not re-colonize them over a 6-year period following the fire (Fig. 3). These findings support our hypothesis that spotted owls are poorly adapted to survive in post-fire landscapes characterized by extensive severe fire. These results also indicate that initial short-term impacts (1-year post-fire) reported by Jones *et al.* (2016) have persisted and thus do not represent an ephemeral effect. Hence, this megafire event caused a persistent loss of spotted owl nesting habitat, which is a primary factor limiting populations of this species across its range (Ganey *et al.*, 2017). For this reason, we reject the notion that owls experiencing large, severe fires within their territories may simply show an initial abandonment of sites but return shortly thereafter.

Rapidly changing fire regimes could pose an existential threat to spotted owls and other forest-dependent species as ecosystems cross ‘tipping points’ and experience type conversion (van Nes *et al.*, 2016). Altered fire regimes, in combination with other stressors such as climate change and logging, can lead to ecosystem collapse (Lindenmayer, Messier, & Sato, 2016) and has led to long-term declines in tree-cavity-dependent species in Mountain Ash forests in Australia (Lindenmayer & Sato, 2018). Recent fires in

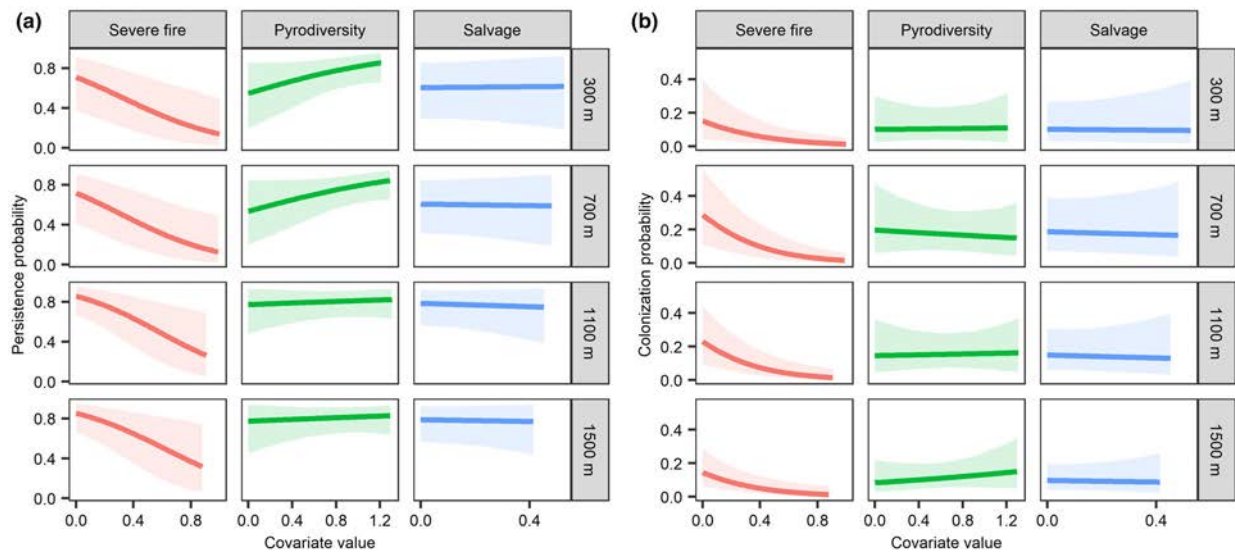


Figure 2 Predicted relationships between covariates (severe fire, pyrodiversity and salvage logging) and dynamic occupancy rates (persistence in panel a; colonization in panel b) across the four scales of analysis (nest area, 300 m; PAC, 700 m; territory, 1100 m and home range, 1500 m). The thick colored lines represent the prediction at the posterior mean, while shaded range represents the upper and lower 95% Bayesian credible intervals. Coefficient estimates used to produce figures can be found in the Table S1 in Appendix [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

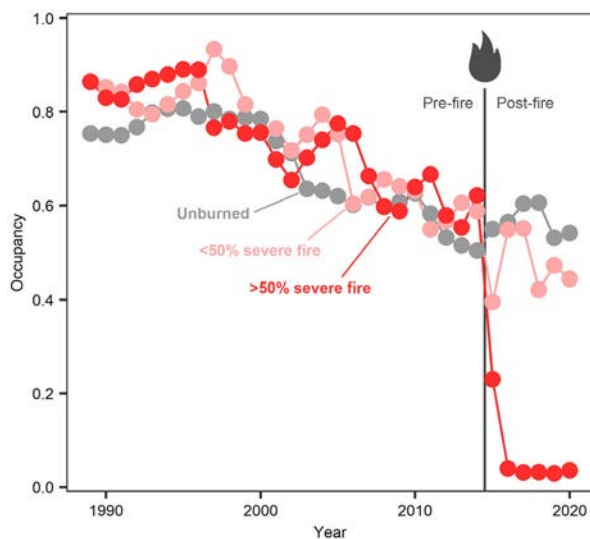


Figure 3 Derived annual occupancy from 1989 to 2020 for spotted owl sites grouped by the percentage of the home-range (1500 m) that experienced severe fire (unburned, <50% severe, >50% severe). The grey vertical line on the x-axis between years 2014 and 2015 indicates the timing of the 2014 King Fire and therefore divides pre- and post-fire occupancy trajectories [Colour figure can be viewed at zslpublications.onlinelibrary.wiley.com.]

California, USA have eclipsed the 2014 King Fire in terms of size and severity (e.g., 2020 Creek fire) and these types of fires could contribute to collapse of dry forest ecosystems through regeneration failure and persistent type conversion (Davis *et al.*, 2019; Stevens *et al.*, 2017). If owl populations

are responding similarly to more recent and widespread fire events, landscape-scale population viability over the coming decades could be threatened. Therefore, our results suggest that forest restoration intended to reduce megafires and increase long-term forest resilience are likely to provide co-benefits for this species, forest ecosystems and the people that depend on long-term sustainability of forest ecosystem services (Stephens *et al.*, 2020; Wood & Jones, 2019), so long as keystone structural features of these ecosystems are retained (Jones, 2019; Jones *et al.*, 2018; Tempel *et al.*, 2014).

Many terrestrial vertebrates may respond positively to forest restoration. Mechanical thinning and fire mosaics produced through prescribed and managed fire (i.e., pyrodiversity) can increase structural diversity in homogenized forests, which could result in increased biodiversity (Fontaine & Kennedy, 2012; Steel *et al.*, 2019; Tingley *et al.*, 2016). It has generally been assumed, however, that spotted owls and other sensitive old-forest species will respond negatively to restoration treatments because these species tend to be associated with ‘dense’ and fire-prone forests. Yet for spotted owls, empirical evidence for negative effects of restoration treatments is sparse. Studies that have inferred or are often cited as evidence for negative treatment effects to owls have demonstrated weak effect sizes (Tempel *et al.*, 2014) or did not distinguish between fire and treatment effects (Seamans & Gutiérrez, 2007). Observed owl declines following restoration treatments in another study occurred alongside declines in control groups, such that effects could not be attributed to treatments themselves (Stephens *et al.*, 2014). Still, other studies have found no measurable effects of treatment, or otherwise weak positive

(beneficial) effects (Tempel *et al.*, 2016). Indeed, restoration that increases landscape-scale heterogeneity in otherwise fire-suppressed, homogenized forests could directly benefit owls by promoting diverse prey habitat and population stability (Hobart *et al.*, 2019). Moreover, restoration that increases the scale of low-severity fire effects through prescribed fire is likely to recruit preferred owl foraging habitat in the short term (Kramer *et al.*, 2021). Therefore, it is likely that although restoration treatments could in some contexts result in weak negative effects, these effects are substantially exceeded by negative effects of megafires over the long term (Jones, 2019; Tempel *et al.*, 2015).

Observations of ecological phenomena are scale dependent (Levin, 1992; Wiens, 1989), which has led to adoption of multi-scale perspectives in ecological analyses (Jackson & Fahrig, 2015; McGarigal *et al.*, 2016). Scale dependence is also apparent in analyses of the effects of ecological disturbances on biodiversity (Hamer & Hill, 2000; Wan, Cushman, & Ganey, 2020). Using four biologically relevant spatial scales (nest area, activity center, territory and home range), we determined that while some disturbance effects were scale invariant, others were scale dependent. The effect of severe fire on both site colonization and persistence was scale invariant; severe fire had clear negative effects on both parameters across all scales examined, with very little variation in effect size or uncertainty (Fig. 2, also see Table S1 in Appendix). This observation may be related to the patterns of severely burned forest within the King Fire where extremely high spatial contagion (Stevens *et al.*, 2017) rendered homogenous severe fire effects across scales. In contrast, higher pyrodiversity has led to increased persistence at finer spatial scales but not at broader spatial scales. Consequently, pyrodiversity at finer scales may result in greater likelihood of nest stand structure preservation or lead to increased diversity of prey habitat near the nest stand (Hobart *et al.*, 2021). The effect of pyrodiversity may diminish at broader scales because these larger scales are more associated with foraging habitat and foray behaviors (Blakey *et al.*, 2019), the former of which is more flexible for spotted owls than is their choice of roosting and nesting habitats (Atuo *et al.*, 2019; Call, Gutiérrez, & Verner, 1992; Williams *et al.*, 2011). This result suggests a potential benefit to increased use of prescribed and managed fire resulting in diverse post-fire conditions in spotted owl core areas and at the scale of protected activity centers (Kramer *et al.*, 2021). Moreover, this result has broader implications for pyrodiversity research, as little existing work has explored the role of scale in mediating pyrodiversity effects on wildlife and the pyrodiversity–biodiversity hypothesis (Jones and Tingley, *in press*).

Following large disturbance events such as megafires, windstorms and droughts, land managers will often engage in post-fire management such as salvage logging and reforestation to recover some economic loss and attempt to rebuild resilient forest ecosystems (North *et al.*, 2019). Salvage logging, in particular, is a controversial practice because of its negative effects on certain taxa and ecosystem processes (Lindenmayer *et al.*, 2008; Thorn *et al.*, 2018). In some cases, scientists have debated whether it is the disturbance itself (e.g.,

fire) or the subsequent management activities (e.g., salvage logging) that has caused estimated effects on sensitive wildlife species such as spotted owls (Hanson, Bond, & Lee, 2018; Jones *et al.*, 2019). It is often the case that fire and salvage effects are confounded and thus cannot easily be separated (Clark, Anthony, & Andrews, 2013; Lee, Bond, & Siegel, 2012). In our study, we were able to separate these two effects and we unequivocally determined that severe fire, and not salvage logging, was correlated with the observed local declines in spotted owl site occupancy. We, thus, reject the hypothesis that salvage logging drove or even contributed to the observed post-fire decline. Given that both severe fire and salvage logging were included as competing covariates, the salvage effects were uninformative across all scales (Fig. 2).

The relative effects of fire and post-fire management on wildlife may, in part, depend on their relative spatial extent. In our study landscape, the spatial extent of severe fire effects not only eclipsed that of salvage logging, but often did so by an order of magnitude (Fig. 4, Table 1). Sites that experienced extensive severe fire (>50%) but very little salvage logging (many close to 0%) remained unoccupied 6 years post-fire, which further indicated that severe fire was more likely of these two forces driving local extirpation and

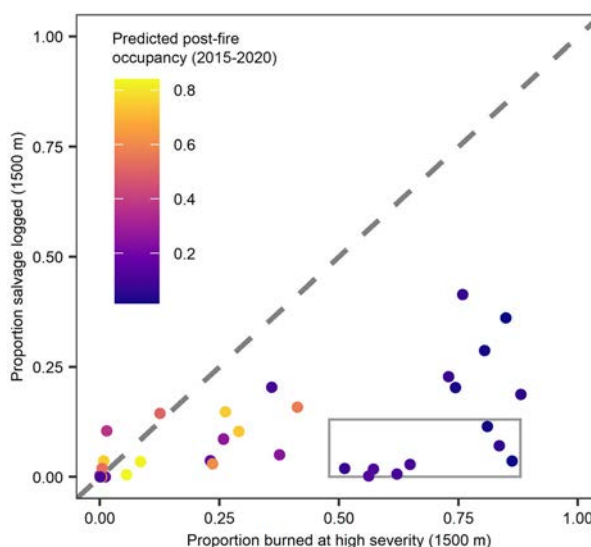


Figure 4 Comparison of the relative extent of salvage logging (y-axis) and severe fire (x-axis) at the home-range (1500 m) scale, where each point represents one spotted owl site. Points are colored by the predicted post-fire (2015–2020) occupancy at each spotted owl site. Points above the grey dashed diagonal 1:1 line indicate sites with a greater extent of salvage logging than high-severity fire; points below the 1:1 line indicate site with more high-severity fire than salvage logging. The grey rectangle in the bottom right surrounds a group of sites that experienced relatively large amounts of severe fire (>50% of home range affected) and relatively little salvage logging (0–12% of home range), highlighting the effect of severe fire on owl occupancy independent of post-fire salvage logging [Colour figure can be viewed at [zslpublications.org/online-library/wiley.com](https://www.zslpublications.org/online-library/wiley.com).]

lack of re-colonization (Fig. 4). In some cases, sites that experienced greater salvage logging had higher post-fire occupancy than sites that had experienced less salvage logging, with differences in occupancy instead being clearly linked to variation in severe fire extent and pyrodiversity, not salvage (Fig. 5). Thus, while it is well known that salvage logging can have negative consequences for spotted owls (Lee *et al.*, 2013; Jones *et al.*, 2020) and biodiversity more broadly (Lindenmayer & Noss, 2006; Thorn *et al.*, 2018), the pattern and extent of salvage logging had no measurable effects on spotted owl occupancy dynamics in this study and was transcended by the extreme nature of the King Fire. It is likely that in other cases where post-fire management (such as salvage logging) is more spatially extensive, determining whether fire or post-fire management caused declines would be challenged because the effects would be confounded.

Long-term monitoring programs offer unmatched value for understanding ecosystem change over prolonged time periods (Hughes *et al.*, 2017; Lindenmayer *et al.*, 2012). Our ability to measure a clear and immediate effect of a random event (the King Fire) on spotted owls was only made possible because of

the intersection of this fire on a long-term population study, even though the original purpose of owl monitoring was to detect population trends, not to detect the effects of disturbance. Our continuing post-fire monitoring of this population has reinforced initial results (Jones *et al.*, 2016), allowed for further accumulation of evidence (Nichols, Kendall, & Boomer, 2019) and expanded understanding of prolonged effects and mechanisms underlying species response. Thus, we emphasize that long-term monitoring can offer surprising and unparalleled opportunities for learning, which allow monitoring programs to provide unexpected value for addressing emerging environmental concerns (Lindenmayer & Likens, 2009). The before–after control–impact natural experimental design – one of the most powerful designs in ecological field studies (Popescu *et al.*, 2012) – is often only possible in the context of long-term monitoring and unexpected environmental changes. In an era of rapid ecological changes and shifting disturbance regimes in ecosystems, the relative value of long-term monitoring programs may increase through time because they will allow researchers to estimate effects of novel changes in ways that more “reactive” research or monitoring may not be able to provide.

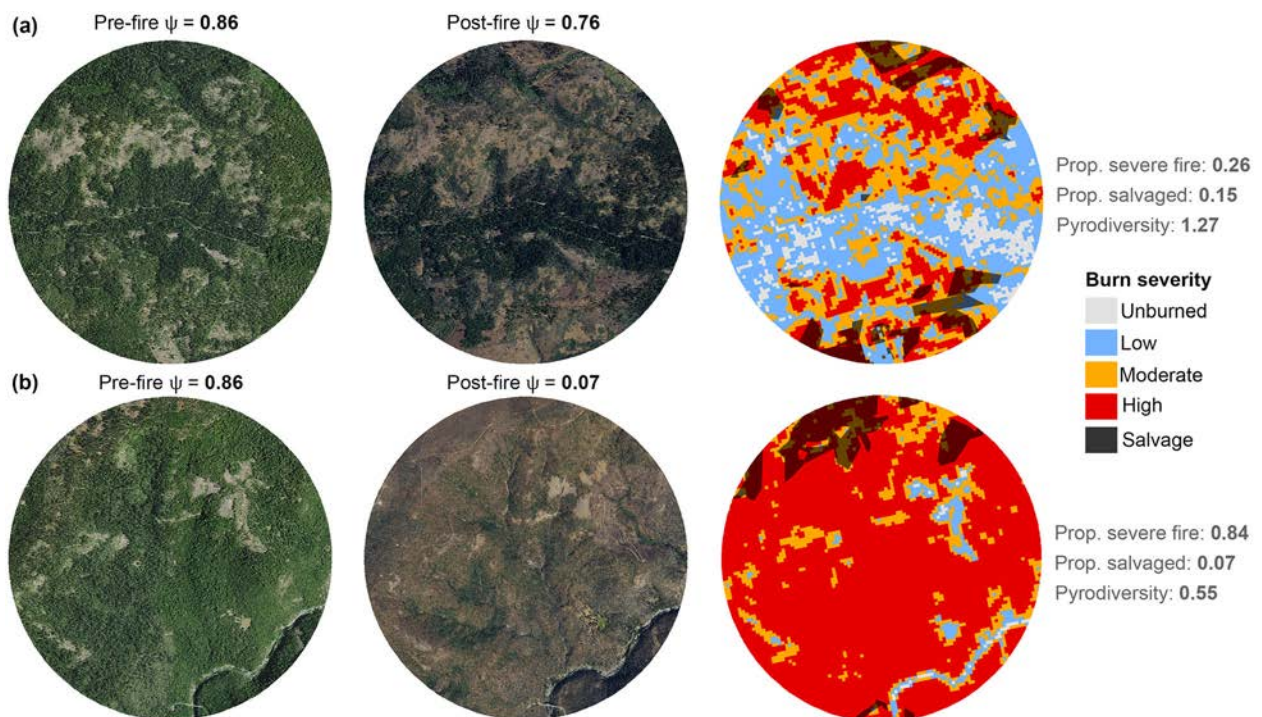


Figure 5 Two selected spotted owl sites (shown at the home-range scale, 1500 m) illustrating the effects of fire severity, pyrodiversity and salvage logging on site occupancy. The owl site in the top row (a; “site A”) and bottom row (b; “site B”) had the same predicted pre-fire occupancy probability ($\psi = 0.86$). After the fire, predicted occupancy declined slightly for site A (0.10 decline) and dramatically for site B (0.79 decline). These different post-fire trajectories can be attributed to differences in high-severity fire exposure and pyrodiversity. Site A experienced relatively little high-severity fire (proportion of home range affected = 0.26) and relatively high pyrodiversity (index = 1.27). Site B experienced extensive high-severity fire (proportion = 0.84) and low pyrodiversity (index = 0.55). Both sites experienced small amounts of salvage logging, with site A experiencing ~2x as much salvage as site B (15% and 7%, respectively). However, salvage logging was an uninformative parameter, so it had no effect on predicted post-fire occupancy. Aerial photos shown in the left and middle columns represent 2014 (pre-fire) and 2018 (post-fire) NAIP imagery. Pre- and post-fire predicted site occupancy was estimated for a 6-year pre-fire period and 6-year post-fire period, respectively [Colour figure can be viewed at [zslpublications.onlinelibrary.wiley.com](https://onlinelibrary.wiley.com).]

Our work offers evidence that the negative effects of novel ‘mega-disturbances’ in some ecosystems may be permanent, not ephemeral, reinforcing the need to re-think the status quo in forest ecosystem conservation (North *et al.*, 2015; Stephens *et al.*, 2019, 2020; Wintle, Legge, & Woinarski, 2020; Wood & Jones, 2019). In this study, there was no evidence of recolonization of sites by owls that burned at >50% high severity even 6 years after the fire. This is not surprising, given that in the Sierra Nevada, the regeneration time for old-forest conditions required by spotted owls exceeds 100 years. However, even a 100+ years hypothesized timeline of habitat regeneration relies on the now questionable assumption that forests will have the capacity to regenerate naturally under climate change and increasing frequency of high-severity fire (Davis *et al.*, 2019; Shive *et al.*, 2018; Stevens *et al.*, 2017). Thus, active management to mitigate disturbance effects, increase forest resilience and/or restore disturbed areas may be required to avoid permanent loss of owl habitat in many areas (North *et al.*, 2019). Forest restoration that increases landscape heterogeneity of forest structure and fuels may increase resilience to disturbances (Koontz *et al.*, 2020). Post-fire reforestation strategies could also increase ecosystem resilience and long-term persistence of seasonally dry forests (North *et al.*, 2019) and the ecosystem services they provide to people (Hurteau *et al.*, 2014; Wood & Jones, 2019). The accumulating evidence, including the evidence provided in this paper, suggests that the conservation of spotted owls, and likely other sensitive wildlife species, and dry forest ecosystem restoration are not in conflict. Therefore, we suggest that sensitive species conservation and forest ecosystem restoration can be mutually reinforcing objectives in bioregional-scale forest management.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Full model results for Bayesian dynamic occupancy models at the four spatial scales examined

Forest restoration limits megafires and supports species conservation under climate change

Gavin M Jones^{1,2*}, Alisa R Keyser^{3,4}, A Leroy Westerling³, W Jonathan Baldwin³, John J Keane⁵, Sarah C Sawyer⁶, John DJ Clare², RJ Gutiérrez^{2,7}, and M Zachariah Peery²

Climate change and fire suppression have altered disturbance regimes in forest ecosystems globally. In the seasonally dry forests of western North America, large-scale restoration may reduce severe fire and increase forest resilience but also eliminate existing habitat for sensitive wildlife species. We modeled bioregional-scale effects of forest restoration on future severe fire activity and occupancy dynamics of an old-forest species declining in abundance, the spotted owl (*Strix occidentalis*), in the Sierra Nevada mountains of California. Our findings suggest restoring historical forest structure may mitigate severe fire activity as the climate warms, particularly when restoration occurs in owl habitat. On average, benefits provided by restoration to owls (reduced severe fire) were found to exceed potential costs (direct habitat alteration) by mid-century. However, the magnitude and direction of restoration trade-offs varied spatially, which informs restoration planning. When large, old trees are maintained, forest restoration can provide co-benefits to old-forest species and forest ecosystem resilience under climate change.

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Climate change is profoundly altering forest distribution and disturbance regimes worldwide (Seidl *et al.* 2017). Humans also continue to shape forests globally. In the seasonally dry forests of western North America, a century of fire suppression and large-tree logging has transformed forest structure away from historical conditions (Collins *et al.* 2017). Forests that were historically open with low tree densities now have high densities of small- and medium-sized trees and a deficit of large trees (Safford and Stevens 2017). These altered forest structures combined with climate change have led to larger, more severe fires (Steel *et al.* 2015; Westerling 2016) and widespread drought-related tree mortality (Fettig *et al.* 2019), with substantial impacts to humans and forests. These increasingly common “mega-disturbance” events pose a major threat to forest persistence, and to forest species and ecosystem services (Stephens *et al.* 2018; Wood and Jones 2019).

Landscape-scale forest restoration may increase seasonally dry forest ecosystem resilience (Stephens *et al.* 2020). Thinning and prescribed/managed fire can reduce accumulation and increase heterogeneity of fuels (Knapp *et al.* 2017); promote development of large, fire-resistant trees (Agee and Skinner 2005); alter fire behavior and lower severe fire likelihood (Tubbesing *et al.* 2019); and reduce risk of drought-related tree mortality (Bradford and Bell 2016). However, restoration alters forests inhabited by wildlife that depend on large, old trees,

high canopy cover, and complex vertical structure (Tempel *et al.* 2014). Concern over wildlife habitat has limited the pace and scale of forest restoration efforts (North *et al.* 2015a). Thus, restoring seasonally dry forest ecosystems while safeguarding vulnerable populations of old-forest species presents a conservation conundrum: how can restoration occur without jeopardizing species that use “departed” forest conditions (Peery *et al.* 2017)?

Solving this conundrum involves understanding whether or how the potential negative short-term impacts of restoration on old-forest species can be outweighed by reducing habitat loss to future severe wildfires. To address this question, we developed a novel bioregional-scale severe fire model (hereafter, “fire model”) that generates robust, fine-grain (30-m) predictions of future severe fire activity linked to climate and vegetation (eg fuels) conditions. We coupled the severe fire model with a spatial occupancy model (“occupancy model”) to evaluate relative and scale-dependent effects of restoration and severe fire on a focal old-forest species, the spotted owl (*Strix occidentalis*) (Figure 1), across the Sierra Nevada mountains of California (~120,000 km²). In doing so, we assessed two central questions about bioregional-scale forest restoration. First, can restoration effectively reduce future severe fire activity in a changing climate? Second, can restoration provide co-benefits to old-forest species?

■ Methods

We fit the fire and occupancy empirical models independently over the period for which common historical data existed (1984–2015), then linked them together during forward simulations of restoration- and climate-induced changes in patterns of severe fire and owl occupancy dynamics (through 2064; WebFigure 1). Climate-change effects in the fire model

¹US Department of Agriculture (USDA) Forest Service, Rocky Mountain Research Station, Albuquerque, NM (gavin.jones@usda.gov); ²Department of Forest & Wildlife Ecology, University of Wisconsin–Madison, Madison, WI; ³Sierra Nevada Research Institute, University of California–Merced, Merced, CA; ⁴Department of Biology, University of New Mexico, Albuquerque, NM; ⁵USDA Forest Service, Pacific Southwest Research Station, Davis, CA; ⁶USDA Forest Service, Pacific Southwest Region, Vallejo, CA; ⁷Department of Fisheries, Wildlife & Conservation Biology, University of Minnesota, St Paul, MN



Figure 1. An adult male spotted owl (*Strix occidentalis*) located in Sequoia and Kings Canyon National Parks in the southern Sierra Nevada, California.

were represented using the Representative Concentration Pathway 8.5 (RCP8.5) and the global circulation model (GCM) CNRM-CM5. We chose RCP8.5 because it reflected a “business-as-usual” emissions scenario; however, we considered only projections through mid-century, when the divergence between RCP8.5 and other more optimistic scenarios is modest compared to the final decades of the 21st century. The CNRM-CM5 model typically reflects moderate to warmer conditions than other commonly used GCMs and therefore represents a “higher end” warming scenario that produced greater future fire activity in our model. The fire model produced annual realizations of severe fire occurrence across the Sierra Nevada through mid-century (2064) that fed into the occupancy model. The behavior of both models was linked to a factorial design that varied the extent and location of restoration activities (changes to “fire regime condition class” [FRCC]; see WebPanel 1) across the landscape (Westerling 2018). By using changes in FRCC to reflect effects of restoration activities (eg fuels reduction), we assume that such activities, however implemented, can return forests to their historical range of variability.

Restoration (or “treatment”) was simulated in areas without substantial mechanical operability constraints on non-subalpine federal lands (hereafter “treatable” lands; Collins *et al.* 2010; North *et al.* 2015a), with total treatment extent varying in equal intervals (20%, 30%, 40%, 50%, and 60% of the Sierra Nevada bioregion treated). Treatable lands (approximately 60,000 km²) excluded wilderness areas, inaccessible areas, and other sensitive areas that cannot be treated under current regulatory frameworks. The highest treatment level (60%) represented ~90% of the total “treatable” area in the

Sierra Nevada. A second set of treatment scenarios maintained the same total treatment extent but excluded treatment from spotted owl territories. Restoration treatments were introduced into the fire and owl occupancy models in year one of the forward projection and were implemented “instantaneously”, meaning that treatment effects were immediate. Consequences of this simplifying assumption likely include an overestimation of the short-term effects of treatments (because they cannot be implemented across such large scales immediately) both in terms of their ability to reduce severe fire behavior and their effects on owl habitat. We evaluated the effect of our assumptions about how treatments would alter owl habitat by conducting a sensitivity analysis in which we varied the extent to which treatment modified habitat within the occupancy model (“no habitat alteration”, “weak habitat alteration”, “strong habitat alteration”; see WebPanel 1).

Fire model

We developed a novel multiscale fire model using remotely sensed burn severity data (WebFigure 1; WebPanel 1). We defined high severity as 90% basal area killed (hereafter “stand-replacing” or “severe” fire). The multiscale fire model consisted of large-scale (~6-km) and fine-scale (30-m) “submodels” that interacted to produce spatial realizations of severe fire. We developed the large-scale submodel by fitting a spatially explicit logistic regression model on a ~6-km grid to estimate the monthly probabilities of the occurrence of at least one fire >400 ha as a function of topography, human population, vegetation fraction, and climate (WebPanel 1; Westerling 2018). Then, for each fire >400 ha, the probability of a minimum threshold (>50 ha) burning in a stand-replacing fire was estimated by fitting a logistic regression with climate covariates. To estimate conditional extent of stand-replacing burned area, we fitted a generalized Pareto distribution with climate and FRCC covariates for each fire with >50 ha stand-replacing burned area (WebFigure 2). We used this model system to simulate large-scale stand-replacing burned area for each climate and treatment scenario (see WebPanel 1).

We developed the fine-scale submodel (a mapping algorithm) by selecting 20 fires for model training that yielded the most complete coverage of latitude, year, ignition month, fire size, and severity in the Sierra Nevada (WebTable 1). Random Forests, a machine-learning algorithm, was used to predict occurrence of stand-replacing fire pixels (30 m) on the landscape as a function of topography, vegetation type, and fire size, and a spatial allocation algorithm was developed to link the large- and fine-scale model to assign severely burned pixels to the 30-m landscape surface using a Monte Carlo simulation. Starting with a randomly assigned ignition point (using a uniform distribution) within the large-scale modeling pixel, the algorithm assigned 30-m pixels as stand-replacing fire (true/false) in an iterative fashion

based on the modeled fine-scale probability surface until the predicted fire size from the large-scale model was reached. This procedure was repeated for the entire suite of models 100 times for each unique treatment scenario, and each individual simulation was delivered to the spatial occupancy model for spotted owls (see below). Full model description, evaluation, accuracy and error assessments, and allocation examples are provided in WebPanel 1.

Occupancy model

We modeled spotted owl territory (hereafter, “site”) occupancy using a Bayesian spatial occupancy model (Chandler *et al.* 2015) with detection/non-detection data from $n = 275$ owl survey areas collected between 1993 and 2011 (WebFigure 1; Tempel *et al.* 2016). The spatial dependence in the model’s structure allowed occupancy dynamics of the 275 surveyed sites to be modeled within a broader network of 1844 known or imputed sites representing nearly all suitable habitat in the Sierra Nevada (see Jones 2019). Site extinction probability and detection probability were modeled as a function of forest structural variables representing the proportion of each owl site containing large trees (quadratic mean stand diameter ≥ 61 cm) and high canopy closure ($\geq 70\%$ canopy cover), and large trees and medium canopy closure (40–70% canopy cover), respectively (WebFigure 1; WebPanel 1; Jones *et al.* 2018).

We combined output from the multiscale fire model with 500 multivariate posterior draws of parameter distributions to project the spotted owl population forward over the period 2012–2064 while incorporating the full parameter uncertainty (WebFigure 1; WebPanel 1). Simulated treatment effects within individual owl territories were modeled by modifying forest structure covariate values (see above) in a manner consistent with expected changes in horizontal canopy structure due to treatments (ie reducing fuel continuity by reducing canopy cover). Severe fire effects were modeled using an empirical effect of severe fire extent (proportion of territory area burned severely) on spotted owl local extinction rates determined by a before–after control–impact natural experiment (WebFigure 1; Jones *et al.* 2016). In forward projections of the model system, we focused on reporting expected (mean) outcomes to guide discussion of management implications, but we also acknowledge and discuss the role of prediction uncertainty in interpretation of results. For full model description and reporting, see WebPanel 1.

Results

In the absence of forest restoration treatments, severe fire was predicted to burn an average of $\sim 24,000$ ha/year (maximum annual prediction 235,000 ha) in the Sierra Nevada, or a total of $\sim 720,000$ ha (range 453,585–1,068,009 ha over 100 simulations) during the years 2035–2064 (Figure 2a; WebFigure 2). Restoration changed the expected

severe fire area by a minimum of -6.8% (a reduction of 45,930 ha of severe fire) to -55.8% (a reduction of 257,880 ha of severe fire) over the period 2035–2064 depending on treatment extent and location (Figure 2, b and c). However, uncertainty in annual decreases of severe fire extent across the stochastic fire replicates resulting from treatment effects was large (orders of magnitude; WebFigure 2). More extensive treatments consistently reduced expected severe fire area across the landscape, and this effect was proportionally larger when treatments were included in owl territories (Figure 2c; WebFigure 2). For example, treating 60% of the landscape but restricting treatments to occur outside of owl territories reduced severe fire area by 29%, whereas allowing treatments to occur in owl territories reduced severe fire by nearly 56%. Moreover, higher levels of treatment (eg $>40\%$ of the Sierra Nevada) appeared to reduce expected severe fire activity even in years when climate models produced extreme fire conditions, most notably when treatments were included in owl territories (WebFigure 3).

The degree to which owl territories were exposed to local extinction-inducing severe fire depended on the spatial extent of simulated restoration treatments and whether treatments were allowed within owl territories (WebFigure 3). Forest restoration has the potential to provide expected net benefits to spotted owls inhabiting the Sierra Nevada by the mid-21st century under all scenarios considered (Figure 3). When treatments were excluded from owl territories (Figure 3a), owl populations experienced expected net benefits that increased with more treatment, but the long-term benefits were lower compared to scenarios where owl territories received treatments (Figure 3, b–d). Owls were expected to benefit most when treatments occurred within territories and when treatments avoided modifying large tree/high canopy cover forest (Figure 3b). When treatments occurred inside territories and owl habitat was modified (Figure 3, c and d), a downward pressure was imposed on owl populations over initial years of the simulation but varied in degree depending on assumptions made about the extent to which treatment directly altered owl habitat. The expected net costs of treatment were offset by the cumulative benefits of reduced severe fire exposure by the 2040s and 2050s for all treatment scenarios (Figure 3, c and d). Importantly, the scenarios involving treatment in owl territories (and therefore simulated changes to forest structure in the owl model) introduced additional variability into the model system because of uncertainty associated with effects of habitat alteration, which resulted in wider prediction intervals (WebFigure 4).

When averaged across the entire Sierra Nevada, expected treatment effects on population occupancy were apparent but modest in magnitude (eg -0.01 to $+0.04$; Figure 3). However, larger expected effects that varied considerably in space were apparent at the territory scale (eg ± 0.30 ; Figure 4; WebFigure 4). When treatments were excluded from owl territories, there

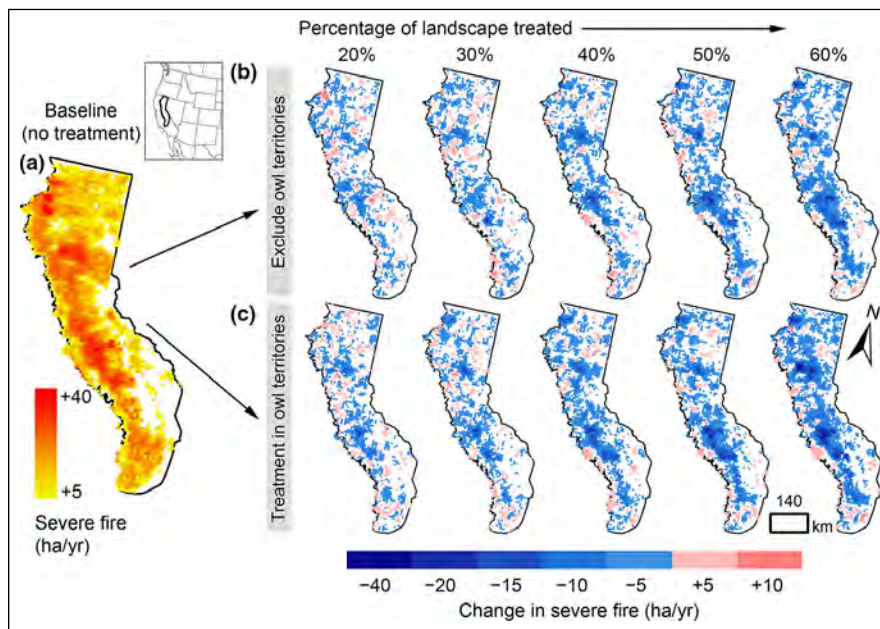


Figure 2. Severe fire activity in the Sierra Nevada is expected to increase by mid-century but was altered by treatment location and extent. (a) Mean annual increase in severe fire (90% basal area killed) over a mid-century climate period (2035–2064) under the baseline no-treatment (0%) scenario; (b) expected effects of treatment on severe fire activity when treatments excluded from spotted owl (*Strix occidentalis*) territories at varying levels of treatment extent (increasing from left to right); (c) expected effects of treatment on severe fire activity when treatments are included in owl territories. The polygon outlined in black depicts the boundary of the Sierra Nevada bioregion. The rectangle in the bottom right is the scale bar, where the horizontal length is equivalent to 140 km. Note that the color ramp intervals for change in severe fire are not all equal.

were relatively uniform expected benefits to mid-century territory occupancy compared to a no-treatment scenario (eg -0.06 to $+0.11$; range of 99th percentile of values; Figure 4b). These benefits grew (eg -0.07 to $+0.20$) when treatments were simulated to occur within owl territories but were assumed to avoid modifying large tree/high canopy cover forest (Figure 4c). When simulated treatments were applied in owl territories and treatment was assumed to modify owl habitat, strong

assumed not to alter key owl habitat, benefits were nearly universal and larger than other scenarios (Figures 3b and 4b) with less prediction uncertainty (WebFigure 4). Optimal management strategies might therefore entail a mixed approach where treatments are excluded from owl territories or designed to avoid high-quality owl habitat in certain regions where expected negative impacts of treatment are greatest, and included elsewhere where expected direct effects

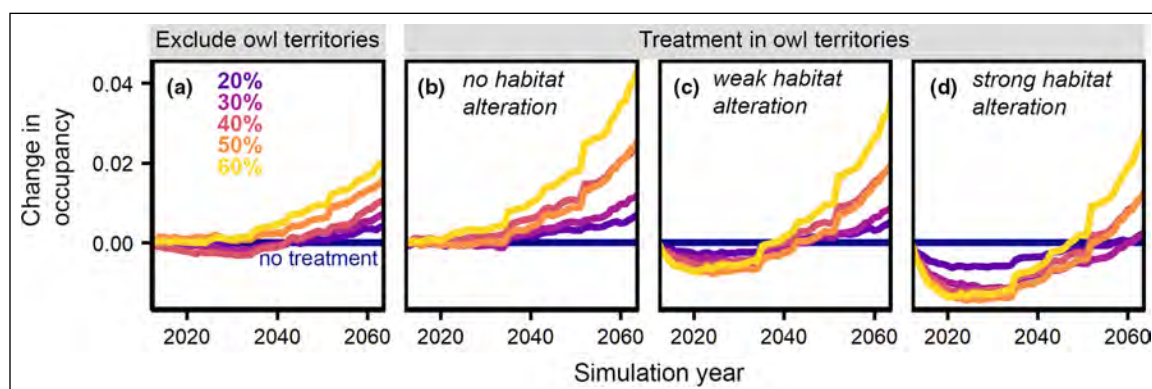


Figure 3. Sierra Nevada-wide site occupancy trajectories for each treatment scenario relative to the baseline no-treatment scenario (dark blue line). (a) Occupancy when treatments are excluded from owl territories; (b–d) occupancy when treatment occurs within owl territories but assumptions about the extent to which treatments alter owl habitat vary (no habitat alteration, weak habitat alteration, strong habitat alteration; see WebPanel 1). Trajectories represent means across 50,000 simulations. For full uncertainty across stochastic replicates, see WebFigure 4.

regional-scale patterns in trade-offs emerged (eg -0.11 to $+0.22$; Figure 4d). Broad-scale patterns in trade-offs were driven by regionally varying treatment effects to owl habitat estimated from occupancy data (WebTable 2) and spatial variation in future severe fire exposure (Figure 2).

Discussion

Our analysis indicates that climate change will result in increased severe fire extent in the Sierra Nevada through mid-century, but that bioregional-scale restoration has the potential to offset this increase. Restoration also appears to support spotted owl conservation, suggesting co-benefits between forest resilience and old-forest species conservation objectives. Owls experienced relatively large expected benefits from treatment in areas where treatments considerably reduced future severe fire (Figures 2 and 4). Conversely, areas where owls experienced net negative treatment effects (eg southern Sierra Nevada) were characterized by lower future exposure to severe fire, more pronounced direct treatment impacts on predicted territory extinction rates, or both (Figures 2 and 4; WebTable 2). When treatments occurred in owl territories but were

of treatment are less negative or are positive (Figure 4).

Landscape fuel treatments will never stop a fire but they can change how fires burn, thereby mediating fire-related tree mortality and resulting effects to species and ecosystems. Both model simulations (eg Collins *et al.* 2011; Tempel *et al.* 2015) and empirical studies (eg Safford *et al.* 2012; Tubbesing *et al.* 2019) have suggested landscape fuel treatments are effective in altering fire behavior and can greatly reduce severe fire activity in seasonally dry forests. In accordance with these findings, our results suggest that returning forest conditions to within the historical range of variability reduces expected high-severity burned area at a bioregional scale (Figure 2; WebFigure 2). Although this was an expectation for fuel-limited seasonally dry forest ecosystems, concern exists that fuels management may be inadequate to modify severe wildfire in a changing climate when extreme fire conditions become more common on an annual basis (Schoennagel *et al.* 2017). Indeed, we observed some degree of increase in severe fire activity under all treatment scenarios with climate warming (eg WebFigure 3). However, as more of the landscape was treated, expected future severe fire extent was reduced (Figure 2) even in years with extreme fire weather, an effect that was particularly notable when larger proportions of landscapes were treated (eg >40%; WebFigure 3). At high levels of treatment extent, expected increases in severe fire activity were completely offset by expected reductions in severe fire due to treatment in some areas (Figures 2 and 4), although real changes could be much larger or smaller because of prediction uncertainty (WebFigure 2). These results suggested that large-scale forest restoration efforts have the potential to meaningfully alter severe fire activity and reduce fire-related risk to spotted owls in a changing climate.

Although our model offers a robust starting point for forecasting wildfire and population dynamics across this large bioregion, we made simplifying assumptions to make our model tractable. We assumed stationarity in fire–climate relationships over the forward simulation period, which may become less likely further into the future (Parks *et al.* 2016; Littell *et al.* 2018). Vegetation (ie fuels) within our models were static, and treatments were introduced once at the beginning of forward simulations and assumed to be maintained when in reality treatments would take decades to implement and maintenance would be variable. As such, effects of treatments to owls via direct habitat alteration only occurred once, whereas maintenance of treated areas could result in recurring effects.

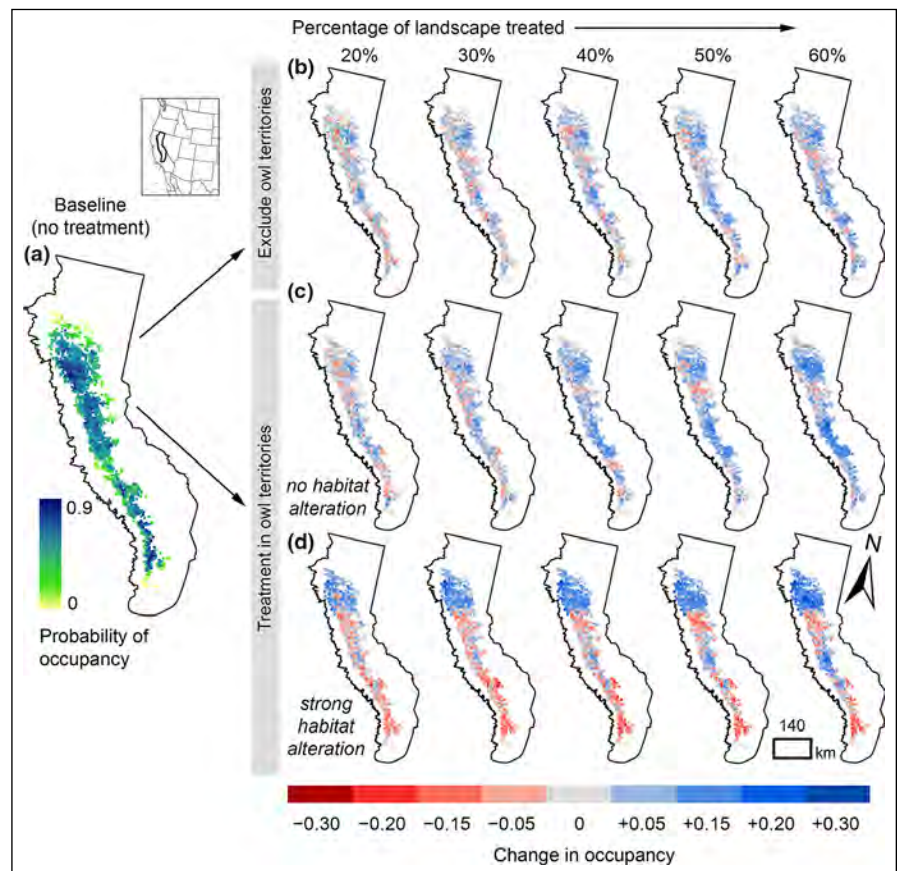


Figure 4. Spatial variation in effects of the location and extent of fuel treatments on spotted owl site occupancy by mid-century (2064). (a) Expected mid-century site occupancy under a no-treatment scenario; (b) difference in occupancy when treatments are implemented but are excluded from owl territories at varying levels of treatment extent (increasing from left to right); (c, d) difference in occupancy when treatment occurs within owl territories but assumptions about the extent to which treatments alter owl habitat vary (see WebFigure 4 for “weak habitat alteration”). Values represent the average across 50,000 simulations (WebPanel 1). The polygon outlined in black depicts the boundary of the Sierra Nevada bioregion. The rectangle in the bottom right is the scale bar, where the horizontal length is equivalent to 140 km. Note that the color ramp intervals for change in occupancy are not all equal.

We also assumed that treatment applications varying in their direct effects to owl habitat (eg Figure 3, b–d) would all be equally effective at altering fire behavior, which is unlikely; in addition, we only considered how the expected changes in forest structure resulting from treatment interacted with our models, not potential effects of the treatment method itself (eg prescribed burning, hand-removal of small trees, thinning and/or logging of medium-sized trees). Finally, treatments were simulated randomly across the landscape because the fine-scale spatial patterning would not influence our statistical fire model, but strategic placement in areas with high baseline fire risk can make treatments more effective at lower treatment extents in the real world (McGarigal *et al.* 2018; Tubbesing *et al.* 2019).

Forest restoration currently occurs below desired levels because of legal, administrative, and financial constraints (Collins *et al.* 2010; North *et al.* 2015a). Increasing the pace and

scale of restoration to levels that will alter fire activity at the bioregional scale (Figure 2) will require greater funding, more effective integration of silvicultural approaches with prescribed and managed fire to increase treatment extent at the landscape scale (North *et al.* 2012, 2021; York *et al.* 2021), and a recognition that while short-term costs may be high, they will be eclipsed by future costs under the status quo (North *et al.* 2015b). Over the past several decades, treatments have sometimes been implemented within portions of owl territories (~300–600 ha), but generally not within the “core” areas of the territory corresponding to management units called “protected activity centers” (PACs; ~121 ha). Our study treated the entire territory as the management unit (including the smaller PAC) and therefore we did not estimate potential effects of treatments at the PAC scale alone. Previous syntheses have recommended lower-intensity fuel treatments at the scale of the activity center (nest, roost) to reduce potential habitat-related negative effects to owls (Peery *et al.* 2017). Our results suggest that implementing treatments within owl territories could have an outsized effect on reducing future severe fire activity in the Sierra Nevada compared to treating the same area outside of owl territories (Figure 2).

Dry forest ecosystems, like those in the Sierra Nevada, face an increased probability of disturbance-initiated transition to non-forest landscapes without active management to restore ecologically appropriate forest conditions and reduce accumulated fuels (Stephens *et al.* 2020). Broadening forest restoration efforts in dry forests has the potential to enhance forest resilience and reduce risk of severe fire that negatively impacts forests, carbon storage, water supply, air quality, and local communities as the climate changes (Wood and Jones 2019; Stephens *et al.* 2020). As a complement to previous mechanistic work that examined forest restoration trade-offs at smaller spatial scales (Scheller *et al.* 2011; Tempel *et al.* 2015), our work suggests bioregional-scale forest restoration appears to be largely compatible with conservation of old-forest-dependent wildlife species.

Fire-suppressed forests that are well outside their historical range of variability are prone to severe fire and are also preferred by many forest-dependent wildlife species. Treatments within these forests are likely to reduce severe fire extent and therefore provide greater long-term benefits to species like the spotted owl. Treatments that increase landscape-scale heterogeneity are likely to provide shorter-term benefits as well by promoting habitat for key prey species (Hobart *et al.* 2019; Kramer *et al.* 2021). Additional targeted research that narrows uncertainties about the effects of different types of treatments (eg hand removal, pre-commercial thinning, prescribed fire) on species habitat will be needed to better inform planning. However, to minimize the effects of fuel reduction and forest restoration on spotted owls and other old-forest species, including the fisher (*Pekania pennanti*), northern goshawk (*Accipiter gentilis*), and American marten (*Martes americana*), it is essential that large, old trees and core nesting/roosting areas

within territories be maintained (Jones *et al.* 2018). When large, old trees are maintained and recruited, fuel reduction and forest restoration in the Sierra Nevada can benefit both old-forest species, forest ecosystem resilience, and people in a changing climate.

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■ Supporting Information

Additional, web-only material may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/fee.2450/supinfo>

Accelerated forest restoration may benefit spotted owls through landscape complementation

G. M. Jones¹ , C. K. Stanley² , M. Z. Peery³, C. Maxwell⁴ & K. N. Wilson² 

¹ USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM, USA

² The Nature Conservancy, San Francisco, CA, USA

³ Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI, USA

⁴ Institute for Natural Resources, Oregon State University, Corvallis, OR, USA

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Correspondence

Gavin M. Jones, USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM, USA.
Email: gavin.jones@usda.gov

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Abstract

Animals often rely on the presence of multiple, spatially segregated cover types to satisfy their ecological needs; the juxtaposition of these cover types is called landscape complementation. In ecosystems that have been homogenized because of human land use, such as fire-suppressed forests, management activities have the potential to increase the heterogeneity of cover types and, therefore, landscape complementation. We modeled changes to California spotted owl (*Strix occidentalis occidentalis*) nesting/roosting habitat, foraging habitat and habitat co-occurrence (i.e. landscape complementation) within a 971 245-ha forest landscape restoration project area, the Tahoe-Central Sierra Initiative (TCSI) landscape, through mid-century as a function of fuels reduction, fire and climate change. Compared to a minimal management scenario, accelerated management within the TCSI landscape was predicted to increase the number of potential 400-ha spotted owl territories containing a high degree of landscape complementation (defined as containing >20% nest/roost habitat and >20% foraging habitat) at lower elevations (<5000 ft.) by an average of 90 to 118 territories by 2050, depending on the climate scenario examined. At higher elevations (>5000 ft.), potential benefits of treatments to spotted owl nesting/roosting and foraging habitat were less evident, but accelerated management did not result in habitat loss. Our results suggest that accelerated fuels reduction and forest restoration treatments within this large landscape are expected to benefit spotted owls by improving the spatial juxtaposition of nesting/roosting and foraging cover types by 2050 compared to a minimal management scenario. Fuels reduction and forest restoration in this landscape thus can both increase the resilience of forest ecosystems to disturbances as well as benefit the habitat of a sensitive old-forest species.

Introduction

Species often require multiple non-substitutable, spatially segregated resources to satisfy their ecological needs. The linking of these resources through animal movement is called landscape complementation (Dunning et al., 1992). For example, Florida manatees (*Trichechus manatus latirostris*) use offshore seagrass beds for feeding but require inland warm-water thermal refugia for overwintering; the spatial juxtaposition of these habitats drives manatee movement ecology (Haase et al., 2017). Landscape complementation has important implications for understanding population ecology as well. In northern leopard frogs (*Rana pipens*), when models excluded the role of upland summer habitat (in addition to breeding season pond habitat), the true presence of a

metapopulation structure was masked (Pope, Fahrig, & Merriam, 2000). Thus, considering the role of landscape complementation is critically important for understanding the nature of population processes.

At the core of the concept of landscape complementation is the concept of landscape heterogeneity. Past and ongoing human land use has substantially reduced landscape heterogeneity in some systems (Schulte et al., 2007; Collins, Everett, & Stephens, 2011), with consequences for biological communities. Fire suppression in the Ozark Mountains, USA produced dense forest thickets between glades used by eastern collared lizards (*Crotaphytus collaris*), resulting in substantially reduced inter-glade movement and widespread local population extinctions (Templeton, Brazeal, & Neuwald, 2011). Landscape heterogeneity also has important implications for ecological

stability and resilience (Holling, 1973). Structurally simplified forests resulting from timber harvest and fire suppression can result in lower resilience and persistent ecological type conversion following wildfire (Hessburg *et al.*, 2019). In contrast, greater local forest structural variability leads to greater resilience to wildfire (Koontz *et al.*, 2020) and drought (Restaino *et al.*, 2019). Landscape heterogeneity, therefore, has important consequences for generating complementary resources for individual species as well as ensuring ecosystem resilience.

In western North America, past logging, fire suppression and other human activities have led to forest structural homogenization and reduced forest ecosystem resilience to disturbances (Coop *et al.*, 2020). Increasingly frequent megafires and drought-related tree mortality events have resulted in pervasive and rapid degradation and loss of conifer forests (Stephens *et al.*, 2020) and sensitive forest species habitat (Steel *et al.*, 2022). While fuels reduction and forest restoration activities at large scales could reduce fire-driven forest loss and increase whole system resilience (North *et al.*, 2021; Jones *et al.*, 2022), considerable apprehension exists among various stakeholders that forest restoration activities themselves could eliminate important habitat elements for species of conservation concern (e.g. spotted owls, *Strix occidentalis*; Jones *et al.*, 2016, 2021). Restoration activities that include removal of live trees through harvesting as well as prescribed and managed fire tend to create more abundant 'open' forest conditions not typically associated with high-quality habitat for old-forest dependent species. However, concerns over potential negative effects of forest restoration to old-forest species rarely recognize the importance of landscape complementarity for species persistence, and the degree to which forest restoration activities could generate heterogeneity and complementarity. More broadly, changes in landscape complementarity are rarely considered in habitat-based projections of how management might impact the future viability of species under changing climate.

Here, we used a forest simulation study to understand the potential effects of landscape-scale fuels reduction and forest restoration activities on promoting landscape complementarity for California spotted owls (*S. o. occidentalis*; hereafter 'spotted owls') in a changing climate (Fig. 1). Spotted owls are known for their dependence on old-growth forest conditions for nesting and roosting (Gutiérrez, Franklin, & Lahaye, 1995). However, spotted owls rely on early-seral and more open forest conditions, particularly at lower elevations, for hunting their preferred prey, dusky-footed woodrats (*Neotoma fuscipes*). When spotted owl home ranges contain sufficient juxtaposition of nest/roost habitat with hunting habitat, individual fitness and other vital rates have been shown to increase (Franklin *et al.*, 2000; Kuntze *et al.*, 2023; Zulla *et al.*, 2023), suggesting the importance of landscape complementation for spotted owl population persistence. Using LANDIS-II, a forest vegetation simulator, we evaluated the influence of fire, forest treatments and climate change from 2020 to 2050 on nesting/roosting habitat, foraging habitat and landscape complementation of these two habitat types in a 971 245-ha landscape restoration project area in the central Sierra Nevada, California, USA.



Figure 1 An adult California spotted owl (*Strix occidentalis occidentalis*). Photo by Rick Kuyper/USFWS.

Our primary objective was to understand whether forest heterogeneity generated by fuels reduction activities could be compatible with the conservation of spotted owls.

Materials and methods

Study area

The Tahoe-Central Sierra Initiative (TCSI) landscape is a 971 245-ha area in the central Sierra Nevada where state, federal, nonprofit and private institutions are partnering to increase the pace and scale of forest restoration and improve ecological and social resilience to wildfire (<https://www.tahoecentralsierra.org/>). Elevations in the TCSI landscape range from ~600 m on the west slope in the foothills of California to ~2700 m at the crest of the Sierra Nevada. The TCSI boundary follows watershed HUC-8 level boundaries to the north and south. The eastern boundary follows the Lake Tahoe Basin watershed and the California-Nevada state line for the Truckee River watershed. The western boundary is roughly uphill of the blue-oak foothill pine and blue-oak woodland vegetation types. TCSI includes portions of four National Forests (Plumas, Tahoe, Eldorado and Humboldt-Toiyabe National Forests) covering 70% of the area, private industrial and non-industrial forest land (15%), and other private land and water bodies (15%).

LANDIS-II model and calibration

To model change in owl habitat under climate change, wildfire and two forest management scenarios, we used the LANDIS-II model (Scheller *et al.*, 2007) with the NECN (v. 6.9) and the SCRPPLE extension (v.3.2.2) (Scheller *et al.*, 2019) following the methods of Maxwell *et al.* (2022). The model simulates forest succession and disturbance of species-age cohorts with multiple cohorts existing in a single cell (180×180 m or 3.24 ha), with the model being flexible in regard to spatial and temporal resolution. In order to run LANDIS, the model requires initial vegetation conditions, information about the species being modeled, spatial information about fires, rates of management and a ruleset for its application and daily weather data (including precipitation, temperature, humidity and wind). The outputs from the model include spatial projections of future vegetation conditions, wildfires and management activities. The NECN extension uses the CENTURY model to track above- and belowground carbon and nitrogen pools and fluxes (Scheller *et al.*, 2011). The SCRPPLE extension simulates both wildfire and prescribed fires across the landscape, with the fire effects determined at the species-age-cohort level by cell which drives changes within the carbon and nitrogen pools. We ran the model from 2020 to 2050 with ten replicates of two climate projections and two management scenarios to capture stochastic variation in wildfire and management. We did not examine potential effects of insect outbreaks and resulting patterns of tree mortality on spotted owls because little is understood about the effects of insect outbreaks on spotted owl habitat suitability.

The initial forest conditions that were entered into the LANDIS-II model were assembled by Natural Capital Exchange (NCX) and were based on the imputation of USDA Forest Service Forest Inventory and Analysis (FIA) plots across the study area using random forest methods involving biophysical variables and represented forest conditions of 2019 (Maxwell *et al.*, 2022). Initial live aboveground biomass stocks for the study area were $218 \text{ Mg ha}^{-1} \pm 91 \text{ Mg ha}^{-1}$, which are comparable against a similar FIA imputed model TREEMAP (mean $185 \pm 159 \text{ Mg ha}^{-1}$). Forest growth and mortality within the model was calibrated against the MODIS 17A3 annual Net Primary Productivity (NPP) product (with modeled NPP of $532 \pm 149 \text{ g C m}^{-2}$ and observed NPP of $506 \pm 145 \text{ g C m}^{-2}$) and the measured annual Net Ecosystem Exchange (NEE) value from the Sagehen Field Station, (with modeled $-60 \pm 140 \text{ g C m}^{-2}$ compared to observed $-66 \pm 72 \text{ g C m}^{-2}$). Fire size and severity were based on the Monitoring Trends in Burn Severity (MTBS) dataset (Eidenshink *et al.*, 2007). The model was calibrated by running the initial conditions using the 2010 climate data (see below) through 2020 to approximate the empirical fire size and severity found in the MTBS dataset.

Climate change

We simulated two climate projections: one based on recent climate conditions from 2010 to 2020 taken from GridMET that

were randomly resampled by year and one based on the multivariate adaptive constructed analogs downscaling of the MIROC5 model using uncontrolled emissions (relative concentration pathway 8.5) available online through USGS Geo Data Portal (<https://cida.usgs.gov/gdp>) (Abatzoglou & Brown, 2012). The climate data were spread across the landscape from their native 6-km grid to larger regions based on elevational gradients. We selected the 2010–2020 period because annual area burned during this period was higher than any other period in recorded history and included the 2014 King Fire, a large fire (39 545 ha) with the largest proportion of high-severity fire (58%) in the MTBS records for this study area. We selected the MIROC5 projections because it was the only climate projection that recreated recent droughts out of the five recommended by the state (Pierce, Kalansky, & Cayan, 2018; Maxwell *et al.*, 2022). We adjusted the calculation of the fire weather index based on expert recommendation specific to CMIP5 and the Sierra Nevada (D. Swain, pers. comm.). Specifically, instead of mean values for all the inputs, we used daily maximum temperature, daily minimum relative humidity and daily average wind speed multiplied by 1.5 to approximate the windiest few hours of each day (Goss *et al.*, 2020).

Wildfire

In the Social-Climate-Fire extension of the LANDIS-II model, wildfire is a function of climate, primarily mediated through the calculated daily Canadian fire weather index values and wind speed, human and/or lightning ignitions, fuels and topography (Scheller *et al.*, 2019). Simulating wildfires is a two-part process and involves calculating where and when a wildfire might start. This required deriving a probability surface for human caused and lightning caused ignitions, which were calculated from historical wildfire ignition data using a kernel density function (Short, 2022). From that surface, fires were allocated based on historical seasonality, with fire size and spread calibrated to the 2010–2021 period and including any past wildfires that intersected the TCSI boundary using fire data from MTBS and California Department of Fire Resource Assessment Program. Total area burned per decade was on average 150 675 ha for the calibration period, compared to 105 797 to 351 240 ha for the 2010–2020 LANDIS-II projection. The largest individual fire in the calibration period was the 2021 Caldor Fire at 89 773 ha, versus a 93 795-ha simulated fire under the 2010–2020 climate projection. The percent high-severity fire ranged from 7 to 73% in the historical period and was 3–96% in the 2010–2020 projection. The greatest proportion of high severity in an exceptionally large (Cova *et al.*, 2023) >40 000 ha fire (King Fire) in the calibration period was 58% and for a similar sized fire (50 000 ha) in the 2010–2020 climate projection it was 80%. A higher proportion of high severity in extremely large fires is reflective of recent 1985–2020 burn trends (Cova *et al.*, 2023).

Forest management scenarios

We identified two forest management scenarios that represented the bookends on a range of possible management

futures from a ‘minimal management’ scenario to an ‘accelerated management’ scenario. The scenarios were designed to bracket the management-as-usual treatment rate from 2010 to 2019 (4348–11 786 ha per year) based on the U.S. Forest Service FACTS database and CalFire private lands database. We divided the TCSI area into seven management zones, five target disturbance return intervals and two slope classes to make forest treatments spatially explicit. The disturbance return interval, time between a wildfire or a treatment, was a range of years based on the mean historical fire return interval (van Wageningen *et al.*, 2018) for different climate zones (Jeronimo *et al.*, 2019). Both management scenarios included fire suppression that matched recent efforts based on fire manager input.

Under the minimal management scenario, timber harvest occurred on private industrial lands every 25 years, private non-industrial lands every 40 years, and on lands in the wildland urban interface (WUI) Defense zone, 402 m from development, based on a target disturbance return interval. Under the accelerated management scenario, forest treatments

expanded beyond the private timber land and WUI Defense to the WUI Threat zone (2102 m from development), general forest and roadless areas. Treatments were triggered based on a minimum target disturbance return interval and a minimum biomass threshold (Maxwell *et al.*, 2022). In the accelerated management scenario (Table 1), treatments matched the historical frequency of fire (20–40-year intervals). Treatments included clear cuts, mechanical thinning and hand thinning. It was assumed that thinning in the general forest and WUI threat zone would include prescribed fire underburn treatment following thinning to reduce surface fuels and increase forest resilience to subsequent wildfires (Prichard *et al.*, 2020). Mechanical thinning followed by prescribed burning in our simulations reduced downed woody debris by 90% and soil organic material by 55%. Treatment prescriptions and fuels reduction percentages were based on expert opinion from forest fire specialists (Table 2). In either scenario, management-induced changes to forest structure were designed to produce conditions that were more resilient and resistant to wildfire (e.g. reduced fire-driven tree mortality)

Table 1 Distribution of simulated treatment prescriptions in the accelerated management scenario

Slopes <30%	Clear cut	Mechanical thin, young stand	Mechanical thin, mature stand	Hand thin
Private non-industrial	–	–	100%*	–
Private industrial	100%*	–	–	–
Defense zone	–	–	100%*	–
Threat zone	–	40%	60%	–
General forest	–	30%	70%	–
Roadless area	–	–	–	100%
Slopes >30%	Clear cut	Mechanical thin, young stand	Mechanical thin, mature stand	Hand thin
Private non-industrial	–	100%*	–	–
Private industrial	–	100%*	–	–
Defense	–	100%*	–	–
Threat	–	–	–	100%
General forest	–	–	–	100%
Roadless	–	–	–	100%

Values marked with an asterisk (*) are those that were implemented under the minimal management scenario. Defense zone = within 400 m of an urban area; Threat zone = between 400 m and 2000 m of an urban area; General forest = non-restricted publicly owned forest 2000 m from an urban area; Roadless area = restricted publicly owned forest.

Table 2 Treatment prescriptions based on species-age ranges

Common name	Scientific name	Clear cut	Mechanical thin, young stand	Mechanical thin, mature stand	Hand thin
White fir	<i>Abies concolor</i>	All	All	All	1–70
Red fir	<i>Abies magnifica</i>	All	All	All	1–71
Jeffrey pine	<i>Pinus jeffreyi</i>	All	1–68	1–140	1–68
Sugar pine	<i>Pinus lambertiana</i>	All	1–57	1–125	1–64
Lodgepole pine	<i>Pinus contorta</i>	All	1–68	1–200	1–88
Western white pine	<i>Pinus monticola</i>	All	1–81	1–200	1–88
Whitebark pine	<i>Pinus albicaulis</i>	All	1–79	1–200	1–87
Ponderosa pine	<i>Pinus ponderosa</i>	All	1–59	1–125	1–68
Washoe pine	<i>Pinus washoensis</i>	All	1–59	1–125	1–60
Douglas fir	<i>Pseudotsuga menziesii</i>	All	All	All	1–56
Incense cedar	<i>Calocedrus decurrens</i>	All	All	All	1–78
Mountain hemlock	<i>Tsuga mertensiana</i>	All	All	All	1–71
California foothill pine	<i>Pinus sabiniana</i>	All	1–50	1–125	1–64

and more representative of historical forest structure compared to present day conditions.

Summarizing vegetation change

We summarized changes in forest and shrub habitat using the California Wildlife Habitat Relationships (CWHR) classification scheme for habitat types. Habitat is based on dominant vegetation type, size measured as the mean diameter at breast height of the predominant trees and canopy cover. We translated species-age-biomass outputs from the LANDIS-II model into CWHR habitat types following recent work (White *et al.*, 2022; Zeller *et al.*, 2023) with a modification to allow for large tree sizes and 0–10% canopy cover. This modification allowed for cells to contain large trees post-fire with very low canopy cover and for larger trees not found in the reference condition.

We classified trees into 5 size classes: seedlings (size class 1: <2.5 cm), sapling (size class 2: 2.5–15 cm), pole trees (size class 3: 15–28 cm), small trees (size class 4: 28–61 cm) and medium/large trees (size class 5: >61 cm). Canopy cover was classified into 5 classes: limited cover (L: 0–10%), sparse cover (S: 10–25%), open cover (P: 25–40%), moderate cover (M: 40–60%) and dense cover (D: >60%). Our classification differs from CWHR habitat types by including the limited cover class, which we did intentionally to capture burned areas with low canopy cover and a few remaining large trees.

Owl habitat summaries

We used classifications of the CWHR database (<https://wildlife.ca.gov/data/cwhr>) to develop vegetation types that are associated with owl habitat to track during LANDIS-II simulations (Table 3). Specifically, we considered all forests falling into 5D, 5M and 5P CWHR classifications to be features associated with California spotted owl nest/roost habitat. We note that CWHR class 5P is typically not considered to be suitable nesting/roosting habitat for California spotted owls; for example, it is not included as suitable in the 2019 California Spotted Owl Conservation Strategy (USDA, 2019).

Table 3 Description of California Wildlife Habitat Relationships (CWHR) classes that were used to track nesting/roosting and foraging habitat during the Landis-II simulations

Habitat type	CWHR classification code	Tree size	Canopy closure
Nesting/ roosting	5P	>24" DBH	25–40%
	5M	>24" DBH	40–60%
	5D	>24" DBH	>60%
Foraging	2P, 3P	<11" DBH	25–40%
	2M, 3M	<11" DBH	40–60%
	2D, 3D	<11" DBH	>60%
	4P	11–24" DBH	25–40%
	1S, 2S, 3S, 4S, 5S	Any DBH	<25%

DBH, diameter at breast height.

However, we view 5P as having a strong potential to serve as nesting/roosting habitat, since it contains large-diameter trees, which are believed to be the primary factor limiting spotted owl populations (Ganey *et al.*, 2017). We think one reason very few contemporary spotted owl nests/roost are found in this vegetation type is simply because it is extremely rare on the landscape, but we predict that owls could use it as it becomes more available in the future. We further considered all mixed chaparral, forests with smaller diameter trees (<11" dbh) with >25% canopy cover, forests with intermediate-sized trees (11–24" dbh) with 25–40% canopy cover, and all forests with <25% canopy cover to represent features associated with California spotted owl foraging habitat, particularly at lower elevations (see below) (Sakai & Noon, 1997; Innes *et al.*, 2007; Kuntze *et al.*, 2023). We tracked these two habitat types (nest/roost and foraging) over the simulation period. We also tracked the co-occurrence of these two habitat types, given that co-occurring nest/roost and foraging habitat are needed to satisfy multiple resource needs of owls.

We reported the area of each habitat type and the extent of co-occurrence across 1857 territory-sized summary units (400 ha) to reflect spotted owl biological needs. Specifically, we tallied the number of 400 ha hexagons (the approximate size of a spotted owl territory; Tempel *et al.*, 2014) that contained at least 20% spotted owl nest/roost habitat, 20% foraging habitat and 20% of both (i.e. 20% of each nest/roost and foraging habitat). We used 20% as a target because previous work has suggested that local territory extinction rates decline substantially when ~20% of the territory contains large, old trees (Jones *et al.*, 2018). We performed a sensitivity analysis to explore robustness of results to threshold selection, examining 5, 10, 15, 20, 30 and 40% as alternative thresholds, but we found to qualitative differences in inferences, so we proceeded with our literature-informed 20% threshold. We further divided summaries of spotted owl habitat into two elevational bins: >5000 ft (1000 hexagons) and <5000 ft (738 hexagons). In the lower elevational zone (<5000 ft.), a mosaic of younger and mature forest has been demonstrated to increase woodrat capture rates and the biomass of prey delivered by spotted owls to their nests (Zulla *et al.*, 2022, 2023; Kuntze *et al.*, 2023). By contrast, at higher elevations (>5000 ft.), mature forest-associated flying squirrels are the dominant prey item (Waters & Zabel, 1995; Kramer *et al.*, 2021) and tend to be captured by spotted owls in areas with large trees (Zulla *et al.*, 2022). Thus, we specifically tracked woodrat foraging habitat at lower elevations and assumed that flying squirrel habitat was consistent with spotted owl nest/roost features at higher elevations.

Finally, we summarized changes in spotted owl habitat in relation to the minimal management scenario. Specifically, we present habitat projections as changes in number of spotted owl territories resulting from accelerated management, relative to the minimal management scenario. This permits clearer visualization of the relative effects of the management alternative and can also lead to more robust interpretations than when using absolute effects in simulations (e.g. in population viability analyses; Beissinger & Westphal, 1998).

Results

The area treated in the accelerated management scenario was greatest in the first decade and decreased slightly over the next 20 years (Fig. 2). The cumulative area treated under the accelerated management scenario (~370 000 ha) was ~12 times higher than the minimal management scenario (~30 500 ha) (Figs 2 and 3). Compared to the minimal management scenario, total fire area was lower on average under accelerated management, but this result was dependent on climate scenario and time period under consideration.

That is, simulations using the 2010–2020 climate scenario generally showed decreases in area burned compared to the minimal management scenario across all time periods, but the MIROC climate tended to show increased area burned relative to the minimal management scenario, except for in earlier decades at high elevations (Fig. 2). Projected high-severity fire showed similar idiosyncrasies. At higher elevations, accelerated management appeared to reduce projected high-severity burned area relative to the minimal management scenario, although we observed a high degree of prediction uncertainty. At lower elevations, we observed a

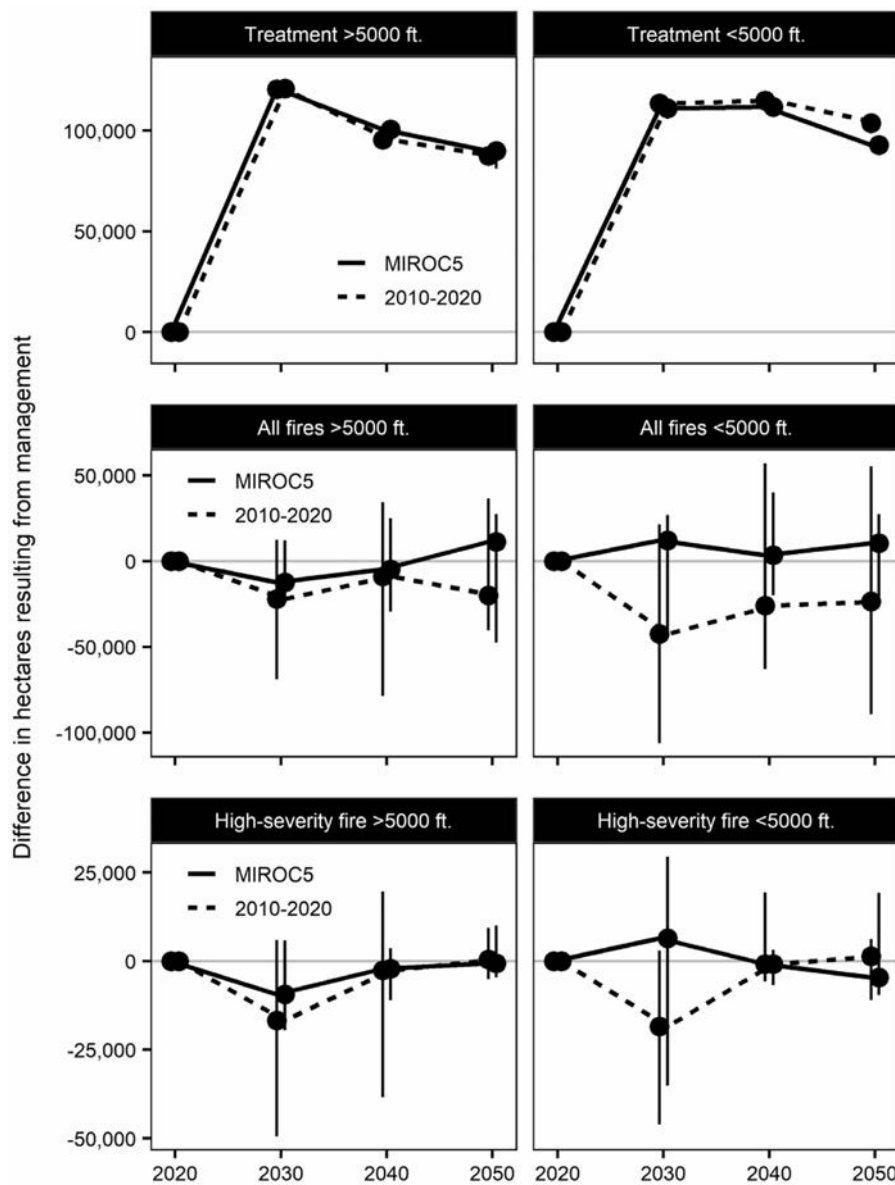


Figure 2 Predictions of future treatments (top row), fire area (middle row) and high-severity fire area (bottom row) relative to the minimal management scenario (gray horizontal line). Lines represent the difference between accelerated management and minimal management scenarios. Vertical error bars indicate the 80% prediction interval based on 10 LANDIS-II replicates, and circles represent the median value across replicates.

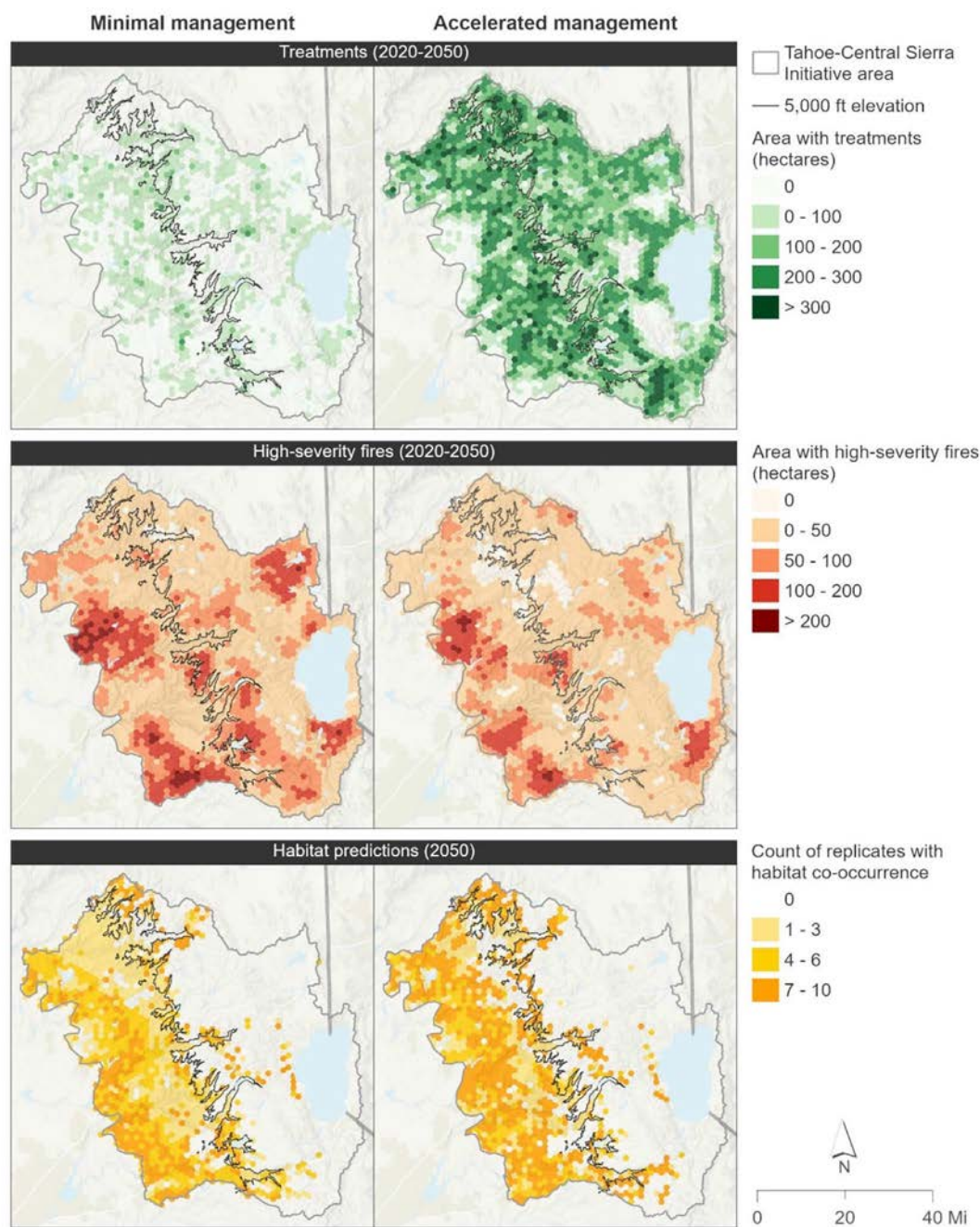


Figure 3 Spatial predictions of treatments (top row), high-severity fire extent (middle row) and landscape complementarity (bottom row) over our simulation period 2020–2050 under the minimal management scenario (left column) and the accelerated management scenario (right column). In the first and second rows, the mean area (of treatments and high-severity fire, respectively) in hectares is shown in each hexagon across 10 LANDIS-II replicates. In the bottom row, the number of LANDIS-II replicates (maximum of 10) showing landscape complementarity within a given hexagon is shown.

similar trend, except for an apparent increase in high-severity fire in the second simulation decade under the MIROC climate scenario (Fig. 2). The cumulative area burned by wild-fire was 2–3 times greater on average in the MIROC5 projection than the 2010–2020 projection while the area of high-severity fire was similar. In general, the lower amount

of high-severity fire in the first decade of the simulation corresponded with increased treatment during that same decade (Fig. 2) and resulted in considerably less cumulative high-severity burned area over the modeling period (Fig. 3). Yet, because of the wide prediction intervals across the LANDIS-II replicates, differences in high-severity fire and

fire at any severity due to treatment were not clearly distinguishable from the minimal management scenario.

In general, treatments across the TCSI landscape resulted in modest to no changes to spotted owl nest/roost habitat conditions at both high and low elevations relative to a minimal management scenario (Fig. 4). Through 2040, treatments resulted in no measurable changes to nest/roost habitat, but modest negative effects emerged by 2050 (median of ~16 potential territories lost) at higher elevations under one climate scenario (Fig. 4, top left). At lower elevations, there was more variation in predicted gains and losses through time, but by 2040 and 2050 the average prediction showed declines in nest/roost habitat (~10 to 34 potential territories lost) (Fig. 4, top right). However, considerable variation across LANDIS-II replicates indicates that potential gains or longer-term losses were not statistically distinguishable from the minimal management scenario; outcomes in the 80% prediction interval ranged from a gain of 56 territories to a loss of 86 territories by 2050. These results remained relatively consistent across both climate scenarios examined.

At lower elevations, treatment across the TCSI landscape resulted in rapid and large increases in the amount of potential woodrat habitat in spotted owl territories. By 2050, the number of spotted owl territories containing at least 20%

woodrat habitat increased by a median of 108 and 146 (depending on the climate scenario used) compared to the minimal management scenario. Across LANDIS-II replicates, these increases were statistically distinguishable from a null result of zero difference in one of two climate scenarios (Fig. 4, bottom left).

At lower elevations, treatment increased the extent of co-occurrence of nest/roost conditions with woodrat habitat within potential spotted owl territories; that is, increased landscape complementation. By 2030, these increases were modest or close to zero (with the 80% prediction interval ranging from a gain of 18 territories to a loss of 12 territories), but thereafter the number increased through 2050. By 2050, we predicted an average increase of 90 to 118 spotted owl territories containing 20% of both nest/roost and woodrat habitat, depending on the climate scenario (Fig. 4, bottom right). Moreover, these differences were statistically distinguishable from the minimal management scenario based on the prediction intervals of LANDIS-II replicates.

Discussion

Results from our analysis suggest a broad compatibility between forest restoration objectives and spotted owl habitat

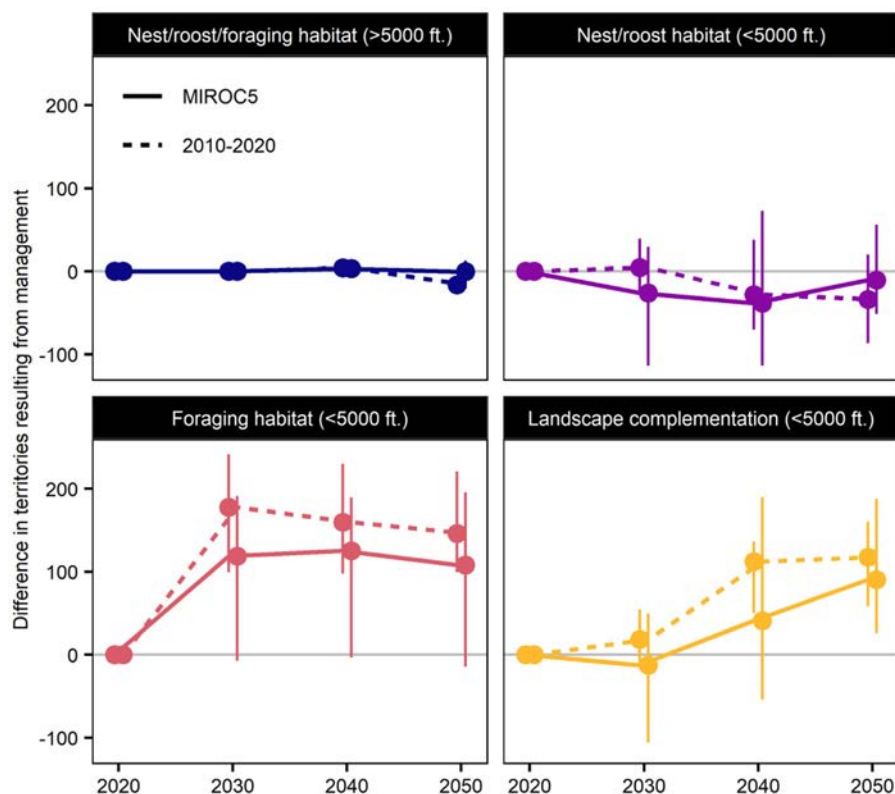


Figure 4 Predictions of spotted owl nest/roost habitat at high (upper left) and low (upper right) elevations; predictions of woodrat habitat at lower elevations (lower left); and predictions of the co-occurrence of nest/roost habitat and woodrat habitat at lower elevations (lower right) on the TCSI landscape. Units are the number of potential spotted owl territories (~400 ha hexagons) containing at least 20% of the noted cover type compared to the minimal management scenario. Vertical error bars indicate the 80% prediction interval based on 10 LANDIS-II replicates, and circles represent the median value across replicates.

conservation in the Sierra Nevada. Most importantly, our habitat projections showed (1) relatively large increases in woodrat habitat (brushy habitat, early-seral conditions and open forests) at lower elevations and (2) increased co-occurrence of spotted owl nest/roost habitat with woodrat habitat at lower elevations compared to the minimal management scenario. This increased co-occurrence of nest/roost habitat with foraging habitat at lower elevations is expected to provide net benefits to spotted owls, suggesting that accelerated management that includes thinning followed by under-burning could benefit spotted owl populations within the TCSI landscape.

One reason we focused on summarizing the co-occurrence of nest/roost habitat with woodrat habitat at lower elevations is that recent research has emphasized that this juxtaposition (i.e. landscape complementation) is important in habitat selection, behavioral ecology, movement, occupancy and fitness of spotted owls in the Sierra Nevada. For example, the mixture of older and younger forest types within a spotted owl territory (Fig. 5) increases the likelihood of capturing woodrats (Wilkinson *et al.*, 2022; Zulla *et al.*, 2022), increases the dietary proportion of woodrats (Hobart *et al.*, 2019), results in higher rates of biomass delivery to nestlings (Wilkinson *et al.*, 2022; Zulla *et al.*, 2023) and yields higher reproductive output (Wilkinson *et al.*, 2022; Zulla *et al.*, 2023). Higher consumption rates of woodrats, driven by vegetation heterogeneity, has been shown to reduce territory extinction rates and promote population stability (Hobart *et al.*, 2019). Other species of management concern inhabiting the Sierra Nevada have shown similar proclivity to landscape complementation, suggesting a broader applicability of our results for conservation. For example, the black-backed woodpecker (*Picoides arcticus*), a species emblematic of post-fire specialization, has recently been shown to be more dependent on burned/unburned forest interfaces than previously thought (e.g. Hutto, 2008). The landscape complementation of recently burned forests with adjacent unburned ('green') forests provides access to both critical nesting habitat (burned forest) as well as refugia for juvenile woodpeckers once they fledge the nest (green forests) (Stillman *et al.*, 2019, 2021).

While the black-backed woodpecker has often been considered an early-seral specialist, spotted owls are often considered to be an old-forest dependent species (Jones *et al.*, 2018). Yet the existence of landscape complementarity (Dunning *et al.*, 1992) may be more important than extensive tracts of mature forest at lower and mid elevations for spotted owls. For example, woodrat abundance was ~2.5 times greater in spotted owl territories with a mixture of vegetation types compared to territories with extensive mature forest, and this increased abundance translated into greater rates of woodrat consumption (and overall biomass consumption; 30% higher) by spotted owls (Kuntze *et al.*, 2023). The idea that heterogeneity in forest cover could benefit individual spotted owl fitness and population growth rates is not new (Franklin *et al.*, 2000), but we are now uncovering one of the key mechanisms for its benefits; landscape complementation. The spatial configuration and patch sizes of foraging habitat are likely

important, but we did not explore those factors here. Previous work has shown that in post-fire landscapes, spotted owls preferred to hunt in smaller patches (< 10 ha) of severely burned forest, which simultaneously provide relatively complete access to forest openings as well as abundant perches to use while searching for prey (Jones *et al.*, 2020). When fuels reduction and forest restoration activities can mimic these smaller patches of early-seral forest openings through either mechanical thinning or mechanical thinning followed by prescribed fire treatments (Fig. 5), we predict that spotted owls will similarly prefer these over larger, homogenous patches of early-seral and open forest conditions.

One potentially counterintuitive result worthy of further exploration is the fact that accelerated management appeared to result in an increased abundance of woodrat habitat in our LANDIS-II simulations (Fig. 4). At least initially, thinning, mastication and prescribed fire would be expected to reduce the abundance of 'brushy' conditions typically associated with woodrats (Collins, Moghaddas, & Stephens, 2007). While shrub abundance has been shown to initially decrease in dry and moist mixed-conifer forests following mechanical treatments, it can increase thereafter, sometimes exceeding initial levels 8-years post-treatment (Vaillant *et al.*, 2015). This could partly explain increased woodrat habitat in our simulations. However, in addition to brushy chaparral conditions, our definition of potential woodrat habitat included sparsely treed forests (those with <25% canopy cover even of larger size classes) and early-seral forests made up of smaller tree size classes and higher canopy cover that woodrats are known to occupy (Sakai & Noon, 1997; Innes *et al.*, 2007; Kuntze *et al.*, 2023). These conditions may be entirely expected to increase in abundance under accelerated fuels reduction scenarios, as the contemporary landscape-scale homogenous dominance of mid-seral conditions gives way to an increase in distributed gaps and openings and lower-density forest conditions produced by mechanical thinning, and as prescribed and managed fire periodically reset local forest succession (Hessburg *et al.*, 2021). Given that treatment area was the main distinguishing feature between the minimal and accelerated management scenarios (Fig. 2), fuels reduction and forest restoration treatments appear to have played an important role in creating and maintaining a landscape-scale shifting mosaic of woodrat habitat over our simulation period.

Yet, it is widely held that the primary factor limiting spotted owl populations is the availability of high-quality nesting habitat (Ganey *et al.*, 2017; Peery *et al.*, 2017). That is, forests dominated by very large, old trees, structural decadence and multi-layered canopies (Gutiérrez, Franklin, & Lahaye, 1995; Jones *et al.*, 2018). As such, it might appear concerning that our simulations indicated that accelerated management would have essentially no effect on recruiting this critical nest/roost habitat across all elevations compared to the minimal management scenario (Fig. 4). However, in absolute terms, our simulation showed a substantial increase in forests that spotted owls use for nesting and roosting (CWHR classes 5D, 5M and 5P). From 2020 to 2050, the abundance of 5D (>24" dbh trees, >60% canopy cover), 5M

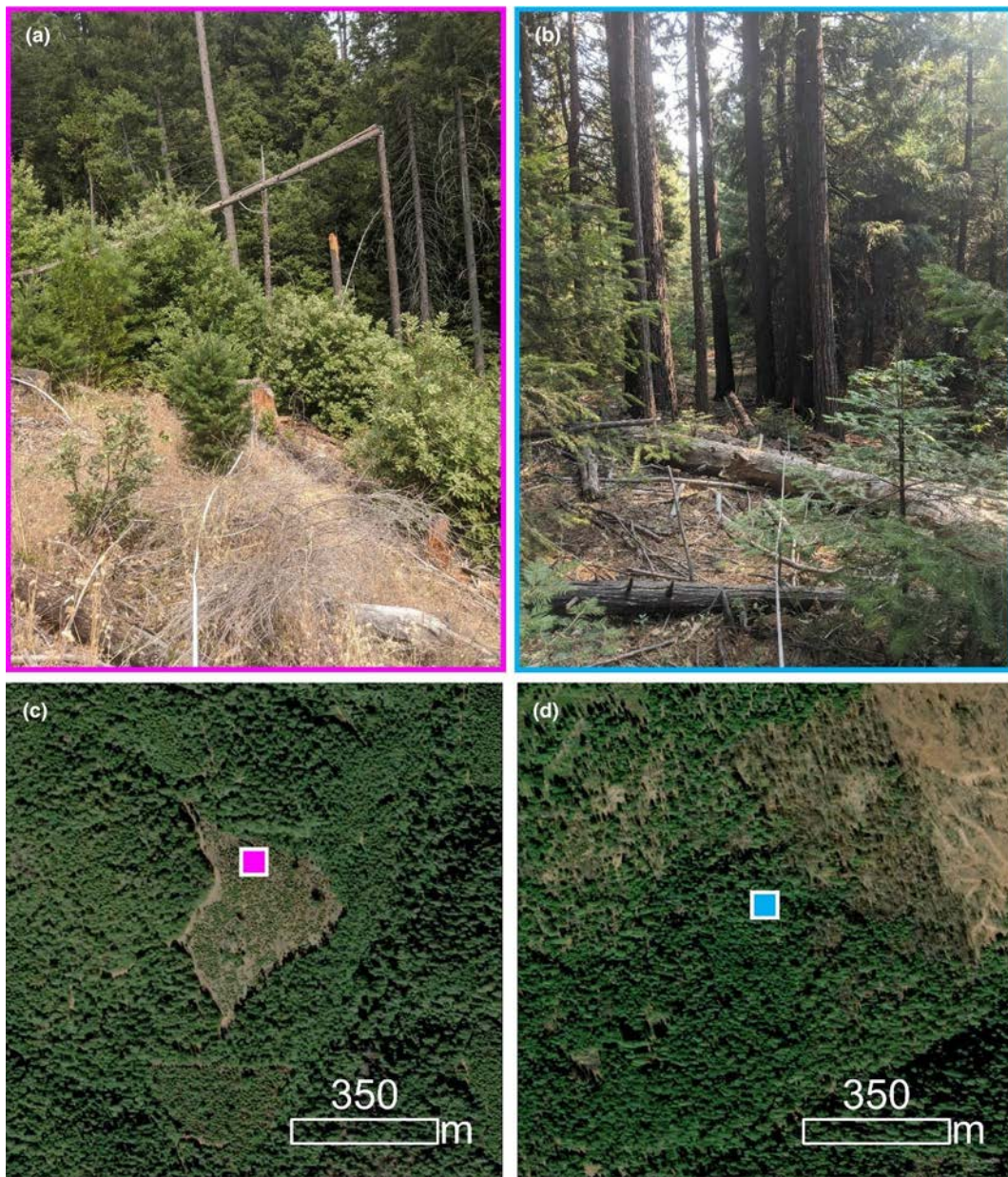


Figure 5 Examples of landscape complementation at an (a) intermediate patch scale and (b) micro-site scale on the Eldorado National Forest, California. Both photos show the juxtaposition of open, early-seral or brushy conditions that tend to be associated with woodrat habitat in the foreground, and later-seral, closed-canopy habitat in the background. Moreover, woodrats were captured at both sites in a different study (Kuntze *et al.*, 2023). The photo in (a) was taken at the location indicated by the pink square in (c), which occurred in a 10-hectare commercially harvested unit that had been recently replanted. The photo in (b) was taken at the blue square located in (d), which was a small forest gap (several meters wide) surrounded by continuous forest cover, but within ~150 m of more open forest conditions. Photo credits for (a) and (b): Corbin Kuntze, used with permission. Images in (c) and (d) obtained from National Agriculture Imagery Program.

(>24" dbh trees, 40–60% canopy cover) and 5P (>24" dbh trees, 25–40% canopy cover) increased by an average of nearly 243 000 ha in the minimal management scenario and nearly 222 000 ha in the accelerated management scenario. Thus, in both the minimal and accelerated management scenarios, many more large trees were simulated to occur in our study region by 2050, and this increase appears to be more

driven by intrinsic forest recruitment processes and climate than management. Given the very high abundance of trees in intermediate size classes (11–24" dbh) at the start of our simulation period (636 698 ha), it is unsurprising that so many trees in this class recruited into the larger size class (>24" dbh) by 2050. Encouragingly, from the perspective of meeting forest restoration goals, it appears that even under

an accelerated management scenario that specifically targets removal of trees in this intermediate size class, the very high initial abundance of intermediate-sized trees means that the overall recruitment into a larger size class was almost entirely unaffected (Fig. 4).

Concluding remarks

Our work demonstrates the importance of considering landscape complementation in habitat modeling efforts. Had we simply considered the changing abundance of typical nest/roost habitat and not the spatial juxtaposition of nest/roost habitat with foraging habitat, we may have concluded that the accelerated management scenario offered no benefits, or even net costs, to spotted owls. In contrast, our results suggest that on our study landscape, accelerated implementation of fuels reduction and forest restoration treatments could benefit spotted owl populations by generating landscape complementation (the co-occurrence of nest/roost with foraging habitat) within territories, particularly at lower elevations. This result is consistent with emerging science suggesting the benefits of landscape heterogeneity to owls, from individual to population scales. There is an increasing recognition that animal movements that produce landscape complementation represent a critical population process, mediating animal responses to rapid landscape changes (Nimmo *et al.*, 2019). Our work provides a simple and generalizable approach for modeling landscape complementation to understand the influence of management interventions on rare or threatened species.

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Author contributions

All authors conceived of the ideas, designed the methodology and participated in numerous discussions about project ideas; CM developed and executed the forest simulations; KNW and CKS summarized and interpreted forest simulation output; GMJ and MZP developed interpretations of the forest simulation model in light of spotted owl ecology; GMJ wrote the first draft of the manuscript and developed most of the data visualizations; CKS developed and produced the maps; all authors contributed to manuscript revisions.

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REPLY

Spotted Owls and forest fire: Reply

DEREK E. LEE †

In response to US Fish and Wildlife Service and USDA Forest Service planning documents that emphasized fire as a primary threat to spotted owl (*Strix occidentalis*) population persistence (e.g., USFWS 2017, USDA 2018), I performed a detailed multifaceted meta-analysis of all published studies of spotted owls and forest fire (Lee 2018). I found significant positive effects on foraging habitat selection and recruitment from mixed-severity forest fires, and significant positive effects on reproduction from high-severity fire. My meta-analysis examined key life history parameters in response to fires as they have burned through spotted owl habitat in recent decades under existing forest structural, fire regime, and climate conditions, including multiple “megafires” with large patches of high-severity burn. The absence of any widespread, consistent, and significant negative fire-induced effects and the presence of significant positive effects indicated forest fire is not a serious threat to owl populations. Therefore, fuel-reduction treatments intended to mitigate fire severity in spotted owl habitat are unnecessary and perhaps counterproductive to the species’ recovery. Planning documents claiming that forest fires currently, or will in future, pose the greatest risk to owl habitat and are a primary threat to population viability are either outdated or highly speculative in light of the Lee (2018) review.

Jones et al. (2020; hereafter Jones et al.) agreed with my most important assumptions, findings,

and conclusions from Lee (2018), namely: my characterization of western US forests inhabited by spotted owls as generally burning in mixed-severity fires where 5–70% of burned area is in high-severity patches with >75% mortality of dominant vegetation; that spotted owl responses to recent mixed-severity fires are variable; that severe fire has not resulted in substantial declines in spotted owl populations; and that fire has not been an overriding driver of recently observed long-term spotted owl population declines. Even though Jones et al. agreed with me that severe fire has not resulted in range-wide spotted owl population declines, and that fire has not been an overriding driver of recently observed long-term spotted owl population declines, Jones et al. questioned the results of my meta-analyses that illustrated why declines are not linked to fire.

The aim of Lee (2018) was to provide forest managers and decision-makers with a clear and concise summary of all evidence for mixed-severity fire effects on spotted owls in order to better inform forest management. Forest Service planning documents assume (paraphrasing): fire can harm owls and therefore owl territories and other owl habitat must be logged to protect owls from fire (e.g., USDA 2019). Jones et al. (2016), a reference often used to justify logging (e.g., USDA 2019), represent 1 fire, 30 burned territories, and 9 radio-tracked owls. Lee (2018) presented management guidelines based on a quantification of all available evidence including more than 20 fires, 425 burned territories, and 37 radio-tracked owls. The much larger dataset in Lee (2018) found mixed-severity fire, including several megafires with large high-severity patches, has mostly neutral effects, but also provides significant benefits to spotted owls.

The strength of meta-analysis as an evidence-based decision support tool is that it enables managers and decision-makers to justify management decisions using patterns and trends from all available data rather than making decisions based on a portion of a single study. I say “a portion of” because Jones et al. (2016) showed both negative and positive effects from a megafire, but typically only the negative effects are

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Biology Department, Pennsylvania State University, University Park, Pennsylvania, USA.

† **E-mail:** dereklee@psu.edu

used to justify management actions while fire-induced positive effects are ignored (e.g., USDA 2019). Similarly, Jones et al. advocate for what they call “context-specific” interpretation of owl responses to fire and emphasize only a few specific results from a few papers to inform forest management against fire while discounting the majority of evidence that indicates fire is neutral or beneficial and could be encouraged.

The observed variation in effects among studies and sites can be considered noise around a mean overall signal. The mean overall signal indicates all fires’ effects on all spotted owls everywhere. Given the Forest Service must manage an enormous area of forest lands for multiple uses, their management must consider mean overall effects as the most parsimonious description of a phenomenon. The evidence synthesized in Lee (2018) indicating that fire is not a grave and immediate threat to owl populations, and has some beneficial outcomes, directly supports management decisions that prioritize allocating wildfire management and suppression resources toward human communities rather than spotted owl habitat. Wildfires can pose a serious threat to human life and property, and wildfire never imparts benefits to human structures. There are limited resources available to protect homes and communities from wildfire (Schoennagel et al. 2017), and treating backcountry forested lands such as in owl habitats has no impact on community safety (Cohen 1999, 2000), so forest fire mitigation resources should be focused on home fire resistance and protection (Schoennagel et al. 2017).

Jones et al.’s comment on Lee (2018) included several suggestions for technical modifications to the meta-analyses (Table 1). Some of these same suggestions for how Lee (2018) could be improved also appeared in Peery et al. (2019). In summary, Jones et al. and Peery et al. (2019) suggested my meta-analyses in Lee (2018) should have: (1) not focused my conclusions on mean effects because of the variation in effects across studies, nor used P values < 0.05 to determine significance; (2) excluded all studies with post-fire logging; (3) accounted for or eliminated data duplication; (4) analyzed subspecies separately; and (5) used different effect sizes and sample sizes for certain papers.

To test whether my original results in Lee (2018) were robust to the above-listed technical criticisms, I reanalyzed the data according to all their suggestions. Details are given below, but to summarize, none of their suggestions changed the results reported in Lee (2018). Regarding criticism 1, Lee (2018) did not focus on mean effects, in fact I thoroughly described and explored the variation among studies by presenting: (1) a random-effects meta-analysis of overall and parameter-specific mean effect sizes; (2) a two-step mixed-effects meta-regression to explain heterogeneity in mean effect sizes that included accounting for among-study and regional variation, time since fire, percent of high-severity fire in the study area, and parameter type (occupancy, survival, reproduction, recruitment, and foraging); and (3) a random-effects meta-analysis of variation to examine differences in parameter variances due to fire. My reporting of mean effect sizes and using $\alpha = 0.05$ for statistical significance are well-established norms for presenting ecological evidence. Many researchers have criticized null hypothesis significance testing using $\alpha = 0.05$, and many have defended it as well (Balluerka et al. 2005). In addition to the technical considerations, Jones et al. also offered their opinions on the ecological and inferential context of Lee (2018). A summary of Jones et al.’s issues with Lee (2018) along with my brief responses to each are found in Table 1.

For my reanalyses here addressing each of Jones et al.’s technical issues, I followed the same methods detailed in Lee (2018). I used: appropriately weighted and standardized effects (to account for different sample sizes and variances among studies); and random-effects and mixed-effects models (to account for non-independence of effects reported in the same study, partially duplicated datasets in a few studies, and other realities of meta-analyses to provide an inference about the average effect in the entire population of studies from which the included studies are considered to be a random selection). For comparison, the original Lee (2018) overall random-effects model standardized mean difference between unburned and burned sites was: -0.095 (95% CI: -0.537 to 0.348), a non-significant, slightly negative effect of mixed-severity forest fire (Fig. 1).

Table 1. Summary of Jones et al.'s issues related to Lee (2018) and responses.

General description	Issue	Response by Lee
Ecological		
Overgeneralization of historical fire regimes within forests inhabited by owls	Forest types and resulting fire regimes vary considerably across the geographic ranges of the three spotted owl subspecies analyzed	Geographic variation was accounted for in Lee (2018). Each parameter (e.g., occupancy) was modeled with effects of each study (e.g., Bond et al. 2009) within geographic region (e.g., Sierra Nevada) as multi-level random effects to properly estimate study site and region-specific variation and to account for repeated measurements (pseudo-replication) within a study or region. Subspecies-specific differences were also empirically tested for and no significant effects were observed. This was clearly stated in Lee (2018).
Statistical/technical		
Focus on the summary (mean) effects in the presence of high among-study variability	There was extremely high variation in effects across studies, including strong negative and positive in addition to neutral effects. In the presence of such high variability, the "average" effect is meaningless	Lee (2018) thoroughly explored and presented heterogeneity in effects, including 1) a random-effects meta-analysis of mean effect sizes including 10 sub-stratifications to specific parameters; 2) a 2-step mixed-effects meta-regression to explain heterogeneity in mean effect sizes that included 17 sub-stratifications accounting for among-study and regional variation, time since fire, percent of high-severity fire in the study area, and parameter type (occupancy, survival, reproduction, recruitment, and foraging); and 3) a random-effects meta-analysis of variation to examine differences in parameter variances due to fire.
Selected data and representation of high-severity fire resulted in reduced variability in ecological effects	Spotted owls respond to fire at the territory level. Using the average value eliminates all variation in severe fire effects among territories that likely mediates spotted owl response within a given study	In meta-analyses such as Lee (2018), each included study can be thought of as a single sample from the population of all possible studies with relevant results (e.g., mean occupancy before and after a fire) and those results can be associated with some study-specific covariate values such as mean proportion of territories burned high severity or time since fire. Meta-analysis summarizes the results from many different studies and looks for patterns in results relative to covariates, but cannot be expected to have access to or use raw data from every study. Lee (2018) followed well-established accepted methods of meta-analysis. Jones et al. are setting an impossibly high standard for meta-analyses.
Inaccuracies in reported fire effect sizes	A requirement for meta-analysis is the ability to obtain accurate and standardized effect sizes from different studies	Reanalysis using Jones et al.'s suggested effect parameters and sample sizes (see Fig. 1) resulted in no change in the results as reported in Lee (2018). Removing problematic studies also resulted in no change to the results reported in Lee (2018).
Transparency in reporting and treatment of studies with confounded salvage logging and fire effects	Studies with confounded fire-logging effects (i.e., when those effects could not be separated) should be treated in the same way: included or excluded. Moreover, we could not reproduce results by Lee (2018) regarding mean salvage logging effects	Lee (2018) removed 3 studies, all from the same study area, where post-fire logging was reported by the authors as so widespread and complete in areas of high-severity fire that essentially no unlogged high-severity patches remained. Reanalysis after removing all studies with any amount of post-fire logging made the overall effect of mixed-severity forest fire on spotted owls positive but not significantly so (Fig. 1).

(Table 1. Continued.)

General description	Issue	Response by Lee
Inclusion of duplicated data from multiple studies	This is referred to as “duplicate study effects.” It is recommended that duplicate study effects be either pooled or discarded from meta-analyses to avoid inferential errors	Lee (2018) accounted for duplicated data in all analyses. The inclusion of all papers, including those with repeated data, is common practice in meta-analyses, and the random-effects and mixed-effects models I used explicitly account for duplicated data. To test Jones et al.’s assertion that data duplication was a problem in Lee (2018), I removed all studies that used some or all of the dataset from another study and reanalyzed. Removing all studies with data duplication made the overall effect of mixed-severity forest fire on spotted owls positive but not significantly so (Fig. 1).
Underestimation and miscalculation of negative effects of fire on occupancy from individual studies	Some of the underlying data included in the meta-analysis of fire effects on owls contain errors or biases and thus may be unreliable	Reanalysis after removing Lee and Bond (2015a), Hanson et al. (2018), and the positive effect of < 50% high-severity burned territories in Jones et al. (2016) resulted in no change to Lee (2018) results (Fig. 1).
Inferential		
Context of changing wildfire trends	A sizeable body of literature suggests that severe fire activity in the spotted owl’s range will continue to increase and will possibly result in the loss of a majority of critical spotted owl nesting habitat by the end of the 21st century	There is considerable uncertainty surrounding recent and prehistoric patterns and trends in fire size and severity in spotted owl habitats. Jones et al.’s narrative was biased and highly speculative. Jones et al. agreed with me that severe fire has not yet resulted in substantial declines in spotted owl populations, and fire has not been an overriding driver of recently observed long-term spotted owl population declines. The years that produced the studies in Lee (2018) were among the biggest fire years in 40 years, so they accurately represent owl responses to fires within an already warmed and changed climate milieu.
The use of meta-analysis to solve complex conservation issues and superseding of existing understanding	Meta-analyses are not replacements for studies that explicitly test mechanisms. Moreover because they are considered a “gold-standard” of evidence synthesis, meta-analyses yielding erroneous inferences can lead to further confusion of complex topics	Meta-analyses are powerful tools for synthesizing results from numerous studies and are designed to deal with heterogeneity and complex varied effects. Lee (2018) found consistent, significant patterns in how owls respond to mixed-severity fire by synthesizing available studies. Namely: a positive effect on recruitment immediately after the fire, with the effect diminishing with time since fire; reproduction positively correlated with the percent of high-severity fire in owl territories; and positive selection for foraging in low- and moderate-severity burned forest while high-severity burned forest was used in proportion to availability but not avoided. Reanalyses did not support any of Jones et al.’s criticisms, and confirmed the results from Lee (2018). Meta-analysis will always be superior to cherry picking one or a few studies to justify “context-specific” management decisions.

REMOVING EFFECTS CONFOUNDED BY SALVAGE LOGGING RESULTS IN AN OVERALL POSITIVE EFFECT OF FIRE

When all studies known to have any amount of post-fire salvage logging were excluded from the analysis, I was left with four papers (Bond

et al. 2002, Roberts et al. 2011, Lee and Bond 2015a, Eyes et al. 2017). The overall difference in effect size between unburned and burned sites in the absence of salvage logging was +0.24 (95% CI: −0.94 to 1.43). Therefore, removing all studies with any amount of post-fire logging made the overall effect of mixed-

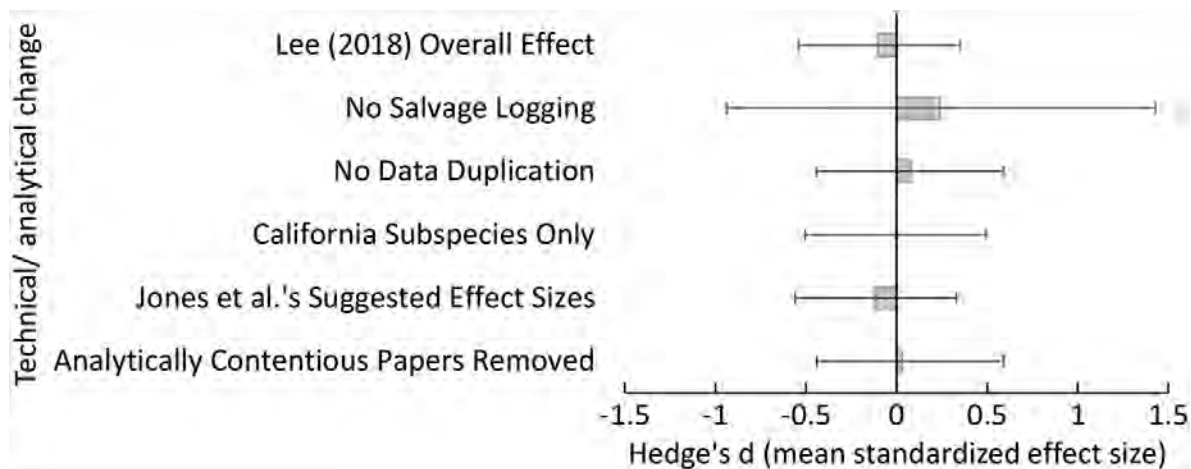


Fig. 1. Results from reanalyses of data used in Lee (2018) meta-analysis of spotted owl responses to mixed-severity forest fire, as suggested in Jones et al. (2020). Whiskers indicate the 95% confidence interval. Jones et al.'s speculations that various changes in data would alter results were not empirically supported.

severity forest fire on spotted owls positive but not significantly so (Fig. 1). No further analyses could be done because the sample of papers was so reduced by removing those with any salvage logging. All of the published peer-reviewed papers on owls and fire that examined salvage logging found negative effects from salvage logging on spotted owls (Lee 2018). Salvage logging has strong negative effects on many aspects of forest ecology and biodiversity (Lindenmeyer et al. 2012, Thorn et al. 2018), so a negative effect of post-fire logging on spotted owls is not surprising.

REMOVING DUPLICATE DATASETS RESULTS IN AN OVERALL POSITIVE EFFECT OF FIRE

The inclusion of all papers, including those with repeated data, is common practice in meta-analyses, and the random-effects and mixed-effects models I used explicitly account for this practice. To test Jones et al.'s assertion that data duplication might be a problem in Lee (2018), I removed studies that used some or all of the dataset from another study. I eliminated older studies and kept the more recent study. I removed Hanson et al. (2018), Roberts et al. (2011), Tempel et al. (2016), the occupancy component of Tempel et al. (2014), Lee et al. (2013), and Lee et al. (2012). The

mean difference between unburned and burned sites in the absence of data duplication was +0.08 (95% CI: -0.44 to 0.59). Therefore, removing all studies with data duplication made the overall effect of mixed-severity forest fire on spotted owls positive but not significantly so (Fig. 1). Removing all studies with data duplication also did not change the results of meta-regression analyses.

ANALYZING SUBSPECIES SEPARATELY IS EMPIRICALLY UNSUPPORTED

My methods to explain heterogeneity in effects included accounting for among-study and regional variation (Table 1). For northern and Mexican subspecies, there was only 1 paper each presenting subspecies-specific data (Jenness et al. 2004, Rockweit et al. 2017). The terms for subspecies in my meta-regression were not significant (Lee 2018), so there was no empirical evidence from these two papers that the Mexican or northern subspecies have responses to fire that are substantially different from the California subspecies. The most parsimonious hypothesis given these data is that subspecies responses to fire are similar. Analyzing the California subspecies data alone did not change the results of overall effects or meta-regression analyses (Fig. 1).

CHANGING DISPUTED EFFECT SIZES TO THOSE SUGGESTED BY JONES ET AL. DID NOT CHANGE RESULTS

The Jones et al. commentary suggested alternative effect sizes and sample sizes for four papers for which analytical issues were raised, Jones et al. (2016), Lee and Bond (2015a,b), and Hanson et al. (2018). Using Jones et al.'s new effect and sample sizes, the overall mean difference between unburned and burned sites was -0.12 (95% CI: -0.56 to 0.33). Changing effect sizes following suggestions by Jones et al. did not change the overall mean effect results (Fig. 1). I also reanalyzed only the occupancy data subgroup using Jones et al.'s suggestions and found no significant mean effect of fire on occupancy (effect = -0.75 , 95% CI: -1.52 to 0.03), the same finding as in Lee (2018). When the four papers for which analytical issues have been raised were simply removed from the analysis, the overall mean difference between unburned and burned sites was $+0.03$ (95% CI: -0.44 to 0.59). Removing studies with analytical issues made the overall effect of mixed-severity forest fire on spotted owls positive but not significantly so (Fig. 1). Neither changing effect sizes nor removing these papers changed the meta-regression results from what was reported in Lee (2018).

THERE WAS NO FOCUS ON MEAN EFFECTS IN LEE (2018), HETEROGENEITY WAS THOROUGHLY EXAMINED, AND GEOGRAPHIC VARIATION WAS ACCOUNTED FOR

Far from ignoring the heterogeneity in effects among studies, in Lee (2018) I used multiple analytical tools (weighted effect sizes, random-effects models, multi-level mixed-effects meta-regressions of Hedge's d against percent of study area burned at high severity and time since fire, and meta-analysis of variation) to describe and examine patterns in the variation of effects among studies. I made 10 sub-strata analyses of mean effects, and 17 sub-strata analyses within the meta-regression. Lee (2018) presented: (1) a random-effects meta-analysis of mean effect sizes that included overall effect, parameter type sub-stratification (occupancy, demography, and foraging), and parameter-specific sub-stratification

(reproduction, survival, recruitment, and foraging in low-, moderate-, and high-severity burn); (2) a 2-step multi-level linear mixed-effects meta-regression to explain heterogeneity in mean effect sizes that included accounting for among-study and regional variation, time since fire, percent of high-severity fire in the study area, and parameter type (occupancy, survival, reproduction, recruitment, and foraging in low-, moderate-, and high-severity burn); and (3) a random-effects meta-analysis of variation to examine differences in parameter variances due to fire.

In addition to finding no significant negative mean effects of fire on owls, Lee (2018) reported multiple significant effects of fire covariates on specific owl parameters. These effects were as follows: a negative correlation of occupancy with time since fire; a positive effect on recruitment immediately after the fire, with the effect diminishing with time since fire; a positive correlation between reproduction and the percent of high-severity fire in owl territories; and positive selection for foraging in low- and moderate-severity burned forest, with high-severity burned forest used in proportion to its availability, but not avoided.

In the meta-regression portion of my paper, I explored how high-severity burned area within territories explained this variation and found a "nearly significant" negative effect across all parameters. I did not discuss the potential meaning of this "nearly significant" result because the more detailed meta-regression of high-severity fire effects partitioned into parameter-specific regressions (occupancy, demography, and foraging) had "clearly significant" results.

Jones et al. also criticized my formulation of the proportion burned at high-severity covariate, but my methods were transparent, used all data available in the published studies that were examined, produced study-specific covariate values representative of the variation among studies, and found numerous significant results. Jones et al. suggested I should have used data from every individual territory ever burned in my meta-regressions, an impossibly high standard for meta-analyses when raw data were not published with every paper. Until all studies make their raw data publicly available, researchers will continue to rely on the methods of meta-analyses and meta-regressions with

study-specific covariates to synthesize the results from different studies as a sample of all possible studies.

Jones et al. also claimed the examination of heterogeneity in Lee (2018) was inadequate because I did not examine high-severity patch size as a covariate. This is surprising given that one of the co-authors (M. P. North) published a paper acknowledging that high-severity patch size is highly correlated with the proportion of fire area burned at high severity (Collins et al. 2017 citing Miller et al. 2009, Harvey et al. 2016). Because high-severity patch size is highly correlated with the proportion of fire area burned at high severity, my meta-regression analysis of effects in relation to high-severity burned area was also an examination of high-severity patch size. Again, the assertions of Jones et al. were not supported by the empirical evidence.

With $\alpha = 0.05$, the criteria most commonly employed in ecological decision making, $P > 0.05$ is not statistically significant. I adhered to the convention of not emphasizing non-significant results, particularly since there were numerous clearly significant results that required discussion. I did discuss the biological significance of the non-statistically significant occupancy result (see *Fire-induced change in occupancy is not greater than annual changes in occupancy in unburned forest* below).

Conservation biology, in its mission to sustain ecological and evolutionary processes, typically espouses conservatism and the precautionary principle when considering unnatural anthropogenic actions such as logging relative to natural disturbances (Noss 1993). Therefore, because Lee (2018) showed there is not strong, widespread, and unequivocal evidence that fire is threatening spotted owl population persistence, it follows that unnatural anthropogenic actions such as logging intended to reduce fire but that can harm owls should not be considered on public lands that are not immediately adjacent to towns and infrastructure. Indeed, rather than high-severity fire, which has burned historically throughout the range of the spotted owl, the novel disturbance to the species is logging (Beardsley et al. 1999). Even the largest most intense fire leaves dead big trees standing for decades, providing many ecological goods and services to the dynamic forest ecosystems.

Logging is the primary reason the spotted owl has declined (USFWS 2011, USFWS 2012), and additional logging, even logging which is called thinning, fuel reduction, or restoration, is unlikely to contribute meaningfully to owl conservation or recovery.

FIRE-INDUCED CHANGE IN OCCUPANCY IS NOT GREATER THAN ANNUAL CHANGES IN OCCUPANCY IN UNBURNED FOREST

In Lee (2018), I provided biological perspective regarding the observed non-statistically significant change in site occupancy probability due to fire (-0.06) by comparing this value to the observed stochastic declines in site occupancy between pairs of sequential years in the unburned Eldorado study area (-0.07). My estimate was based on Jones et al. (2016) time series of annual proportion of sites occupied from 1993 to 2015 (Fig. 2A). Each year the proportion of sites occupied could be the same relative to the previous year's occupancy (zero change), higher (a positive number), or lower (a negative number). So each year's stochastic change in occupancy relative to the previous year can be seen as a zero indicating no change, or a positive or negative departure from zero (Fig. 2B).

To describe the magnitude of annual departure from zero change in annual proportion of sites occupied ($\psi_t - \psi_{t-1}$) for the time series in the unburned Eldorado study area, I used the mean of all negative changes (-0.07), but I could also have used the mean of all positive changes (0.06), the mean absolute value of all changes (0.07), the mean proportional change (ψ_t / ψ_{t-1}) applied to mean occupancy (0.07), or the standard deviation of occupancy (0.15). For example, if occupancy over four years was 0.5, 0.6, 0.4, and 0.5, then annual changes in occupancy would be $+0.1$, -0.2 , and $+0.1$ (the results of: $0.6 - 0.5$, $0.4 - 0.6$, and $0.5 - 0.4$). Jones et al.'s proposed method of simple averaging would estimate the mean annual change in occupancy was 0.0, which is clearly not the case, whereas the absolute value method I described would estimate mean annual change in occupancy as 0.13, and the standard deviation of the four hypothetical occupancy values above is 0.08. Jones et al.'s method of averaging the positive and negative changes was wrong because any average of positive and negative

random numbers will tend to have a mean of zero (Fig. 2B). The -0.02 overall mean reported by Jones et al. was actually the slope of the trend line through the time series of Eldorado owl occupancy with y -intercept at 1.0 (Fig. 2A).

To revisit the biological significance of the nearly statistically significant change in mean occupancy after fire (-0.06), I did the following: (1) detrended the Jones et al. (2016) occupancy data by subtracting the trend line estimate from each observation in the series; (2) calculated the mean and standard deviation of the detrended occupancy data; (3) computed the year-on-year change in occupancy for each year by subtracting occupancy in year $t-1$ from occupancy in year t (Fig. 2B); (4) computed the absolute value of each year's change in occupancy; and finally (5) calculated the mean of the absolute values of each year's change in occupancy. The mean of the absolute value of each year's change in occupancy in the unburned forests of Jones et al. (2016) is 0.063. Thus, the mean raw effect size of mixed-severity fire on occupancy (0.060) is less than the mean annual change in occupancy in unburned forest owl sites of the Eldorado study

area (0.063), and less than the standard deviation of detrended occupancy probabilities (0.077). As reported in Lee (2018), the mean effect size of mixed-severity fire on spotted owl site occupancy is neither statistically nor biologically significant.

ECOLOGICAL AND INFERENTIAL CONTEXT OF LEE (2018) WAS APPROPRIATE

Jones et al. claimed I overgeneralized historical fire regimes within forests inhabited by spotted owls, and did not address changing wildfire trends due to global warming. In Lee (2018), I acknowledged both sides of the ongoing unsettled debate about whether fires in forests inhabited by spotted owls are becoming larger or more severe at evolutionary timescales, while Jones et al. present a narrower perspective. I assert that climate change is not a future event, but one we have been experiencing for decades (Westerling 2016, USGCRP 2017). The years that produced the studies analyzed in Lee (2018) were among the biggest fire years in 50 years, so they accurately represent owl responses to fires within an

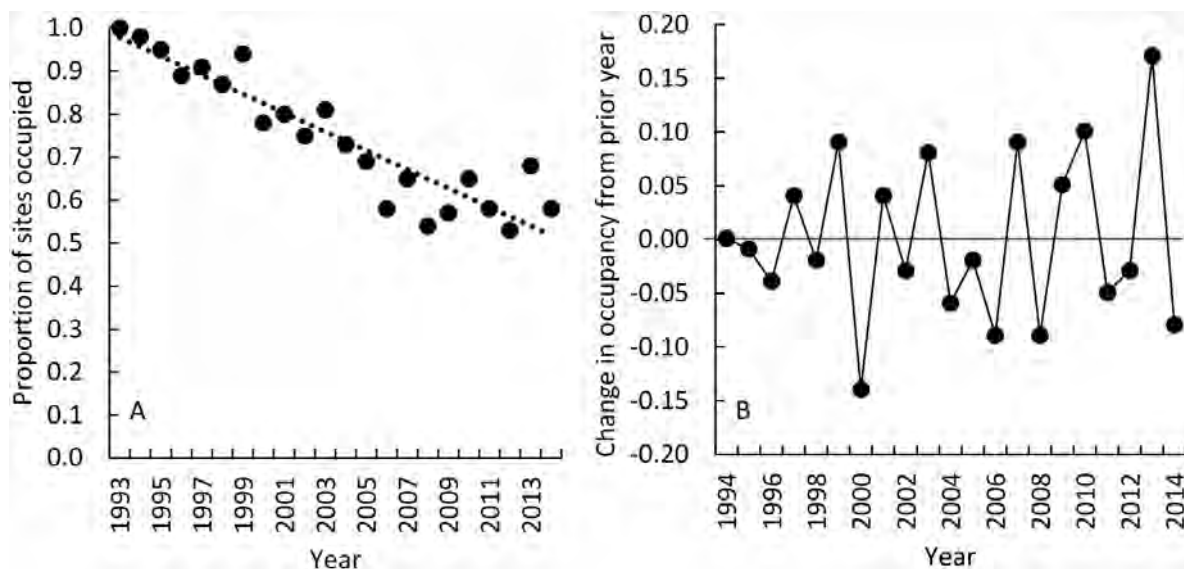


Fig. 2. (A) Annual estimates of spotted owl site occupancy (ψ) in Eldorado, California study area 1993–2014 (data from Jones et al. 2016: Fig. 3e). The dotted line represents a regression line fitted to the time series ($y = -0.02x + 1.0$). (B) Change in spotted owl site occupancy probability from year $t - 1$ to year t calculated using detrended occupancy data. Raw mean of changes is 0.0 (SD = 0.08). Mean of absolute value of changes is 0.063 (SD = 0.043).

already warmed and changed climate milieu (Littell et al. 2009, Miller et al. 2009, Parks et al. 2015, Westerling 2016). Thus, the results from Lee (2018) are directly applicable to climate change predictions for western forests.

The topic of fire regimes and natural range of variability is fraught with uncertainty, and tangential to my synthesis of published literature. In Lee (2018) I thoroughly accounted for regional geographic variation in my analyses. Each parameter (e.g., occupancy) was modeled with effects of each study (e.g., Bond et al. 2009) within geographic region (e.g., Sierra Nevada) as multi-level random effects to properly estimate study site and region-specific variation and to account for repeated measurements (pseudo-replication) within a study or region. Regions were defined as Sierra Nevada, southern California, national parks, not California, and the Eldorado density study area. Subspecies-specific differences were also empirically tested for and no significant effects were observed. This was all clearly explained in Lee (2018).

I find it useful to consider the evolutionary past when contextualizing perceived threats to an ecosystem and its natural disturbances. Fire is a natural and widespread mechanism of changes in vegetation community structure and distribution (Pickett and White 1985, Sugihara et al. 2006). There is evidence that native plants and animals such as spotted owls are well adapted to take advantage of large patches of high-severity burn found in recent megafires, indicating that large high-severity patches are not novel conditions (Tingley et al. 2016, Downing et al. 2020). The spotted owl and the older forests it inhabits have experienced numerous very warm and dry periods during their evolutionary history that were likely similar to the current and predicted near-future climate (LaMarche 1974, Graumlich 1993, Stine 1994). Mixed-severity fires that included large patches of high-severity fire have likely often been found in western forests, and even if one is uncertain of exactly how much high-severity fire was on the landscape at different points in time, it is clear that at least a few times in the past few thousand years, there have been droughts and climate swings that likely led to more fire than is currently observed (Pierce et al. 2004, Power et al. 2008, Marlon et al. 2012). The spotted owl survived those episodes. I find

this to be compelling evidence for built-in adaptation and resilience in the forest-owl system that the novel disturbance of logging could disrupt.

The notion that logging or thinning might somehow avert large, weather-driven, mixed-severity forest fires with large patches of high-severity burn is not well supported by the evidence (reviewed in Kalies and Kent 2016, Schoennagel et al. 2017). Approximately 90% of the forested acres burned at high severity occur each year in a few extreme climate- and weather-driven mixed-severity fire events that thinning treatments are unlikely to interact with, let alone slow or stop (Flanagan and Wotten 2001, Williams 2004, Lydersen et al. 2014, Kalies and Kent 2016). In fact, some evidence supports the observation that thinning and other logging can exacerbate fire severity (Raymond and Peterson 2005, Cram et al. 2006, Wimberly et al. 2009, Cruz et al. 2014, Bradley et al. 2016), while spotted owl nesting and roosting habitat (old-growth forest characterized by large trees and high canopy cover) is naturally more resistant to high-severity fire than younger forest (Weatherspoon and Skinner 1995, Odion et al. 2014, Lesmeister et al. 2019). Logging of green trees also can exacerbate competition between invasive barred owls (*Strix varia*) and spotted owls (Dugger et al. 2011).

Another aspect of thinning and other logging activities considered fuel reduction that is underappreciated is the genetic variation among trees that is the raw material for forest adaptation in a changing climate (Kolb et al. 2016, Prunier et al. 2016, Pinnell 2016, Six et al. 2018). Until foresters can identify exactly which individual trees are most genetically and epigenetically adapted to be resilient and resistant to drought, higher temperatures, fire, disease, and insects, and can use that genetic information to preserve those specific locally well-adapted individual trees, then random thinning and logging will inevitably impoverish the genetic variation of our forests and impair their natural processes of adapting to a changing climate.

CONCLUSIONS

None of the issues raised by Jones et al. regarding Lee (2018) were supported by reanalyses (Table 1). Most were not truly issues at all, but

misunderstandings by Jones et al. about meta-analysis in general and the specific methods used in Lee (2018). Jones et al. espouse the belief, based on a small subset of available data, that because mixed-severity fire with large patches of high-severity burn *can* sometimes harm some spotted owl territories or individual owls, thinning or other logging within owl habitat is justified if it can reduce fire severity. That is a highly questionable management recommendation, particularly when a different subset of the available data showed high-severity fire *can* be significantly preferred by foraging owls and more high-severity fire *can* increase reproduction. Crucially, thinning logging is rarely effective at mitigating fire severity during the large, climate- and weather-driven fires that burn 90% of burned area each year.

Given the known absence of consistent negative effects, and the significant positive effect of high-severity fire on spotted owls, I propose that the limited resources available for forest fire mitigation should be prioritized for human community protection in the wildland–urban interface rather than in remote spotted owl territories. When all available data are examined objectively in meta-analysis, the larger pattern is revealed that high-severity fire patches from climate-changed wildfire events are used by spotted owls for foraging in proportion to their availability, and more high-severity fire significantly increases reproduction, but no strong consistent negative effects are apparent. This is exactly why meta-analyses such as Lee (2018) are so valuable, because they provide decision-makers with the broader consistent patterns found among all studies so that decisions need not be based on single studies or so-called “biological intuition.”

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RESEARCH ARTICLE

Occupancy of California Spotted Owl sites following a large fire in the Sierra Nevada, California

Derek E. Lee^{1*} and Monica L. Bond¹

¹ Wild Nature Institute, Hanover, New Hampshire, USA

* Corresponding author: derek@wildnatureinstitute.org

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ABSTRACT

High-severity forest fire often is presumed to adversely affect the occupancy of territories by California Spotted Owls (*Strix occidentalis occidentalis*) because these owls are associated with mature and old-growth forests. We used single-season, multi-state occupancy statistics to estimate site occupancy probability for Spotted Owls at 45 historically occupied sites during the breeding season immediately following the 2013 Rim Fire, which was one of the largest forest fires on record in California. We quantified how occupancy probability was influenced by the amount of high-severity fire occurring in mature forested habitat within Protected Activity Centers (PACs). The model-averaged estimate of site-occupancy probability for at least a single owl was 0.922 ($\pm$ SE = 0.073), which was higher than other published occupancy probability estimates for this subspecies in either burned or long-unburned sites in the Sierra Nevada. Mean site-occupancy probability for pairs was 0.866 ($\pm$ 0.093), and most sites (33) were occupied by pairs. The amount of high-severity fire in the PAC did not affect pair occupancy. Occupancy probability by at least a single bird was negatively correlated with the amount of high severity fire in the PAC but remained >0.89 in 100% high-severity burned PACs. These data add to observations that California Spotted Owls continue to use post-fire landscapes, even when the fires were large and where large areas burned at high severity, suggesting that owls are not generally negatively impacted by high-severity fire. Based on this and other studies of Spotted Owls, fire, and logging, we suggest land managers consider burned forest within and surrounding PACs as potentially suitable California Spotted Owl foraging habitat when planning and implementing management activities, and we recommend against logging burned forest within at least 1.5 km of nests or roosts for the conservation and recovery of this declining subspecies.

Keywords: California Spotted Owl, *Strix occidentalis occidentalis*, occupancy, forest fire

Ocupación de sitios de *Strix occidentalis occidentalis* luego de un gran incendio en la Sierra Nevada, California

RESUMEN

Generalmente se supone que los incendios forestales de alta severidad afectan la ocupación de los territorios de *Strix occidentalis occidentalis* debido a que estos búhos se asocian con bosques maduros y primarios. Usamos estadísticos multiestado de ocupación de una temporada para estimar la probabilidad de ocupación de un sitio por *S. occidentalis* en 45 sitios históricamente ocupados, durante la temporada reproductiva que siguió inmediatamente al incendio Rim de 2013, uno de los incendios forestales más grandes registrados en California. Cuantificamos cómo la probabilidad de ocupación se vio influenciada por la cantidad de incendios de alta severidad en bosques maduros dentro de Centros de Actividad Protegida (PAC, por sus siglas en inglés). El estimado promedio de los modelos de probabilidad de ocupación de sitios para al menos un individuo fue de 0.922 ($\pm$ EE = 0.073), lo que es mayor que otras probabilidades de ocupación estimadas para esta subespecie en sitios con o sin incendios recientes en la Sierra Nevada. La probabilidad promedio de ocupación de sitios para parejas fue de 0.866 ($\pm$ 0.093), y la mayoría de los sitios (33) fueron ocupados por parejas. La cantidad de incendios de alta severidad en los PAC no afectó la ocupación de las parejas. La probabilidad de ocupación por al menos un individuo se correlacionó negativamente con la cantidad de incendios de alta severidad en los PAC, pero permaneció mayor a 0.89 en el 100% de los PAC severamente incendiados. Estos datos complementan las observaciones de que *S. o. occidentalis* sigue usando los paisajes incendiados, aún cuando los incendios fueron grandes y donde grandes áreas se incendiaron con alta severidad, lo que sugiere que los búhos generalmente no sufren un impacto negativo por los incendios de alta severidad. Basados en este y otros estudios sobre *S. occidentalis*, incendios y tala de bosques, sugerimos que los administradores de la tierra consideren los bosques incendiados dentro y alrededor de los PAC como hábitats de alimentación potencialmente apropiados para *S. o. occidentalis* durante la planeación e implementación de las actividades de manejo. No recomendamos la tala de los bosques incendiados en un radio

menor a 1.5 km alrededor de los nidos y dormitorios para la conservación y recuperación de esta subespecie en declive.

Palabras clave: incendios forestales, ocupación, *Strix occidentalis occidentalis*

INTRODUCTION

For more than 25 years, the California Spotted Owl (*Strix occidentalis occidentalis*) has been a species of concern throughout its range because it selects commercially valuable mature and older conifer forests for nesting, roosting, and foraging (Verner et al. 1992). Recent evidence from long-term demographic studies in the Sierra Nevada show that California Spotted Owl populations are declining significantly on managed national forest lands (Conner et al. 2013, Tempel and Gutiérrez 2013). At the same time, populations are apparently stable in Sequoia and Kings Canyon national parks where forests are largely unmanaged (Conner et al. 2013).

Forest fire has long been hypothesized to be a major threat to California Spotted Owls (Verner et al. 1992, USFWS 2006), but recent studies have shown that owls persist for years in landscapes burned by all fire intensities (Roberts et al. 2011, Lee et al. 2012, 2013). Despite this evidence, forest managers continue to assume that large areas of high-severity fire adversely affect Spotted Owl occupancy to the extent it renders forests unsuitable as habitat (USFS 2004). As a result, post-fire salvage logging is routinely proposed and permitted in severely burned forests, even within administrative designations established to conserve owl habitat, such as 121 ha Protected Activity Centers and 405 ha Home Range Core Areas surrounding nests and roost sites (USFS 2004).

In August 2013, the Rim Fire burned a large (>100,000 ha) area within and around the Stanislaus National Forest and Yosemite National Park, California. The year following the fire, biologists from the USDA Forest Service (USFS) conducted surveys in all previously occupied (occupied ≥ 1 year before the fire) California Spotted Owl sites (Protected Activity Centers, see Methods) within the Rim Fire area to determine site occupancy status. These data provided an excellent opportunity to estimate single-season occupancy of Spotted Owl breeding sites within one of the largest forest fires in recent Sierra Nevada history and to compare occupancy with previously reported rates in burned and long-unburned forests. The USFS also maps burn severity of vegetation, which we used as a site-specific covariate to determine how the amount of high-severity burned forest within Spotted Owl Protected Activity Centers affected occupancy status. This information is important for developing appropriate post-fire forest management policies and activities to conserve this declining management indicator species.

METHODS

Study Area and Species

The Rim Fire started near the confluence of the Clavey and Tuolumne rivers about 32 km east of Sonora, California, and burned primarily eastward into the Sierra Nevada (USFS 2014a). Elevations within the Rim Fire area ranged from 300 to 2,100 m. The fire area included a variety of habitats and vegetation age classes; forest types pertinent to Spotted Owls included Sierran mixed-conifer, white fir (*Abies concolor*), red fir (*A. magnifica*), montane hardwood-conifer, ponderosa pine (*Pinus ponderosa*), and Jeffrey pine (*P. jeffreyi*) (USFS 2014b).

The California Spotted Owl occurs in conifer and mixed conifer-hardwood forests in the Sierra Nevada, central and southern coastal, and southern interior mountain ranges of California (Gutiérrez et al. 1995). This nocturnal raptor primarily preys on small mammals but also eats insects, birds, and bats (Thraillkill and Bias 1989, Munton et al. 2002, Bond et al. 2013). California Spotted Owls are territorial with high site fidelity (Gutiérrez et al. 1995, Blakesley et al. 2006) and select nest and roost sites in older forests containing large live trees typically >61 cm diameter at breast height, with multi-layered structure, high canopy cover (>40% but typically >70%), and abundant large snags and downed logs (Call et al. 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004, Blakesley et al. 2005). Foraging habitat is more variable and can include forest areas with high canopy cover (Call et al. 1992, Gutiérrez et al. 1992), medium-sized forest (Williams et al. 2011), and forest burned at any severity (Bond et al. 2009).

Defining Spotted Owl Habitat and Protected Activity Centers (PACs)

The USFS manages wildlife habitat using a classification system based on the California Wildlife Habitat Relationships system (CWHR) developed by the California Department of Fish and Game (now California Department of Fish and Wildlife). The CWHR types 6, 5D, 5M, 4D, and 4M denote stands dominated by larger-sized trees and high canopy cover, and these CWHR types are considered highly and moderately suitable “Spotted Owl habitat” for the California subspecies (CDFG 2008). The USFS delineates for management purposes a 121 ha Protected Activity Center (PAC) consisting of Spotted Owl habitat CWHR types in as compact a unit as possible around owl detection locations on National Forest System lands (Verner et al. 1992). Owl detection locations are

based on (1) the most recent documented nest site, (2) the most recent known roost site when a nest location remains unknown, and (3) a central point based on repeated daytime detections when neither nest nor roost locations are known (USFS 2004). In addition, a 405 ha Home Range Core Area (HRCA), consisting of Spotted Owl habitat CWHR types, is established around each owl detection location and includes the PAC.

The guiding USFS management document for the Sierra Nevada (USFS 2004) states that PACs are maintained regardless of California Spotted Owl occupancy status, but after a “stand-replacing event,” habitat conditions are to be evaluated within a 2.4 km radius around the activity center. The PAC may be re-mapped to exclude high-severity fire areas or can be removed from the conservation network altogether (USFS 2004). The elimination of PAC protections enables areas to be logged following impact by high-severity fire (i.e. “salvage” logging). Prior to post-fire salvage logging in former PACs, portions of former PACs, or HRCAs, surveys for Spotted Owls are conducted in accordance with 1995 Pacific Southwest Region survey protocol (USFS 1995), but burned stands may be logged even if owls are detected during these surveys.

Data Collection and Analysis

We organized and analyzed survey data using a single-season, multi-state occupancy modeling approach (MacKenzie et al. 2006, 2009, 2010). We followed as much as possible the methods of data collection and analyses of MacKenzie et al. (2006, 2009, 2010) where suitably defined geographic units or “sites” are repeatedly surveyed for detections of the species of interest to define presence at a site in 1 of 2 “states.” Here we use the term “site” to mean a PAC, which was our sampling unit (MacKenzie et al. 2006, 2009, 2010), and defined “state” as the detection of either a single or pair of owls. This allowed us full use of survey data while incorporating information about single- vs. pair-detection data (MacKenzie et al. 2006, 2009, 2010). Our population of interest was all historical Spotted Owl sites that were burned during the Rim Fire, so it was appropriate to use data from sites that were not randomly selected (MacKenzie and Royle 2005).

At our request, the USFS provided field data forms from Spotted Owl surveys conducted within the boundary of the Rim Fire. The standardized data forms contained the following information: survey location (PAC number and site name), date, observers, starting latitude and longitude, specific survey times, survey duration, weather and moon phase, age and sex of owls detected, detection type (seen or heard), latitude and longitude for nest and roost trees, and a detailed narrative about the survey. A narrative typically included the time and place that surveyors began broadcasting vocal lures, the time when an owl was seen

or heard and the sex of the owl, the time a mouse was offered to an owl to assess reproduction and when the owl took the mouse, and the fate of each mouse (eaten, cached, offered to a mate or to young, or undetermined). The USFS also provided us with quadrangle maps associated with each survey that identified the survey routes and owl locations by sex if owls were detected. Although we did not conduct the surveys ourselves, we assumed that the USFS provided us with all available data forms for the PACs within the Rim Fire and that the data on the forms were accurate. Thus, we acknowledge that factors unknown to us could have affected the reliability of the data.

USFS biologists who gathered the data surveyed for Spotted Owls at all of the 45 historically occupied PACs within the Rim Fire using the 1995 Pacific Southwest Region survey protocol from 24 March through 5 August 2014 (USFS 1995). Surveyors used vocal lures at 3–11 ($\bar{x}$ = 6) calling stations per PAC at night. Following a nighttime detection, they conducted daytime follow-up surveys by feeding owls live mice (1) to locate active nest trees, (2) to locate roosts of pairs and resident singles, and (3) to monitor reproduction (USFS 1995). Protocols required a minimum of 6 site surveys during a single year, with at least 4 of these surveys occurring before 30 June. If no detections were recorded during any survey, a site may be designated as not occupied. Six PACs in the Rim Fire were not surveyed enough times to meet protocol standards, but we included these in our analyses to avoid potential bias owing to censoring and because a minimum of 3 visits is generally sufficient when detection probability is >0.5 (MacKenzie and Royle 2005), as was the case for our pairs data (see Results).

We examined all USFS field data forms, notes, and associated maps depicting owl survey routes and detections or nondetections and created a database of the results of every survey for each site. We incorporated both nocturnal and daytime detections in our occupancy analysis to increase sample size. We attributed a state for each survey of each site as: pair detected, single owl detected, or no detection. To reduce the possibility of detecting an animal from a neighboring site, we excluded detections whenever surveyors suspected an owl came from another territory and recorded such suspicions in the narrative on the field forms. We did not consider nesting status or reproductive success as a state for occupancy modeling because surveyors had insufficient data to determine reproduction by owls at 14 of the 33 sites where pairs were detected. When a single male was detected at a site during a survey and, during a subsequent survey, a female was detected at that same site <400 m from the male's location or vice versa, we coded the second detection status as a pair following the 1995 Pacific Southwest Region survey protocol (USFS 1995). We used data from surveys conducted >72 hr apart to ensure

independence and included results from complete surveys only (i.e. when >90% of all point stations were surveyed) and omitted surveys aborted because of inclement weather or other reasons.

We calculated a naïve occupancy estimate (number of sites with detections per total number of sites surveyed) and estimated site occupancy using single-season, multi-state site occupancy statistics. Naïve occupancy is the simple proportion of total sites surveyed where the species was detected. Owls may be present at a site but not detected, however, and the ability of surveyors to detect owls may vary throughout the season or depend on whether the site is occupied by a pair or a single owl. Surveyors may also misclassify a site as occupied by a single, when in fact a pair is present at the site. Estimation of site occupancy accounts for probabilities of detection and misclassification based on repeated surveys at a given site in a given year; thus, estimates of site-occupancy probabilities are unbiased by imperfect probabilities of detection and classification during a given survey (MacKenzie et al. 2006, 2009, 2010).

We modeled occupancy using Program Presence 4.0 (USGS-Patuxent Wildlife Research Center, Laurel, MD 2006) to analyze the survey histories of the 45 historical Rim Fire Spotted Owl sites and to estimate 5 parameters: probability a site was occupied (ψ_1), probability a site was occupied by a pair (ψ_2), detection probability of single occupancy (p_1), detection probability of pair occupancy (p_2), and probability of correct classification of pair-occupied sites (δ) (MacKenzie et al. 2010). For each survey, we coded owl detections as: 0 = no detection, 1 = single owl, and 2 = pair. We divided the survey season into 2-week sampling periods (i.e. 1–15 April, 16–30 April, etc.), and assigned the highest state detected within a sampling period to the site (e.g., see Tempel and Gutiérrez 2013).

We made a site-specific covariate of occupancy and detectability as the percentage of each owl PAC burned at moderately high to high severity (hereafter referred to as “high severity”). We obtained burn severity data from the Stanislaus National Forest’s 2014 Biological Assessment, Evaluation, and Wildlife Report (USFS 2014b). The USFS mapped burn severity of vegetation after the Rim Fire using Landsat TM satellite imagery and RdNBR classification (Miller and Thode 2007, USFS 2014c). Areas with $\geq 75\%$ basal area mortality were categorized as moderately high to high fire severity (USFS 2014c).

We first ranked temporal models of detection (p_1 and p_2) and classification (δ) as all possible combinations of survey-specific (t), constant (.), and linear temporal trend (T) structure. We then ranked all possible combinations of models of detection and classification probabilities using the percent of PAC area burned at high severity as a site-specific covariate, while maintaining the same temporal structure as the best-ranked temporal model. Finally, we

ranked occupancy as a function of the site-specific covariate percent of PAC burned at high severity.

We ranked all models using Akaike’s Information Criterion (Burnham and Anderson 2002). Site-specific covariates were standardized by subtracting each site’s value from the mean and dividing by the standard deviation (Burnham and Anderson 2002). To protect against spurious conclusions based only on a single top model and to account for model selection uncertainty, we present all results as the model-averaged parameter estimates (Burnham and Anderson 2002, Doherty et al. 2010). We presented estimates as means ($\pm$ SE).

Occupancy Model Assumptions

Occupancy models rely on 4 major assumptions: (1) occupancy state is unchanged during the sampling season (also known as “closure”); (2) sites are independent, and animals do not move among sites; (3) there is no unexplained heterogeneity in detectability; and (4) there is no unexplained heterogeneity in occupancy. Regarding the first assumption, occupancy biases potentially occur in single-season models when sites are colonized or vacated during the sampling period (Kendall 1999, Otto et al. 2013), but we believe the closure assumption was not violated in our data because trend models for p were not highly ranked (Kendall 1999). Given our top model structures and our estimates of ψ and p , if colonization = 0.05 and extinction ranged from 0.0 to 0.1, then closure violation bias in ψ would be approximately +0.05 (Otto et al. 2013). Furthermore, random violations of closure do not bias estimators (Kendall 1999), but estimates in these cases correspond to sites being “used” by the species rather than “occupied” (MacKenzie et al. 2006, Kendall et al. 2013). Regarding the second assumption, some lack of independence among sites may have occurred because animals were free to move among nearby sites, but we were unable to quantify this because owls were not individually marked, although survey design and protocols should minimize this possibility. We also deleted records of owls that surveyors suspected were from outside the PAC being surveyed, but if we were not perfect in identifying such individuals, our estimates of occupancy could be biased high. For the third assumption, the standardized sampling design for Spotted Owl surveys should reduce detection heterogeneity (USFS 1995, Lee et al. 2012). We also included temporal and site-specific covariates to minimize unexplained variation in detectability (Popescu et al. 2012), but any extraneous heterogeneity in detectability would only negatively bias our occupancy estimates (MacKenzie et al. 2006). Finally, heterogeneity in occupancy is not known to cause excessively biased parameter estimates, but it can overestimate standard errors (MacKenzie et al. 2006). Our site-specific covariates also accounted for extra variation in occupancy and detect-

ability due to fire, our main factor of interest; thus, our primary results are likely unbiased due to this effect (Popescu et al. 2012).

Because occupancy models rely on assumptions, problems with study design can bias resulting estimates and their interpretation. Tempel and Gutiérrez (2013) eliminated nocturnal detections >400 m from a site's nest or roost core area and used data from color-band resights to maximize independence among sites. USFS Spotted Owl surveyors often cannot determine nest and roost locations, and individual owls are not marked for identification because of logistical or budgetary constraints, but occupancy modeling was specifically developed to inform management using less expensive and less intensive presence-absence surveys than mark-recapture studies (MacKenzie et al. 2006). Here we provided analyses to inform post-fire forest management decisions affecting California Spotted Owls using data as they are typically collected under current USFS survey practices. The USFS survey data we used may have included some detections of owls from neighboring sites, but our estimates remain valid in terms of quantifying occupancy of PACs by owls and comparing with previous occupancy studies. The survey data also may have included some detections of nonresident "floater" owls, but these individuals are essential to the population as a source of breeding recruitment, and their use of sites should not be discounted (Franklin 1992). Any detected presence of owls from occupancy surveys, whether they are floaters or residential singles and pairs, should be interpreted as use, if not occupancy, of those forest stands (MacKenzie et al. 2006).

RESULTS

All 45 sites were surveyed ≥ 3 times from 28 March to 5 August 2014. The median number of surveys was 5, the mean number of surveys was 6, and maximum number of surveys was 10. At one site (Middle Fork Tuolumne), 2 pairs were detected during a survey and the USFS delineated a new site (Mather), so we included these as 2 distinct sites for determining the naïve occupancy. A male owl was detected at one site (Brushy Creek), but surveyors speculated the male was from a nearby site, so we considered the status of this site to be 0 = no detection. We calculated a naïve occupancy rate of 0.848 ± 0.053 (39/46). Naïve occupancy rate of pairs was 0.717 ± 0.066 (33/46).

In our estimated occupancy analysis we excluded the owl pair detected at the new Mather site because it lacked survey data. The top-ranked model was constant occupancy, detection, and classification, with the site-specific covariate describing percent of PAC burned at high severity affecting detectability but not occupancy (Table

TABLE 1. Model selection results for multi-status, single-season occupancy modeling of California Spotted Owl breeding sites in the Rim Fire, 2014. Parameter notation: site-occupancy probability of at least one owl (ψ_1), site occupancy probability of pairs (ψ_2), survey-specific detection probabilities of singles (p_1) and pairs (p_2), and correct classification probability of pair-occupied sites (δ). ΔAIC = difference in a model's AIC relative to the AIC of the best-ranked model in the set (minimum AIC = 428.21), W = AIC Weight, a measure of the strength of evidence for a given model to be the best in the set, and k = number of parameters. "Burn" indicates a covariate model where parameter is a function of the percent of the site's PAC that burned at high severity.

Model	ΔAIC	W	k
$\psi_1, \psi_2, p_1(\text{burn}), p_2(\text{burn}), \delta(.)$	0	0.23	7
$\psi_1, \psi_2, p_1(.), p_2(\text{burn}), \delta(.)$	0.10	0.21	6
$\psi_1(\text{burn}), \psi_2, p_1(\text{burn}), p_2(\text{burn}), \delta(.)$	0.22	0.20	8
$\psi_1, \psi_2, p_1(\text{burn}), p_2(\text{burn}), \delta(\text{burn})$	1.89	0.09	8
$\psi_1(\text{burn}), \psi_2(\text{burn}), p_1(\text{burn}), p_2(\text{burn}), \delta(.)$	2.09	0.08	9
$\psi_1, \psi_2, p_1(.), p_2(\text{burn}), \delta(\text{burn})$	2.10	0.08	7
$\psi_1, \psi_2, p_1(.), p_2(.), \delta(.)$	4.02	0.03	5
$\psi_1, \psi_2, p_1(\text{burn}), p_1(\text{burn}), p_2(\text{burn}), \delta(.)$	5.11	0.02	8
$\psi_1, \psi_2, p_1(.), p_2(.), \delta(T)$	5.79	0.01	6
$\psi_1, \psi_2, p_1(\text{burn}), p_2(.), \delta(.)$	5.79	0.01	6
$\psi_1, \psi_2, p_1(.), p_2(T), \delta(.)$	5.96	0.01	6
$\psi_1, \psi_2, p_1(.), p_2(.), \delta(\text{burn})$	5.99	0.01	6
$\psi_1, \psi_2, p_1(T), p_2(.), \delta(T)$	7.79	0	7
$\psi_1, \psi_2, p_1(\text{burn}), p_2(.), \delta(\text{burn})$	7.86	0	7
$\psi_1, \psi_2, p_1(T), p_2(T), \delta(.)$	7.96	0	7
$\psi_1, \psi_2, p_1(T), p_2(.), \delta(.)$	9.43	0	6
$\psi_1, \psi_2, p_1(T), p_2(T), \delta(T)$	9.74	0	8
$\psi_1, \psi_2, p_1(.), p_2(t), \delta(.)$	11.18	0	14
$\psi_1, \psi_2, p_1(.), p_2(t), \delta(t)$	12.94	0	15
$\psi_1, \psi_2, p_1(t), p_2(.), \delta(t)$	16.10	0	15
$\psi_1, \psi_2, p_1(.), p_2(.), \delta(t)$	16.63	0	14
$\psi_1, \psi_2, p_1(t), p_2(t), \delta(.)$	24.97	0	23
$\psi_1, \psi_2, p_1(t), p_2(t), \delta(t)$	37.59	0	32

1). The model-averaged estimate of site-occupancy probability for at least a single owl (ψ_1) was $0.922 (\pm 0.073)$, after accounting for detection and classification probabilities. Mean site-occupancy probability for pairs (ψ_2) was $0.866 (\pm 0.093)$. Detection (p) was 0.196 for singles (± 0.122) and 0.613 for pairs (± 0.038). Probability that pair-occupied sites were correctly classified (δ) was $0.555 (\pm 0.046)$.

Model-averaged estimates of occupancy showed a slight decrease in occupancy as the percent of PAC burned at high severity increased ($\psi_1 \beta = -0.216 \pm 0.155$), but occupancy when the PAC burned at 100% high severity remained higher than 0.89, and no decrease was evident for sites occupied by a pair (Figure 1). Detection probability for both singles and pairs decreased as a function of the covariate describing percent of PAC burned at high severity ($p_1 \beta = -0.871 \pm 0.884$; $p_2 \beta = -0.223 \pm 0.087$). An average of 37% (SD = 35%, range 0–100%) of the area of pre-fire 121 ha PACs burned at high severity.

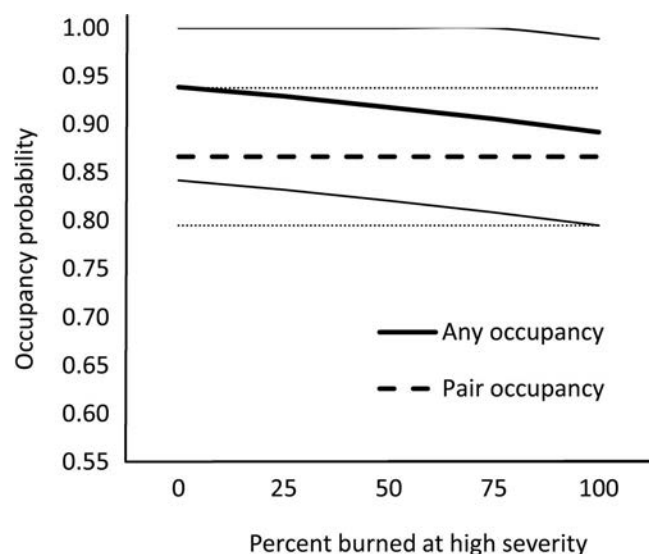


FIGURE 1. Model-averaged site occupancy probability in 2014 for occupancy by at least a single owl (thick solid line) and pairs (thick dashed line) in known California Spotted Owl sites burned during the 2013 Rim Fire. Site occupancy probability is presented as a function of the percent of the site's 121 ha Protected Activity Center that was burned at high severity. Thin solid lines and thin dotted lines are ± 1 SE for any occupancy and pair occupancy, respectively.

DISCUSSION

We examined the short-term response of California Spotted Owls to a large wildfire using survey data collected by USFS biologists. We documented high occupancy probabilities for historical California Spotted Owl sites during the first breeding season after the Rim Fire. Our estimated site occupancy probability after the Rim Fire was greater than estimates from burned and long-unburned sites previously reported for the subspecies in the Sierra Nevada, although there were some differences in methods among studies. Lee et al.'s (2012) estimated annual occupancy in sites throughout the Sierra Nevada from 1997 to 2007 was 0.80 in burned forests and 0.76 in forests without recent fire and encompassed longer-term effects of up to 7 years post fire. Tempel and Gutiérrez (2013) estimated 0.67 occupancy probability in the most recent year of their study (2010) in forests of the central Sierra Nevada that were largely unaffected by recent fire.

Our occupancy estimates for California Spotted Owls after the Rim Fire could be higher, lower, or the same as pre-fire occupancy. Occupancy status was known for only 9 of the 45 sites 1 year prior to the Rim Fire and for 6 sites 2 years prior to fire (USFS personal communication). The paucity of these data preclude modeling for occupancy estimates, but naïve occupancy estimates of the 13 sites surveyed during any of the 2 pre-fire years showed: 2 sites with no detections before the fire were occupied by pairs

after the fire; 1 territorial single had a mate after the fire; 8 were occupied by pairs both before and after the fire; 1 territory with a pair had a single bird after the fire; and 1 territory with a single bird before the fire became unoccupied after the fire. Therefore, 3 sites had upgraded occupancy status post-fire, 2 had downgraded occupancy status, and 8 were unchanged, which supports the hypothesis that the Rim Fire was not detrimental to Spotted Owls in the short term. We were unable to examine effects of the Rim Fire on California Spotted Owl reproduction with these data, but data from other study areas have shown no effect of fire on reproductive success in occupied burned sites (Bond et al. 2002, Roberts 2008, Lee and Bond personal communication). Longer-term monitoring of owl sites in the Rim Fire—particularly monitoring of reproduction—without the confounding effect of post-fire salvage logging within home ranges will be essential to elucidate the influence of fire-induced vegetation changes on California Spotted Owls.

Our results indicate that forests within the Rim Fire area contained adequate amounts of Spotted Owl habitat for continued post-fire occupancy in the first breeding season following the fire. Site occupancy probability is positively correlated with habitat quality when animals tend to consistently occupy the highest-quality habitats (Rodenhous et al. 1997, Sutherland 1997, Sergio and Newton 2003) and is likely the case for California Spotted Owls in the Sierra Nevada because site occupancy, reproductive output, and apparent survival are all positively correlated with the amount of Spotted Owl habitat in a 200–800 ha area surrounding the nest (Blakesley et al. 2005). The high occupancy rates in this study could indicate that Spotted Owl territories of the Rim Fire area are (or were, prior to fire) of above-average quality relative to other burned and long-unburned sites throughout the Sierra Nevada. However, the high site fidelity of the subspecies (Gutiérrez et al. 1995, Blakesley et al. 2006) could also mean that some owls may have remained in burned territories that are no longer of high habitat quality because they had occupied the site in the previous year. Importantly, vegetation changes and subsequent changes in prey species composition and/or abundance as a result of the Rim Fire began 6 months before surveys were initiated, providing resident owls time to evaluate post-fire habitat conditions and distribute themselves accordingly (Zimmerman et al. 2003). We believe the high rates of occupancy 1 year after the Rim Fire compared favorably with other study areas, and that the post-fire increase in naïve occupancy status compared with pre-fire suggested that the burned sites retained sufficient suitable owl nesting, roosting, and foraging habitat, at least in the short term. Longer-term monitoring of these sites will determine the temporal durability of our observed high occupancy rates.

Estimated occupancy by at least a single bird in the Rim Fire was negatively correlated with amount of high-severity fire in the PAC. Spotted owls likely occupy sites according to an ideal despotic distribution, with the highest-quality sites claimed by the most dominant pairs (Fretwell 1972, Zimmerman et al. 2003). Thus, high-severity fire may have reduced occupancy only in lesser-quality sites. The amount of high-severity fire in the PAC did not affect pair occupancy, and the majority of sites (33 of 46 of the naïve estimate) were occupied by pairs. Notably, 6 pair-occupied PACs had >70% habitat burned at high severity. Thus, the occurrence of even high levels of high-severity fire within these PACs did not alter or reduce habitat such that occupancy of the site by pairs was immediately affected.

Studies from the Sierra Nevada indicate that the “complex early seral forest” created by high-severity fire, with its structural complexity such as abundant snags and downed logs, pockets of surviving trees, montane chaparral patches, and natural conifer regeneration (DellaSala et al. 2014), may provide habitat for the small mammal prey of California Spotted Owls (Bond et al. 2009, 2013). Additionally, even within high-severity fire areas, considerable numbers of overstory trees can survive the fire, often containing no green needles immediately after fire when satellite imagery is taken for fire-severity mapping but flushing with new foliage 1 year post-fire (Hanson and North 2009). The USFS (2014c) mapped areas with $\geq 75\%$ basal area mortality as high severity in the Rim Fire, therefore incorporating some moderately burned stands with surviving overstory trees into the high-severity category. Thus, a substantial amount of vegetation heterogeneity can occur even within areas mapped as high severity, potentially contributing to habitat structure used by Spotted Owls, and residual pockets of surviving trees can serve as Spotted Owl nesting areas (LaHaye and Gutiérrez 1999).

Our findings add to the growing body of research that fire, even high-severity fire, is not a major threat to the persistence of California Spotted Owls in the Sierra Nevada (Bond et al. 2002, 2009, Roberts 2008, Roberts et al. 2011, Lee et al. 2012). No difference in occupancy rates was detected between 41 burned and 145 long-unburned breeding sites throughout the Sierra Nevada up to 7 years post-fire in managed national forests (Lee et al. 2012), and occupancy rates were similar between burned (within 2–15 years) and long-unburned randomly selected survey areas in unmanaged forests in Yosemite National Park (Roberts et al. 2011). Further, radio-tagged California Spotted Owls in the southern Sierra Nevada selected forest patches burned at high severity for foraging within 1.5 km of their core nest and roost areas 4 years after fire (Bond et al. 2009), and radio-tagged Mexican Spotted Owls (*S. o. lucida*) moved to wintering areas that burned 4–6 years earlier and had a greater abundance and biomass of small

mammal prey than nest core areas (Ganey et al. 2014), demonstrating that high-severity fires can provide foraging benefits during both breeding and nonbreeding seasons.

In contrast to fire, multiple studies show that logging is detrimental to this declining subspecies (Seamans and Gutiérrez 2007, Tempel et al. 2014), even when the largest trees and a minimum of 40% canopy cover is retained (Stephens et al. 2014). Post-fire logging also apparently reduces site occupancy; Lee et al. (2012) reported 7 sites that were burned and later salvage-logged were occupied by owls after the fire but not after logging. Tempel et al. (2014) compared occupancy dynamics in 12 burned sites relative to 62 unburned sites over 7 years and concluded that burned sites had lower colonization rates, but this inference suffered from small sample size (5 of 9 sites burned in the largest fire remained occupied every year post-fire so were unavailable for colonization), and post-fire salvage logging occurred in the remaining sites (M. Bond personal communication), which confounded the effects of fire with logging.

Our results indicate that managers should not immediately assume Spotted Owls vacate burned sites, even with large areas of high-severity fire in a PAC. We believe it is valid to reconfigure PACs after high-severity fire to incorporate and conserve closed-canopy nesting–roosting–foraging habitat because this important habitat type can be patchily distributed in the vicinity of owl nests or roosts, especially after fire. However, conservation of burned foraging habitat is also likely necessary to maintain site occupancy. Results from this and other studies suggest that the most prudent course of action is to forgo logging activities in burned forests within 1.5 km of the post-fire nest or roost core to provide easily accessible potential foraging habitat within the larger home range (Bond et al. 2009). Lee et al. (2012) recommended a minimum of 2 years of adequate occupancy surveys to demonstrate that owls are no longer occupying a site, but the probability that unoccupied burned sites were recolonized by owls was 0.381 per year (± 0.051), so even post-fire unoccupied sites stand a good chance of being utilized in the future. Therefore, we also suggest retaining burned sites within the PAC network for the conservation and recovery of this declining subspecies. Overall, we encourage land managers to recognize fire as a natural rejuvenating process of Sierra Nevada forests (DellaSala et al. 2014) and to no longer assume burned forest is unsuitable California Spotted Owl habitat when planning and implementing management activities in PACs and HRCAs.

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RESEARCH ARTICLE

Previous year's reproductive state affects Spotted Owl site occupancy and reproduction responses to natural and anthropogenic disturbances

Derek E. Lee* and Monica L. Bond

Wild Nature Institute, Hanover, New Hampshire, USA

* Corresponding author: derek@wildnatureinstitute.org

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ABSTRACT

Understanding interactions among site occupancy, reproduction, vegetation, and disturbance for threatened species can improve conservation measures, because important aspects of vegetation and disturbances may be identified and managed. We used 9 yr of survey data collected at 168 sites to investigate dynamic site occupancy and reproduction in a declining population of California Spotted Owls (*Strix occidentalis occidentalis*) in southern California, USA. We used multistate models to examine the relationship among owl site occupancy, reproduction, high-severity wildland fire, and postfire logging, while accounting for variation in vegetation characteristics and variation in detectability. Both occupancy and reproduction were positively correlated with successful reproduction in the previous year. Tree cover (ha) in a site's 203-ha core area also was positively correlated with both occupancy and reproduction. We detected no effect of disturbance covariates on reproduction, given that a site was occupied. Fire and logging covariates were both negatively correlated with the probability of site occupancy, and the effect sizes of these disturbances were large in sites that were occupied by owls that were nonreproductive the previous year (reduced 0.19 by fire and 0.26 by post-fire logging), but small in sites that were occupied by owls that were reproductive the previous year (reduced 0.02 by fire and 0.03 by postfire logging). This study illustrates the important contribution of consistently occupied and productive breeding sites to this population of Spotted Owls, and demonstrates that both occupancy and reproduction at these productive sites exhibited negligible effects from disturbances. Our results suggest that sites with recent owl reproduction and sites with more tree cover in this study area should receive enhanced protection from management actions that modify vegetation utilized by Spotted Owls.

Keywords: Spotted Owl, occupancy, reproduction, fire, logging, southern California

El estado reproductivo del año anterior afecta la ocupación de sitios y la respuesta reproductiva de *Strix occidentalis* a los disturbios naturales y antrópicos

RESUMEN

Entender las interacciones entre la ocupación de sitios, la reproducción, la vegetación y los disturbios puede mejorar las medidas de conservación de las aves en peligro ya que importantes aspectos de la vegetación y de los disturbios pueden ser identificados y manejados. Empleamos 9 años de datos de muestreo colectados en 168 sitios para investigar la dinámica de ocupación de sitios y la reproducción en una población en disminución de *Strix occidentalis occidentalis* en el sur de California. Empleamos modelos de estado múltiple para examinar la relación entre la ocupación de sitios, la reproducción, los fuegos de gran intensidad de ambientes silvestres y el aprovechamiento forestal post-incendio, mientras consideramos las variaciones en las características de la vegetación y en la detectabilidad. La ocupación y la reproducción se correlacionaron positivamente con una reproducción exitosa en el año anterior. Las hectáreas de cobertura arbórea en un sitio de 203 ha de área núcleo también se correlacionaron positivamente con la ocupación y la reproducción. Considerando que un sitio estaba ocupado, no detectamos un efecto de las covariables del disturbio sobre la reproducción. Las covariables de fuego y aprovechamiento forestal estuvieron negativamente correlacionadas con la probabilidad de ocupación del sitio, y los efectos del tamaño de estos disturbios fueron grandes en los sitios que no fueron usados para reproducción en el año anterior (reducido 0.19 por fuego y 0.26 por aprovechamiento forestal post-incendio), pero fueron pequeños en los sitios usados previamente para reproducción (reducido 0.02 por fuego y 0.03 por aprovechamiento forestal post-incendio). Este estudio ilustra la contribución significativa de los sitios constantemente ocupados y usados para reproducción para esta población de *S. occidentalis*. La ocupación y la reproducción en estos sitios productivos no se vieron afectados por los disturbios. Nuestros resultados sugieren que los sitios reproductivos y los sitios con más cobertura arbórea en esta área de estudio deberían recibir una mayor protección a partir de acciones de manejo que modifiquen la vegetación utilizada por *S. occidentalis*.

Palabras clave: aprovechamiento forestal, fuego, ocupación, reproducción, *Strix occidentalis*, sur de California

INTRODUCTION

Analyzing patterns of site occupancy and reproduction for territorial species can improve conservation measures, because characteristics of the landscape that are important to the species can be identified, measured, and, if possible, managed (Conroy et al. 1995, Dunning et al. 1995, Hurme et al. 2008). The importance of a territory, or breeding site, is best defined by the survival and reproduction of individuals who occupy the site through time (Van Horne 1983, Newton 1989, Franklin et al. 2000), but the site's capability to support occupancy or reproduction may be temporally dynamic as a result of natural and anthropogenic disturbance events (Sutherland 1998, Lee et al. 2012, 2013).

Methods are now well developed for using presence-absence survey data to estimate site occupancy and reproduction probabilities, while accounting for imperfect detectability and state misclassification and incorporating both time- and site-specific vegetation covariates (Nichols et al. 2007, MacKenzie et al. 2009, 2010). Multistate modeling provides a useful measure of productivity by estimating the probability that young are produced at a site, while accounting for imperfect detectability and examining the effects of a site's state during the previous year: (1) vacant, (2) occupied with no young, or (3) occupied with young. Within this framework, we examined the effects of vegetation and disturbance interactions on site occupancy and reproduction for an important indicator of late-seral forests, the California Spotted Owl (*Strix occidentalis occidentalis*), in southern California, USA.

Site occupancy and reproduction of California Spotted Owls are influenced by site-specific vegetation characteristics (Blakesley et al. 2005, Seamans and Gutiérrez 2007). Wildland fire is a major natural disturbance that has affected forests within the range of the Spotted Owl for millennia, with varying pattern, frequency, and intensity across forest types, regions, and time (Swanson et al. 2011). High-severity fires—also called stand-replacement or crown fires—cause widespread mortality of existing vegetation and result in a forest structure no longer dominated by live trees but by herbs, shrubs, and dead trees (Swanson et al. 2011). Only high-severity fires burn intensely enough to initiate ecological succession and restore essential habitat for a variety of fire-dependent and early-seral-stage species (Smucker et al. 2005, Kotliar et al. 2007, Hutto 2008, Fontaine et al. 2009), but data are scarce regarding the specific effects of this type of fire on wildlife characteristically associated with older forests, such as the Spotted Owl. Furthermore, high-severity burned forest is frequently logged—often called 'salvage logging'—which has additional effects on wildlife (Lindenmayer et al. 2004).

Vegetation disturbances such as timber harvest (Seamans and Gutiérrez 2007) and high-severity fire (Lee et al.

2013) may adversely affect the site occupancy dynamics of California Spotted Owls when alterations of forest within a territory exceed a certain threshold. Alternatively, these disturbances may have positive effects on occupancy (Lee et al. 2012) or reproduction (Franklin et al. 2000) by creating heterogeneity, such as complex early seral stands that are used for foraging (Bond et al. 2009) interspersed with older forest stands that are required for nesting and roosting (Gutiérrez et al. 1992).

Site occupancy and reproduction also could be correlated with the state of the site in the previous year. The probability of a site being occupied or supporting reproduction in a given year could be lower when young were produced the previous year because of 'resource depletion' in the territory (Carey et al. 1992, Ganey et al. 2014). Conversely, the probability of a site being occupied or supporting reproduction in a given year could be greater when young were produced the previous year if the site's capability to support occupancy and reproduction ('reproductive capability') is consistently high (Przybylo et al. 2001). The effect of the previous year's state also could vary among years in a complex interaction of state and time (MacKenzie et al. 2009, 2010), or could be absent (no effect of previous year's state).

We investigated dynamic site occupancy and reproduction of California Spotted Owls over a 9-yr period in relation to site-specific vegetation and topographic characteristics, and in response to the disturbances of high-severity wildland fire and postfire logging, in the San Bernardino and San Jacinto mountains of southern California, where populations have declined over the past 2 decades (LaHaye et al. 1994, 2004, Lee et al. 2013). We examined the influence of site- and year-specific covariates of the amount and structure of vegetation, which varied spatially because of climate and geography and temporally because of natural and human-caused disturbances. We performed multistate model selection and estimated the dynamic probability of annual occupancy and reproduction by Spotted Owls in known sites according to the reproductive state of the owls in the site in the previous year, and according to dynamic site-specific vegetation disturbance covariates that we used to classify sites as: (1) unburned, (2) burned and not logged postfire, or (3) burned and logged postfire. All burned sites were surveyed before and after fires, so that prefire occupancy and reproduction data existed for a before-after control-impact analysis (Popescu et al. 2012).

We did not know which owls occupied a given site in our study because birds were not individually marked. Thus, herein we consider occupancy, reproduction, and effects of previous year's state to be characteristics of the site, and these were our metrics of the site's capability to support reproduction in relation to disturbance covariates.

METHODS

Study Area

The San Bernardino Mountains (SBM) and San Jacinto Mountains (SJM) are located ~140–150 km east of Los Angeles, California. The climate is Mediterranean, with most precipitation (500–1,000 mm per year) falling during the winter as rain at lower elevations and as rain and snow at higher elevations (Minnich 1988).

In southern California, Spotted Owls inhabit isolated upper-elevation (915–1,525 m) forests surrounded by lower-elevation desert and semidesert vegetation (Gutiérrez and Pritchard 1990, Gutiérrez et al. 1992, LaHaye et al. 1994, 1997, 2001). Forest fires in these southern Californian forests occur largely as a result of human-caused ignition (Halsey 2005) and typically burn in a mosaic of severities (Weatherspoon et al. 1992, Stephenson and Calcarone 1999), with the largest high-severity fires burning under extreme Santa Ana weather conditions typical of the region (Keeley et al. 2009). Fire has been proposed as a factor in the regional Spotted Owl population decline (LaHaye and Gutiérrez 2005), although empirical evidence is lacking.

In the period 2003–2011, a large proportion (0.42) of Spotted Owl breeding sites in the SBM were affected by wildland fire, which occurred during drought conditions and warmer-than-average temperatures. Two large fires in 2003 and 2007, and several smaller fires during this period, burned through 71 of 181 owl sites that were regularly monitored by U.S. Forest Service biologists. Postfire logging occurred on a subset of 21 sites, and provided us with the opportunity to examine the effects of high-severity fire and postfire logging on Spotted Owl dynamic breeding site occupancy and reproduction from 2003 to 2011.

Spotted Owl Surveys

We defined an owl site as a distinct geographical area deemed to be occupied by seeing or hearing a single or pair of territorial Spotted Owls during surveys from 1989 to 2001. From 1989 to 2001, 181 California Spotted Owl sites within the boundaries of the San Bernardino National Forest in the SBM and SJM (2,140 km²) were identified by annually surveying all forested stands (LaHaye et al. 2004, Gutiérrez et al. 2011). For our study, each year from 2003 through 2011, the U.S. Forest Service attempted to survey as many known Spotted Owl sites as possible from March 1 to August 31, following standardized methods described by Forsman (1983) and Franklin et al. (1996). The U.S. Forest Service provided us with the raw survey data, which we then used to construct an occupancy history database. Because we did not collect data ourselves, we acknowledge that there may be problems with the data that are unknown to us. We

analyzed the data from sites surveyed for >2 consecutive years from 2003 to 2011 ($n = 168$ sites). Our population of interest was historical Spotted Owl sites that were subsequently burned (or not burned) by fire, so it was appropriate to use data from sites where occupancy status had been previously established, rather than from randomly selected sites where previous occupancy status was unknown (MacKenzie and Royle 2005).

Within each year, 2 types of surveys were conducted: (1) presence–absence surveys to initially locate owls in an area, and (2) reproductive surveys to find roosts and nests and to assess the reproductive status of owls detected during presence–absence surveys. All surveys were separated by >48 hr. The presence–absence surveys were conducted by imitating Spotted Owl vocalizations between dusk and dawn from a series of fixed calling stations. If a Spotted Owl responded during a nighttime survey, the presence–absence survey ended, and dusk or dawn reproductive surveys were conducted. Reproduction was estimated by feeding owls live mice (Forsman 1983, Franklin et al. 1996). Successful reproduction was documented when at least 1 owlet was observed outside the nest. A maximum of 6 presence–absence surveys and 4 reproductive surveys were conducted at Spotted Owl sites every year.

The maximum number of surveys at any site in a year was 8, but both the median and mode number of visits across all sites each year was 6, so we truncated all within-year survey histories at 6 surveys for this analysis to reduce the number of missing observations (Olson et al. 2005, Kroll et al. 2010).

Characteristics of Sites

We quantified site-specific vegetation covariates as hectares within a 203-ha circular ‘core area’ around the most recently used Spotted Owl nest tree location or roost centroid (geometric mean of roost locations) for the following variables: total tree cover; amount of coniferous, hardwood, and old-growth (≥ 5 trees ha⁻¹ with crown diameter >9 m) forest; and area of riparian vegetation. The core area was approximately half of the average breeding-season home-range size for California Spotted Owls in the SBM (Zimmerman et al. 2001), and was intended to represent the area of most concentrated use by Spotted Owls during the breeding season (Blakesley et al. 2005, Lee et al. 2012, 2013). We also assigned a site-specific topographic covariate for elevation at the nest tree or roost centroid for each site. Table 1 shows the definitions of our temporal and vegetation covariates.

We used a landscape-level vegetation map developed by GIS analysts from the U.S. Forest Service’s Adaptive Management Services Enterprise Team (AMSET). The base map consisted of a layer of joined and orthorectified 1-m resolution infrared aerial photographs taken of the

TABLE 1. Temporal and vegetation covariates used in modeling detection, occupancy, and reproduction of California Spotted Owls in the San Bernardino Mountains, California, USA, 2003–2011. Predicted effects were: x = no prediction, but effect could be present; + = positive correlation predicted between covariate and parameter; – = negative correlation predicted; +/- = either positive or negative correlation predicted. If predicted effect is blank, the covariate was not modeled for that parameter.

Covariate name	Type	Definition	Predicted effect on parameter				
			δ	$p1$	$p2$	$C\psi$	CR
<i>Survey</i>	Binomial	Within-year, survey-specific variation coded as 5 categorical dummy variables.	x	x	x		
<i>S</i>	Continuous	Linear within-year temporal trend according to survey.	x	x	x		
<i>S2</i>	Continuous	Quadratic within-year temporal trend according to survey.	x	x	x		
<i>S1diff</i>	Binomial	First survey in a year is different from subsequent surveys.	x	x	x		
.	Constant	Constant parameter value through time coded as an intercept only (used within and among years).	x	x	x	x	x
<i>Year</i>	Binomial	Year-specific annual variation coded as categorical dummy variables (7 variables in $C\psi$ and CR ; 8 in δ , $p1$, and $p2$).	x	x	x	x	x
<i>Y</i>	Continuous	Linear annual temporal trend.	x	x	x	x	x
<i>Y²</i>	Continuous	Quadratic annual temporal trend.	x	x	x	x	x
<i>EO</i>	Binomial	Even–odd year effect where alternate years are coded 1 or 0.	x	x	x	x	x
<i>SB</i>	Binomial	Difference between SBM and SJM study sites.	x	x	x	x	x
<i>Elev</i>	Continuous	Site elevation standardized as (elevation – mean) / SD [mean = 0, range = –3 to 3].				+	+
<i>Rip</i>	Continuous	Amount of riparian vegetation computed as hectares in 203-ha core area [mean = 13, range = 0 to 96].	–	–	–	+	+
<i>Tree</i>	Continuous	Amount of tree cover computed as total hectares of conifer and hardwood tree cover in 203-ha core area [mean = 106, range = 44 to 149].				+	+
<i>OG</i>	Continuous	Late-seral stage ‘old growth’ trees in a 203-ha core area computed as hectares with ≥ 5 large trees (>9 m crown diameter) [mean = 30, range = 0 to 148].				+	+
<i>HW</i>	Continuous	Amount (ha) of hardwood tree cover in 203-ha core area [mean = 63, range = 0 to 130].				+	+
<i>Burn</i>	Binomial	Intercept effect of fire between 2003 and 2011 coded 0 in unburned sites in all years, 0 in burned sites in prefire years, and 1 in burned sites in postfire years.	+	+	+	–	+/–
<i>Hisev</i>	Continuous	The amount of suitable forest vegetation burned at high severity within a 203-ha core area [mean = 44, range = 0 to 140].				+/–	+/–
<i>Hisev²</i>	Continuous	The square of <i>hisev</i> , used to model occupancy and reproduction as a quadratic function of the amount of suitable forest vegetation burned at high severity.				+/–	+/–
<i>Salvage</i>	Continuous	Amount (ha) of burned forest clear-cut postfire [mean = 63, range = 0 to 150].				–	–

entire San Bernardino National Forest in 2002. Vegetation was mapped within the Spotted Owl core area circles with a minimum map unit of ~ 2 ha.

We defined burned Spotted Owl sites as those in which the core area was inside or included the perimeter of one of the fires. M. Borchert and C. Hanson provided us with vegetation change data for our analyses. M. Borchert determined the number of hectares of tree cover that burned at high severity by overlaying burn severity and vegetation maps to quantify change in tree cover resulting from fire. High-severity fire induced changes in dominant vegetation by killing $\geq 75\%$ of trees. C. Hanson quantified postfire logging using aerial photographs, obtained from Google Earth, by imposing a grid of 1-ha cells in the 203-ha circle around the nests or roost centroids and estimating the amount of the circle affected by extensive (i.e. clear-cut) postfire tree removal.

GIS Map Accuracy Assessment

To confirm the GIS base map's accuracy in representing the vegetation variables in our analysis, we used field data collected by AMSET biologists within 81 variable-radius plots in 15 randomly selected owl sites. For each owl site, 6 plots were located at fixed distances in randomly selected directions from the most recently occupied nest tree. Plots ranged from a minimum distance of 50 m to a maximum distance of 500 m from the nest. At each plot, AMSET biologists estimated the number of large trees per acre and percent tree cover, and we compared these values (after conversion to hectares) with classifications of those covariates at the same locations from the landscape-level map. We considered percent tree cover to be accurate if the map's estimate was within 10% of the ground-plot estimate. Producer's accuracy was 63% for large tree density and 68% for percent tree cover, and user's accuracy was 58% for large tree density and 64% for percent tree cover. Our map accuracy was somewhat lower, but still comparable to other remotely sensed maps used to analyze Spotted Owl habitats (e.g., accuracy for mature conifer forests = 50–84%, Clark 2007; and 50–71%, Williams et al. 2011).

Statistical Analysis

We used raw survey data to compile occupancy histories for 168 California Spotted Owl sites. Our 9-yr dataset included 97 unburned control sites and 71 burned sites, of which a subset of 21 were logged postfire. We created occupancy histories in which each survey of each site was coded according to observed state: '0' for no Spotted Owls observed, '1' for >0 adults observed, and '2' for >0 owlets observed outside the nest. We used program Presence 4.0 (USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA) to fit models and estimate parameters from occupancy histories following methods developed by MacKenzie et al. (2009, 2010). Readers are directed to

those papers for more detail on the statistical foundation and methods.

We modeled the process that gave rise to our detection history data using the following notation and parameters (from MacKenzie et al. 2009, 2010): ψ = the probability that the area was occupied by the species during the first year of the study; R = the probability that successful breeders were present in the first year of the study, given that the area was occupied by the species; $C\psi x_i$ = the probability that the area was occupied in year i , conditional upon state ($x = 0, 1$, or 2) in year $i - 1$; CRx_i = the probability that successful breeders were present in year i , conditional upon state ($x = 0, 1$, or 2) in year $i - 1$; $p1_i$ = the probability of detecting adult nonbreeders or unsuccessful breeders in year i ; $p2_i$ = the probability of detecting successful adult breeders in year i ; and δ_i = the probability of correctly identifying reproduction (observing young) in year i , given presence ($1 - \delta_i$ = the misclassification parameter).

Model selection. Because we had a large number of temporal and vegetation covariates to consider in detection, occupancy, and reproduction parameters, we adopted a multistage process to build models, similar to the methods in Olson et al. (2005), MacKenzie et al. (2010), and Dugger et al. (2011). We selected the best model within each stage using Akaike's Information Criterion adjusted for small sample size (AIC_c) to rank models (Burnham and Anderson 2002), and the best model structure from a given stage was then used in subsequent stages. Model selection proceeded as follows (a full table of model selection is provided in [Supplementary Material Table S1](#)):

- (1) First, we tested for within-year, survey-specific temporal variability in detection probabilities ($p1$, $p2$, and δ), while holding occupancy and reproduction in their fully time-dependent forms (*state * year*). Detection probabilities could vary because of survey-specific differences in survey staff, weather conditions, and other unmeasured factors. We considered 5 different models of within-year temporal variation: survey-specific (*survey*), constant ($\cdot$), linear trend (S), quadratic trend (S^2), and first survey different from all subsequent surveys (*s1diff*). These models are typical temporal models that have been used in previous occupancy analyses of Spotted Owls (Olson et al. 2005, Dugger et al. 2011).
- (2) We examined whether and how previous year's reproductive state was correlated with current year's occupancy and reproduction by ranking 6 state models. Each model's structure represented a competing hypothesis. The model (*year*) represented no correlation between previous year's state and current year's occupancy or reproduction, so all states were equivalent. The model (*state + year*) represented a

correlation between previous year's state and current year's occupancy or reproduction that was consistent through time, and the competing hypotheses of 'resource depletion' or 'reproductive capability' of a site were differentiated by whether sites that were previously occupied by nonreproductive vs. reproductive owls had greater occupancy and reproduction probabilities. If site occupancy and reproduction probabilities varied because of previous state, such that nonreproductive > reproductive, then 'resource depletion' would be supported. If the opposite (reproductive > nonreproductive) occurred, then 'reproductive capability' would be supported. The model ($state * year$) indicated a complex interaction of state and time (MacKenzie et al. 2009, 2010).

- (3) We examined among-year annual temporal variability in detection probabilities ($p1$, $p2$, and δ), while holding occupancy and reproduction in their previously determined best state- and time-dependent forms ($state + year$). Parameters were modeled as year-specific ($year$), a linear year trend (Y), a quadratic year trend (Y^2), an even-odd year effect (EO), and constant ($.$). We expected that detection, occupancy, and reproduction probabilities could exhibit annual variation due to fluctuations in weather or prey populations, and similar temporal model structures have been detected in previous studies of Spotted Owl occupancy or reproduction (Franklin et al. 2000, Seamans et al. 2002, LaHaye et al. 2004, Blakesley et al. 2010, Lee et al. 2013).
 - (4) We tested for among-year annual temporal variability in occupancy and reproduction probabilities, while holding detection probabilities in their best previously determined structures. Parameters were modeled as in step 3 above.
 - (5) We tested for the effects of fire and study area covariates on detectability. We included site-specific covariates of detection probabilities for burned vs. unburned sites ($burn$), and differences between study areas (SB).
 - (6) We investigated prefire vegetation covariate models of occupancy probability. We included 6 site-specific core area vegetation covariate models of occupancy: hectares of tree cover ($tree$), hectares of hardwood tree cover (HW), hectares of late-seral 'old growth' (OG), hectares of riparian vegetation (rip), elevation ($elev$), and differences between the San Bernardino and San Jacinto mountains (SB).
- California Spotted Owls are typically associated with habitats characterized by large trees and high canopy cover (Gutiérrez et al. 1992, Blakesley et al. 2005, Seamans 2005), and previous work has documented occupancy dynamics related to the site-specific amount of tree cover and elevation (Lee et al. 2013). Therefore,
- we predicted that occupancy would be positively correlated with the amount of tree cover ($tree$) or 'old growth' (OG) within 203 ha of the nest or roost centroid. We expected elevation ($elev$) to be negatively correlated with occupancy probability because of gradients in vegetation type, prey biomass (Smith et al. 1999), and climate (LaHaye et al. 2004). Spotted Owls seek cool roosting sites during periods of warm weather as an adaptation to heat stress (Barrows 1981), and radio-tagged Northern Spotted Owls (*S. o. caurina*) in dry forests of southwestern Oregon select foraging locations closer to perennial streams (Clark 2007); therefore, we predicted that occupancy would be positively correlated with the amount of riparian vegetation (rip). Our model set also included 3 models of occupancy with >1 vegetation covariate: ($tree + elev$), ($tree + rip$), and ($tree + OG$); and 5 models of reproduction with >1 vegetation covariate: ($tree + elev$), ($tree + rip$), ($tree + OG$), ($tree + SB$), and ($tree + elev + OG$).
- (7) We examined prefire vegetation covariate models of reproduction probability. We predicted that there would be site-specific, vegetation-related effects on reproduction, such that elevation ($elev$) would be negatively correlated with reproduction (LaHaye et al. 1997, Blakesley et al. 2005), and that the following covariates would be positively correlated with reproduction: tree cover ($tree$; Blakesley et al. 2005, Forsman et al. 2011), hardwood tree cover (HW ; LaHaye et al. 1997), 'old growth' (OG ; Blakesley et al. 2005), and riparian vegetation (rip ; Clark 2007).
 - (8) We tested high-severity fire and postfire logging covariate models of occupancy probability. We ranked 6 models of fire and postfire logging effects. We modeled fire effects as a postfire change in intercept ($burn$), and with continuous covariates of vegetation change from high-severity fire as linear ($burn + hisev$) and quadratic ($burn + hisev^2$) functions of the hectares of trees killed by fire within the core area. We modeled the intercept effect of fire between 2003 and 2011 as a time-varying, site-specific, categorical covariate that was coded 0 for unburned sites in all years, 0 for burned sites in years before the fire, and 1 for burned sites in years after the fire. All fires burned after surveys ended for the year, so fire did not affect within-season conditions in this study.

Linear and quadratic covariates of tree cover burned at high severity were previously shown to affect California Spotted Owl site occupancy in southern California (Lee et al. 2013). We included a site-specific covariate for postfire logging ($burn + salvage$) as a linear function of the hectares of postfire clear-cut within the core area. Our model set also included ($burn + hisev^2 + salvage$), and a null (no fire effects) model.

- (9) Finally, we tested fire and postfire logging covariate models for reproduction probabilities that were the same as for occupancy probabilities in step 8 above.

We assessed support for models of the effects of vegetation, high-severity fire, and postfire logging on occupancy, reproduction, and detection parameters using AIC_c weights (Burnham and Anderson 2002, Doherty et al. 2010). The effect of a specific covariate was inferred to be significant when the 95% confidence interval of the beta coefficient did not include zero.

RESULTS

The mean number of Spotted Owl sites surveyed each year (2003–2011) that had also been surveyed in the previous year was 76 for unburned sites (SD = 24, minimum = 39) and 52 for burned sites (SD = 16, minimum = 31). In years after the first fire burned in 2003, the mean annual proportion of surveyed sites that were in the burned group was 0.37 (SD = 0.09).

Site-Specific Covariates

The mean amount of prefire tree cover within all (168) core areas was 106 ha (SD = 24, range = 44–149). The mean amount of tree cover that burned at high severity within the 71 burned core areas was 24 ha (SD = 31, range = 0–120). Postfire logging occurred on 21 burned sites. The mean amount of postfire logging in logged burned sites was 63 ha (SD = 53, range = 0–150). Sites at higher elevations tended to support a greater amount of tree cover prefire ($t_{167} = 2.77$, $P = 0.006$), but among burned sites the amount of tree cover burned at high severity within a core area was similar at all elevations ($t_{70} = -1.19$, $P = 0.23$).

Detection

The top-ranked model of detection probability was $\{\delta(Y + s1diff + burn + SB), p1(year + . + burn + SB), p2(year + s1diff + burn + SB)\}$, which indicated that the probability of correctly identifying reproduction (δ) increased linearly across years (Figure 1), and that, within years, the probability of correctly identifying reproduction was significantly lower during the first survey than in all subsequent surveys (mean 1st survey $\hat{\delta} = 0.012$, mean 2nd–6th surveys $\hat{\delta} = 0.331$). The probability of detecting owls given that they were unsuccessful or nonbreeders ($p1$) varied annually (Figure 2), but was constant within years (mean $\hat{p1} = 0.315$). The probability of detecting owls given that they were successful breeders ($p2$) varied annually (Figure 2), and, within years, the probability of detecting owls during the first survey was significantly lower than in all subsequent surveys (mean 1st survey $\hat{p2} = 0.756$, mean 2nd–6th surveys $\hat{p2} = 0.873$). Beta coefficients and 95%

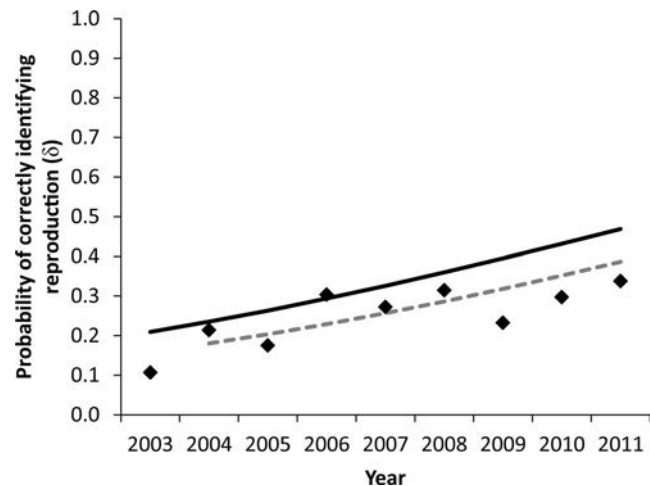


FIGURE 1. The probability of correctly identifying reproduction (δ) during surveys for California Spotted Owls in unburned sites (solid black line) increased linearly across years in the San Bernardino Mountains, California, USA. There was a lower probability of correctly identifying reproduction in sites that burned (dashed gray line). Linear estimates are from the top-ranked model (Supplementary Material Table S1). Black diamonds are annual estimates of δ from the fully parameterized (state * year) model of all parameters.

confidence intervals are presented in Supplementary Material Table S2.

The probability of correctly identifying reproduction (δ) in burned sites was 0.068 lower than in unburned sites, the probability of detection of unsuccessful or nonbreeders ($p1$) was 0.063 lower in burned sites relative to unburned sites, and the probability of detection of successful breeders ($p2$) was 0.024 greater in burned sites relative to unburned sites (Figures 1 and 2). Although none of the effects of high-severity burns on detection probabilities were statistically significant (Supplementary Material Table S2), we retained these effects on detection probabilities when modeling occupancy and reproduction because they were present in most of the top detection probability models, and because ignoring covariates of detection probabilities can introduce biased results into the main effects of interest (Popescu et al. 2012). The SBM study area had significantly greater δ , $p1$, and $p2$ than the SJM study area (Supplementary Material Table S2).

Occupancy and Reproduction

Influence of previous state. Reproductive state in the previous year was significantly correlated with the current year's occupancy and reproduction (Supplementary Material Table S1, section 2). Occupancy and reproduction probabilities were consistently much greater for sites that were occupied by reproductive owls in the previous year vs. sites that were previously occupied by nonreproductive

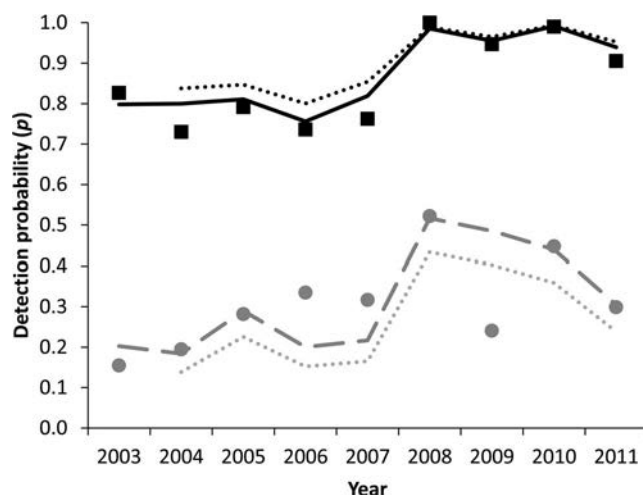


FIGURE 2. The probability of detecting California Spotted Owls at occupied sites in which owls were either reproductive (p_2 , solid black line) or nonreproductive (p_1 , dashed gray line) in the San Bernardino Mountains, California, USA, 2003–2011. In sites that burned, there was a lower probability of detecting nonreproductive owls (dotted gray line) and a higher probability of detecting reproductive owls (dotted black line). Linear estimates are from the top-ranked model (Supplementary Material Table S1). Squares (■) and filled circles (●) are year-specific estimates of p_2 and p_1 , respectively, from the fully parameterized (state * year) model of all parameters.

owls or vacant (Figures 3 and 4). This result supports the ‘reproductive capability’ hypothesis.

The top-ranked temporal model was $C\psi(\text{state} + Y^2)$ and $CR(\text{state} + \text{year})$. Mean initial site occupancy probability was $\hat{\Psi} = 0.65$, and mean initial probability of reproduction was $\hat{R} = 0.56$. Mean state-dependent occupancy probability was $\hat{C}\Psi = 0.126, 0.759$, and 0.985 for sites which in the previous year were vacant, held nonreproductive owls, and held reproductive owls, respectively. Mean state-dependent reproductive probability was $\hat{C}R = 0.048, 0.283$, and 0.819 for sites which in the previous year were vacant, held nonreproductive owls, and held reproductive owls, respectively. The coefficient of variation (SD / mean across all years) in reproduction probability was $R\text{ CV} = 0.76, 0.56$, and 0.13 for sites which in the previous year were vacant, held nonreproductive owls, and held reproductive owls, respectively.

Prefire vegetation. The top-ranked vegetation covariate model of occupancy was $C\psi(\text{tree} + \text{elev})$, and the second-ranked model was $C\psi(\text{tree})$. $CR(\text{tree})$ was the only statistically significant vegetation covariate of occupancy or reproduction (Supplementary Material Table S2).

Fire and logging. The top-ranked model of the effects of fire on occupancy revealed significantly lower occupancy in burned vs. unburned sites, and showed that occupancy was further significantly reduced according to

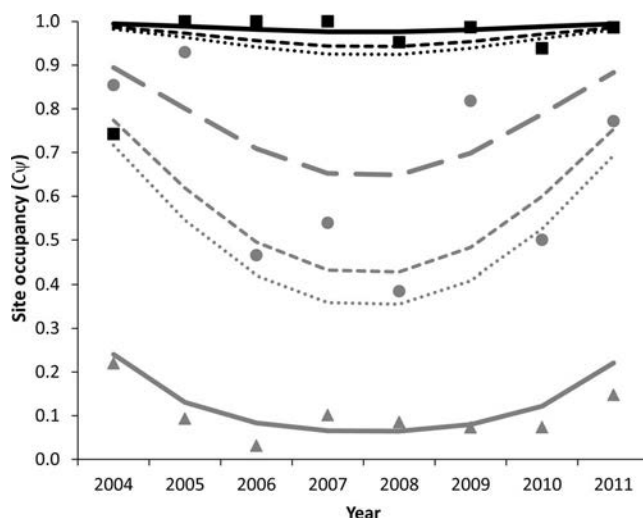


FIGURE 3. California Spotted Owl dynamic occupancy probability ($C\psi$) at sites which in the previous year supported reproductive owls (state 2, solid black line), nonreproductive owls (state 1, long-dashed gray line), or were vacant (state 0, solid gray line) in the San Bernardino Mountains, California, USA, 2004–2011. There was a reduced probability of occupancy in sites that burned relative to unburned sites (state 2, short-dashed black line; state 1, short-dashed gray line), and site occupancy was further reduced by postfire logging (state 2, dotted black line; state 1, dotted gray line), but the effect sizes were much smaller in sites that previously supported reproductive owls (black lines). Linear estimates are from the top-ranked model (Supplementary Material Table S1). Squares (■), filled circles (●), and triangles (▲) are year-specific estimates of occupancy for the 3 states from the fully parameterized (state * year) model of all parameters.

how much of the core area was logged postfire (Figure 3, Supplementary Material Table S2). The occupancy of sites that supported reproductive owls the previous year was reduced 0.02 by fire and 0.03 by postfire logging. The occupancy of sites that were occupied by nonreproductive owls the previous year was reduced 0.19 by fire and 0.26 by postfire logging. The top-ranked model of fire and logging effects on reproduction indicated no significant effects of either covariate (Supplementary Material Table S2). The final, top-ranked model was $\{C\psi(\text{state} + Y^2 + \text{tree} + \text{elev} + \text{burn} + \text{salvage}), CR(\text{state} + \text{year} + \text{tree}), \delta(Y + s1\text{diff} + \text{burn} + SB), p1(\text{year} + \text{burn} + SB), p2(\text{year} + s1\text{diff} + \text{burn} + SB)\}$.

DISCUSSION

Our study used multistate modeling of dynamic site occupancy and reproduction of California Spotted Owls in southern California to examine the effects of previous reproductive state and site-specific vegetation characteristics on responses to wildland fire and postfire logging for this important management indicator species.

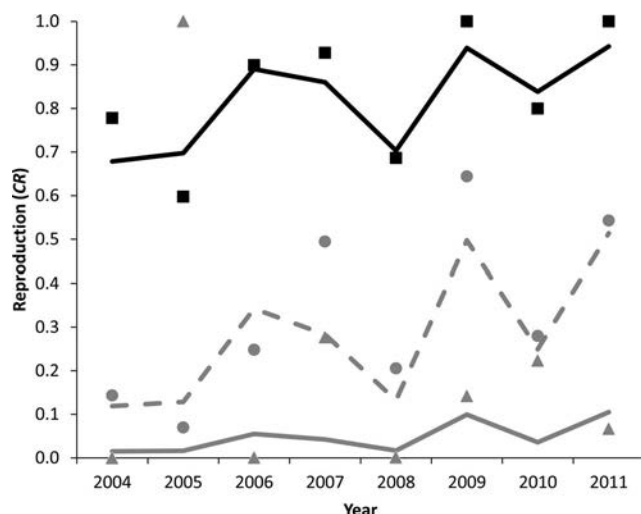


FIGURE 4. Dynamic probability of reproduction (CR) of California Spotted Owls at sites which in the previous year supported reproductive owls (state 2, solid black line), nonreproductive owls (state 1, dashed gray line), or were vacant (state 0, solid gray line) in the San Bernardino Mountains, California, USA, 2004–2011. Linear estimates are from the top-ranked model (Supplementary Material Table S1). Squares (■), filled circles (●), and triangles (▲) are year-specific estimates of occupancy for the 3 states from the fully parameterized (state * year) model of all parameters.

Effects of Previous State

Both occupancy and reproduction probabilities of California Spotted Owls were much greater at sites that were occupied by breeding owls in the previous year (Figures 3 and 4), after accounting for variation in vegetation characteristics. This result supports predictions from the ‘reproductive capability’ hypothesis. We interpret this to indicate the presence of sites that were consistently occupied by successfully reproductive owls over time. It could be that variation in geography or vegetation influenced a site’s habitat and prey base and led to these sites being consistently occupied and productive regardless of the reproductive abilities of the individual owls present, or that individuals with high reproductive abilities occupied the sites with the best habitat and that this combination of individual and habitat attributes led to consistent occupancy and reproduction. Our inferences cannot extend to individual owls when our sampling unit was the site, but one can expect positive correlations between individual and site reproductive capability when intrinsically superior individuals settle preferentially in the sites with the best habitat (Fretwell 1972, Lomnicki 1988). Additionally, many avian species, including California Spotted Owls, exhibit a pattern of greater fidelity to breeding sites for individuals that were reproductively successful than for those that were not (Greenwood and Harvey 1982, Blakesley et al. 2006, Gutiérrez et al. 2011).

Our methods attempted to account for variation in site vegetation characteristics while examining evidence for ‘reproductive capability’ vs. ‘resource depletion’ effects, but our GIS map for vegetation was not highly accurate. Thus, the ‘reproductive capability’ effect could result from variation in site-specific characteristics that we could not account for with our vegetation covariates.

Our results differ from those of 2 similar studies of a population of California Spotted Owls in the central Sierra Nevada (Eldorado study area), where previous year’s reproductive state was not an important determinant of occupancy or reproduction (MacKenzie et al. 2009, 2010). Our methods were based directly upon the methods of those 2 studies, so comparisons are valid. Differences in habitat–demography relationships, mediated by the different vegetation, climate, and anthropogenic impacts in the 2 regions, could explain the observed patterns. One possibility may be that the Sierra Nevada population is at or above carrying capacity while the southern California population is below carrying capacity, in which case we would expect demographic patterns to be obscured in the Sierra Nevada relative to southern California (Pulliam 2000). Spotted Owl populations have declined in the Sierra Nevada (Tempel and Gutiérrez 2013, Conner et al. 2013), but it is likely that the amount of habitat has also declined because of extensive commercial logging (Seamans and Gutiérrez 2007), therefore the Sierra Nevada population could be at or above carrying capacity while also at a substantially lower population size than previously documented. California Spotted Owl populations in southern California have declined as well (LaHaye et al. 1994, 2004, Lee et al. 2013), but forests here are much less affected by recent commercial logging, and more affected by drought, water diversions, and urbanization (LaHaye and Gutiérrez 2005).

Effects of Disturbance

Site-specific vegetation covariates, including our disturbance variables of interest, high-severity fire and postfire logging, were important factors affecting detection and misclassification probabilities. It is now well established that vegetation and other site-specific covariates should be included in model selection procedures for detection and other ‘nuisance’ probabilities, in order to produce unbiased estimates of occupancy and reproduction (Popescu et al. 2012, Lee et al. 2012, 2013). It is particularly important to examine the influence of a study’s main effect of interest upon ‘nuisance’ parameters if researchers hope to produce robust results (Popescu et al. 2012).

In southern California, we found that high-severity fire and postfire logging were correlated with a significant reduction in Spotted Owl site occupancy probability, but that the negative effects were small in sites that supported reproductive owls the previous year (reduced 0.02 by fire

and 0.03 by postfire logging, respectively) and pronounced in sites that were occupied by nonreproductive owls the previous year (reduced 0.19 by fire and 0.26 by postfire logging; Figure 3). As with the influence of prior reproductive state, the effects of high-severity fire on Spotted Owl site occupancy also differed between southern California and the Sierra Nevada. Burned sites in the Sierra Nevada had slightly greater occupancy relative to unburned sites (Lee et al. 2012). Although the mean percentage of high-severity burned tree cover in owl core areas was similar between the 2 regions, owl sites in the Sierra Nevada had substantially greater amounts of prefire tree cover and thus retained more postfire unburned or lightly burned closed-canopy nesting and roosting habitat, potentially explaining the differences in the effects of fire on occupancy between the 2 areas (Lee et al. 2012, 2013). Further, vegetation and climate differ substantially between the regions.

Reproduction in occupied sites in our study area was unaffected by high-severity fire and postfire logging during the study period. Our results agree with previous studies on reproduction of Spotted Owls after fire, indicating that productivity in occupied burned sites is no different from (Jenness et al. 2004, Clark 2007), or may be greater than, productivity in occupied unburned sites (Bond et al. 2002). Our multistate modeling using 9 yr of owl survey data for 168 sites in 2 mountain ranges that experienced multiple fires corroborates results from earlier studies in other regions. Our and other studies suggest that, in Spotted Owl breeding sites with habitat characteristics that support occupancy, reproductive rates are similar in both burned and unburned areas.

We found no significant effect of elevation on reproduction, but elevation was found to be a significant factor in previous studies of Spotted Owl reproduction (LaHaye et al. 1997, Blakesley et al. 2005). The number of young fledged per pair could have been greater at lower elevations in our study, but our multistate modeling quantified reproduction at a site as binomial (0 or 1). Thus, the probability of successfully reproducing at lower-elevation sites is not greater than at higher-elevation sites, but more juveniles per pair apparently are fledged at lower elevations in this region (LaHaye et al. 1997). These lower-elevation owl sites were more vulnerable to high-severity fire during our study period (Lee et al. 2013). Therefore, we recommend strengthening efforts to reduce human-caused ignitions at the wildland–urban interface in the lower elevations of the San Bernardino and San Jacinto mountains to reduce the potential for high-severity fire to exceed critical thresholds in owl sites.

Importance of Productive Breeding Sites

This study illustrates the important contribution of productive breeding sites to this population of Spotted

Owls. Zimmerman et al. (2003) noted that Spotted Owls in our study population tended to occupy sites where they were more likely to replace themselves. Although fire and postfire logging covariates were associated with reduced site occupancy, the effect sizes of these disturbances in the sites where owls reproduced the previous year were small. We were unable to quantify whether owls rearranged themselves according to an ideal despotic distribution after disturbance because we did not have data on individual survival and fecundity (*sensu* Franklin et al. 2000), but the greater overall productivity at sites where young were produced the previous year compared with sites where breeding did not occur, regardless of disturbance, indicates that some sites were more important than others.

The majority of Spotted Owl core areas in the SBM and SJM experienced high-severity fires that were below the critical threshold that reduced occupancy (>50 ha forested area in the 203-ha core), even during this period of extreme drought and elevated fire activity (Lee et al. 2013). Severe fire that burned owl core areas throughout the Sierra Nevada from 2000 to 2007 also did not reduce site occupancy (Lee et al. 2012), and severely burned forests in the southern Sierra Nevada that were not logged after fire had a greater probability of use by foraging Spotted Owls than unburned forests (Bond et al. 2009). Therefore, the occurrence of high-severity forest fire does not necessarily translate into adverse effects on California Spotted Owls.

In contrast, prior studies have demonstrated that Spotted Owls and other species have been adversely affected by logging projects intended to reduce the future risk of high-severity fire, including postfire logging and green-tree thinning. California Spotted Owls in the Sierra Nevada avoided foraging and showed reduced occupancy in recently implemented landscape-scale logging projects designed as firebreaks (Stephens et al. 2014), and Northern Spotted Owls avoided foraging in stands that were logged postfire (Clark 2007). In addition, many avian species that colonize postfire forests were significantly less abundant in postfire-logged patches (Saab et al. 2007, Hanson and North 2008, Hutto 2008, Cahall and Hayes 2009). Therefore, we urge managers to consider that the purpose and need for postfire logging, and for fuels treatments intended to reduce the risk of high-severity fire, conflicts with conservation of the Spotted Owl and other species.

Assessments of Spotted Owl sites based on recent reproductive output can provide an efficient and accurate measure of the relative contribution of specific sites to population growth (Sergio and Newton 2003, Peery and Gutiérrez 2012), and can enable managers to prioritize conservation efforts at sites that support high levels of reproduction (Sergio et al. 2009). In southern California, where both demographic and site-occupancy data strongly indicate a declining owl population, sites with successfully reproducing owls likely are making consistent, relatively

large contributions to overall population growth (Runge et al. 2006). Our results indicate that occupancy of these important sites that consistently supported reproductive owls exhibited negligible effects from high-severity fire. Protective measures should be in place for all known Spotted Owl sites, but sites with recent owl reproduction and sites with higher amounts of tree cover in the 203-ha core area should receive enhanced protection from management actions that modify vegetation utilized by Spotted Owls, including fuels treatments and postfire logging.

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Dynamics of Breeding-Season Site Occupancy of the California Spotted Owl in Burned Forests

Author(s): Derek E. Lee , Monica L. Bond and Rodney B. Siegel

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DYNAMICS OF BREEDING-SEASON SITE OCCUPANCY OF THE CALIFORNIA SPOTTED OWL IN BURNED FORESTS

DEREK E. LEE¹, MONICA L. BOND, AND RODNEY B. SIEGEL

The Institute for Bird Populations, P. O. Box 1346, Point Reyes Station, CA 94956

Abstract. Understanding how habitat disturbances such as forest fire affect local extinction and probability of colonization—the processes that determine site occupancy—is critical for developing forest management appropriate to conserving the California Spotted Owl (*Strix occidentalis occidentalis*), a subspecies of management concern. We used 11 years of breeding-season survey data from 41 California Spotted Owl sites burned in six forest fires and 145 sites in unburned areas throughout the Sierra Nevada, California, to compare probabilities of local extinction and colonization at burned and unburned sites while accounting for annual and site-specific variation in detectability. We found no significant effects of fire on these probabilities, suggesting that fire, even fire that burns on average 32% of suitable habitat at high severity within a California Spotted Owl site, does not threaten the persistence of the subspecies on the landscape. We used simulations to examine how different allocations of survey effort over 3 years affect estimability and bias of parameters and power to detect differences in colonization and local extinction between groups of sites. Simulations suggest that to determine whether and how habitat disturbance affects California Spotted Owl occupancy within 3 years, managers should strive to annually survey ≥ 200 affected and ≥ 200 unaffected historical owl sites throughout the Sierra Nevada 5 times per year. Given the low probability of detection in one year, we recommend more than one year of surveys be used to determine site occupancy before management that could be detrimental to the Spotted Owl is undertaken in potentially occupied habitat.

Key words: *California Spotted Owl, colonization, extinction, occupancy, site-occupancy modeling, Strix occidentalis.*

Dinámicas de la Ocupación de Sitio por *Strix occidentalis occidentalis* en la Estación Reproductiva en Bosques Quemados

Resumen. Entender la manera en que los disturbios de hábitat, como los incendios forestales, afectan la extirpación y la probabilidad de colonización—el proceso que determina la ocupación del sitio—es crucial para desarrollar un manejo forestal adecuado para la conservación de *Strix occidentalis occidentalis*, una subespecie cuyo manejo es preocupante. Usamos datos de 11 años de monitoreo de la estación reproductiva de 41 sitios de presencia de *S. o. occidentalis* quemados en seis incendios forestales y 145 sitios en áreas no quemadas a lo largo de Sierra Nevada, California, para comparar las probabilidades de extirpación y colonización en sitios quemados y no quemados tomando en cuenta las variaciones en detectabilidad anuales y específicas de cada sitio. No encontramos efectos significativos de los incendios en estas probabilidades, sugiriendo que los incendios, incluso aquellos que queman en promedio 32% del hábitat adecuado con una alta severidad dentro de un sitio de presencia de *S. o. occidentalis*, no amenazan la persistencia de la subespecie en el paisaje. Empleamos simulaciones para examinar como diferentes asignaciones de esfuerzo de monitoreo a lo largo de tres años afectan la capacidad de estimación y sesgan los parámetros y el poder para detectar diferencias en colonización y extirpación entre los grupos de sitios. Las simulaciones sugieren que para determinar si y cómo los disturbios de hábitat afectan la ocupación de *S. o. occidentalis* a lo largo de tres años, los gestores deberían esforzarse para monitorear anualmente ≥ 200 sitios históricos de la especie afectados y ≥ 200 no afectados a lo largo de Sierra Nevada cinco veces por año. Dada la baja probabilidad de detección en un año, recomendamos que se use más de un año de monitoreo para determinar la ocupación antes de aplicar manejos que podrían ser negativos para *S. o. occidentalis* en sitios potencialmente ocupados.

INTRODUCTION

Reliable estimates of a population's vital rates are essential for wildlife conservation and management (Williams et al. 2002). Local extinction from occupied sites and colonization of unoccupied sites over time are the dynamic processes that govern changes in occupancy, and the rates of these processes provide

important information about the long-term sustainability of a population and effects of management (Mazarolle et al. 2005, MacKenzie et al. 2006). The development of statistical methods for estimating site occupancy and local rates of local extinction and colonization while accounting for imperfect detectability has increased the potential for understanding the

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¹Current address: Wild Nature Institute, P. O. Box 165, Hanover, NH 03755. E-mail: derek@wildnatureinstitute.org

effects of natural processes and human disturbance on wild-life populations (MacKenzie et al. 2003, 2006, Kendall et al. 2009).

The California Spotted Owl (*Strix occidentalis occidentalis*) is a subspecies of management concern in the Sierra Nevada of California because it is strongly associated with older coniferous forests for nesting, roosting, and foraging (Gutiérrez et al. 1992, Blakesley et al. 2005, Seamans 2005). The California Spotted Owl is territorial, with high fidelity to breeding sites (Gutiérrez et al. 1995, Blakesley et al. 2006). Occupancy, site fidelity, adult survival, and reproductive success are positively associated with the amount of older conifer-dominated forest at a site (Blakesley et al. 2005, Seamans 2005, Seamans and Gutiérrez 2007). Modifications of old forests by logging and forest fire are believed by land and wildlife managers to be the greatest habitat-driven influences on California Spotted Owl populations (Verner et al. 1992, USFS 2004). Understanding how these habitat disturbances affect probabilities of local extinction from and colonization of breeding sites—the processes that determine occupancy—is critical for developing appropriate forest-management policies and activities to benefit the Spotted Owl. Moreover, managers with limited budgets need guidance on the amount of survey effort required to monitor Spotted Owl occupancy efficiently, so they can estimate detection probabilities and occupancy rates accurately with the minimum expenditure of effort.

The relationship between forest fire and the California Spotted Owl is relatively understudied although this natural disturbance has influenced the structure and function of habitat in California for millennia (Weatherspoon et al. 1992). The influence of fire on the occupancy dynamics of the California Spotted Owl's breeding sites is an important question for management and conservation of the subspecies, but the obvious logistical and political difficulties of conducting large-scale experiments with forest fire and a sensitive species necessitate collecting data opportunistically and taking advantage of natural experiments. The few existing studies of fire's effects on rates of occupancy of Spotted Owl sites have found no significant effects (Bond et al. 2002, Jenness 2004, Roberts et al. 2011), but all were limited either by small sample size or lack of prefire survey data. An experimental design in which occupancy rates are estimated at many burned and unburned sites both before and after forest fire would allow for a stronger inference that any observed changes in occupancy are due to fire (Smucker et al. 2005).

To assess demographic rates and explore ecological relationships, biologists have surveyed California Spotted Owl sites annually for more than 20 years in three areas of the Sierra Nevada (see Blakesley et al. 2010). In other areas of the Sierra Nevada, biologists with the U.S. Forest Service (USFS) surveyed historically occupied Spotted Owl sites prior to forest management such as logging. Over the past decade some known and repeatedly surveyed sites in national forests were

subsequently burned by forest fires. These surveys represent some of the best data available for investigating effects of fire on occupancy dynamics of California Spotted Owl sites.

We compiled a long-term (11-year) data set of surveys of California Spotted Owl sites throughout the Sierra Nevada, comprising 41 burned and 145 unburned control sites and including data from ≥ 3 years pre-fire for all burned sites. We used these data to determine whether rates of local extinction and/or colonization at burned and unburned sites differed before fire and for 5 to 7 years after fire, while accounting for annual and site-specific variation in detectability. We also quantified how fires affected vegetation characteristics at burned sites.

Additionally we used simulations to examine how different allocations of survey effort affected parameter estimability and bias and power to detect differences between groups of sites (i.e., burned and unburned). Our simulations continue the work of previous investigators in this field, providing guidance for research designed to examine differences in occupancy dynamics between groups of sites (objective ii in MacKenzie and Royle 2005). MacKenzie et al. (2002) provided early guidance for the number of occupancy surveys required for parameters to be estimated precisely. Field et al. (2005) used simulations to guide allocation of survey effort given budgetary constraints and concluded that three surveys per site are generally sufficient, but more surveys are required if the occupancy rate is high, as is the case with historical Spotted Owl sites (Olson et al. 2005, Dugger et al. 2011). Using simulations, MacKenzie and Royle (2005) provided additional guidance for allocating survey effort but in their simulations constrained detection probability to be constant through time, an assumption that may not be true for the Spotted Owl (Olson et al. 2005, Roberts et al. 2011, but see Seamans and Gutiérrez 2007). Bailey et al. (2007) further expanded these explorations and introduced software (GENPRES) for exploring study-design options and trade-offs in light of the realization that allocation of survey effort is sufficiently complex that designs should be evaluated on a case-specific basis. Following the methods of Bailey et al. (2007) we simulated 3 years of Spotted Owl occupancy data for two groups of sites with realistic but different parameter values, various numbers of surveys per year, and various numbers of sites.

METHODS

STUDY AREA

We obtained data on the California Spotted Owl's occupancy of burned and unburned sites throughout the Sierra Nevada, California. The Sierra Nevada is 650 km long, trends north-south, and composed of granitic rock. Its climate is Mediterranean, with cold, wet winters and hot, dry summers (Sierra Nevada Ecosystem Project 1996).

Sierran mixed-conifer forest was the dominant vegetation type in our study areas, with a canopy consisting largely of

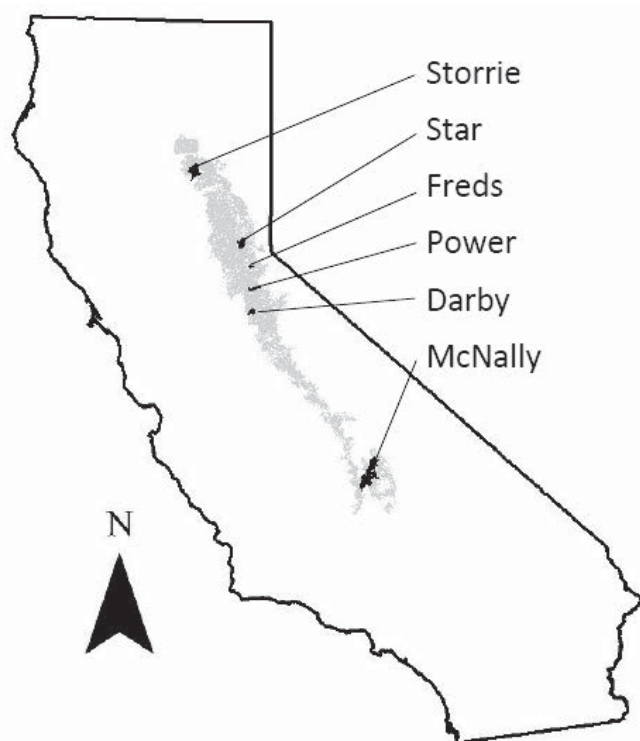


FIGURE 1. Location of six major fires (shaded black) that burned from 2000 to 2004 in California Spotted Owl habitat (conifer, mixed-conifer, and hardwood vegetation types [shaded gray]) in the Sierra Nevada, California.

ponderosa pine (*Pinus ponderosa*) or Jeffrey pine (*P. jeffreyi*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), incense-cedar (*Calocedrus decurrens*), and Douglas-fir (*Pseudotsuga menziesii*) and an understory of black oak (*Quercus kelloggii*), tanoak (*Lithocarpus densiflorus*), and bigleaf maple (*Acer macrophyllum*) (Sierra Nevada Ecosystem Project 1996). Higher-elevation sites were dominated by red fir (*Abies magnifica*).

Our sample of 41 burned Spotted Owl sites had been burned in the following six fires (north to south): the 2000 Storrie Fire in the Lassen and Plumas national forests, the 2001 Star Fire in the Tahoe and Eldorado national forests, the 2004 Freds and Power fires in the Eldorado National Forest, the 2001 Darby Fire in the Stanislaus National Forest, and the 2002 McNally Fire in the Sequoia National Forest (Fig. 1).

SPOTTED OWL OCCUPANCY DATA

The USFS provided us with records of occupancy surveys at California Spotted Owl sites that were conducted annually between 1 April and 31 August from 1997 to 2007 by methods described in its Spotted Owl inventory and monitoring handbook (USFS 1988). We used this window in time because (1) remotely sensed GIS data of fire severity were generally unavailable before about 2000, (2) we knew of six large fires after 2000 in which Spotted Owl sites were burned, and (3) we were striving for at least three years of pre-fire occupancy

data. We used these data to compile occupancy-survey histories for 41 sites throughout the Sierra Nevada that were influenced by fires and 145 sites unaffected by fire. We defined a site as a distinct area in which a single territorial Spotted Owl or pair had been detected. These sites could include multiple locations of roosts and nests. All sites had USFS-defined protected activity centers (PACs) associated with them. A PAC is an administratively designated polygon surrounding a California Spotted Owl nest or core roost area that delineates for management planning approximately 121 ha of forest dominated by the largest trees and highest canopy cover.

USFS biologists conducted or oversaw surveys in or near PACs at each site. Each site contained multiple permanent call stations. Surveys to elicit responses consisted of either 10 min of vocal imitations or playback of recorded Spotted Owl calls at these stations or >1 hr of vocalizing or playback at sites of historical nesting or roosting. The minimum time elapsed between consecutive surveys was 24 hr. We restricted our database to include only sites that had been surveyed in ≥ 3 years from 1997 to 2007, with at least 2 years being consecutive so colonization and local extinction rates could be estimated. We used data only from nighttime surveys conducted between dusk and dawn. To reduce the number of missing observations we used only the first five surveys in any single year. We defined a site as occupied if a Spotted Owl was detected whether or not it was paired.

Previous studies in unburned landscapes have investigated the effects of habitat variables on California Spotted Owl occupancy and vital rates at two spatial scales surrounding nests and core roost areas, 200 ha (circle of radius 800 m) and 400 ha (circle of radius 1128 m). The 200-ha circle marks approximately half the distance between nest sites of adjacent pairs in the Lassen National Forest in the northern Sierra Nevada (Blakesley et al. 2005), and the 400-ha circle marks half the mean distance between occupied sites in the Eldorado and Tahoe national forests in the central Sierra Nevada (Seamans and Gutiérrez 2007). These circles represent regions within an owl's home range that receive concentrated use. We used the smaller 200-ha circle to conservatively classify whether sites were "burned," but, to be inclusive about fire effects at the site, we used the larger 400-ha circle to describe the severity at which the vegetation burned.

Burned sites were those where a 200-ha circle around the best pre-fire owl location was inside or included the perimeter of one of six major forest fires that burned from 2000 to 2004. In defining a "best detection location" for the Spotted Owl at each site from available survey data we used the following hierarchical criteria: (1) most recent pre-fire nest site; (2) most recent pre-fire detection of a pair; (3) most recent pre-fire detection of a single owl. At 34 of the 41 burned sites the best pre-fire detection locations were within the perimeter of the fires. At the remaining seven sites, the best pre-fire detections were located outside but <400 m from the fire's perimeter.

We also compiled records of occupancy surveys from 1997 to 2007 at 145 unburned California Spotted Owl sites throughout the Sierra Nevada. We obtained available survey data from owl sites within the same national forests as the six fires but where the best detection location was >1500 m from the nearest fire. We defined sites this distance from any recent fire as “unburned” because previous studies in unburned landscapes of the central Sierra Nevada found California Spotted Owls’ occupancy rates were influenced by characteristics of the forest within 1128 m of their nest or core roost area (Seamans 2005, Seamans and Gutiérrez 2007), and the probability of an owl’s foraging is minimal beyond 1500 m from its nest or core roost area (Bond et al. 2009). These sites served as unburned controls that represented latitudes, altitudes, and pre-fire vegetation similar to those of burned sites. We excluded sites where the best pre-fire detection was 400–1500 m from the fire perimeter because we wished to distinguish clearly sites we defined as burned or unburned. Surveys at unburned sites followed the same field methods as at the burned sites and included sites in the Lassen and Plumas national forests in the north and the Eldorado and Tahoe national forests in the central Sierra Nevada. The majority (82%) of the unburned controls were from two areas of demography studies (Plumas–Lassen and Eldorado–Tahoe administrative studies). Our data do not encompass all Spotted Owl sites and surveys in the Sierra Nevada during our study period but rather consist of a subset of survey data that had been provided to the regional office of the USFS and that met our criteria for inclusion.

STATISTICAL ANALYSES

Occupancy analysis. Following MacKenzie et al. (2003), we used the program Presence 3.0 (Hines 2006) to fit models and estimate survey-specific detection probabilities, initial occupancy, and annual probabilities of colonization and local extinction from survey histories. Our analytical design allowed us to examine potential pre-fire differences between burned and unburned sites and determine whether differences existed between groups after fire. Our population of interest was historical Spotted Owl sites that subsequently were burned (or not burned) by fire, so it is appropriate to use data from sites where occupancy status had been previously established rather than from randomly selected sites where previous occupancy status was unknown (MacKenzie and Royle 2005). Unbalanced sample sizes (number of sites) in each category (burned or unburned) are not an issue in occupancy analysis, so long as numbers of sites in each category are adequate (MacKenzie et al. 2003).

We estimated the following four parameters. Detection (p) is the probability that an occupied site is correctly identified as such. Colonization (γ) is the probability that a site unoccupied in year $t - 1$ becomes occupied in year t . Local extinction (ϵ) is the probability that a site occupied in year $t - 1$ becomes unoccupied in year t . We were most interested

in colonization and local extinction processes that determine occupancy, but the probability of occupancy (ψ) in year t can be calculated from occupancy in year $t - 1$, local extinction, and colonization rates (MacKenzie et al. 2003).

We ranked models by Akaike’s information criterion (AIC) and used AIC weight as a measure of the strength of evidence supporting a given model (Burnham and Anderson 2002). We used a multi-stage (stepwise) approach to keep the number of models in our set reasonable (Lebreton et al. 1992, Doherty et al. 2012, Dugger et al. 2011). We began with the most highly parameterized form of general model [$\gamma(\text{year} + \text{fire}) \epsilon(\text{year} + \text{fire}) p(\text{year} \times \text{survey} + \text{dem})$] (notation defined below). First, we tested for pre-fire differences in detection, colonization, and local extinction between burned and unburned sites. Next, we constrained our model set in a stepwise manner beginning with detection probability. We then held p in its most parsimonious form while we constrained temporal variation in colonization and local extinction parameters. Finally, we added fire effects to the most parsimonious model of colonization and local extinction. We used likelihood-ratio tests to evaluate the significance of fire effects by comparing models that included fire effects against a null model with no fire effects. Because of uncertainty in model selection, we considered all models with $\Delta\text{AIC} \leq 2$ to be potentially the highest-ranking in a set. We used model-averaged parameter estimates to reduce bias and account for model-selection uncertainty in estimating and inferring final parameters for colonization, local extinction, and occupancy (Burnham and Anderson 2002, Doherty et al. 2012).

We modeled the pre-fire difference between burned and unburned sites in mean probabilities of colonization and local extinction as a time-varying individual (site-specific) categorical covariate, coded 0 for unburned sites in all years, 0 for burned sites post-fire, and 1 for burned sites pre-fire. Thus, models with pre-fire effects had structure for a pre-fire difference between burned and unburned sites in the mean estimates of probabilities of colonization and local extinction. We also examined a model in which mean probabilities of detection at burned and unburned sites differed. We found no evidence for a difference in detectability between burned and unburned sites ($\chi^2_1 = 0.64$, $P = 0.36$) and no pre-fire difference in rates of colonization ($\chi^2_1 = 1.95$, $P = 0.11$) or local extinction ($\chi^2_1 = 0.40$, $P = 0.51$). Therefore, we considered burned and unburned sites equivalent and proceeded with examination of fire effects.

To determine the most parsimonious form for detection probability, we first ranked 18 competing models of p while keeping ϵ and γ in the form $[(\text{year} + \text{fire})]$ (Table 1). We modeled survey-specific detection within a season as a constant ($\cdot$), a linear trend (T), a quadratic trend (T^2), and a log-linear trend ($\ln/T$). We modeled annual probabilities of detection as a constant ($\cdot$) and as year-specific (year). We included an additional detection effect (dem) between sites that were part of intensive demography studies and all other sites because survey effort at

TABLE 1. Model-selection results for probabilities of detection (p) of the California Spotted Owl at sites in Sierra Nevada national forests, 1997–2007. Model notation is (year, survey, covariates), so $p(\text{year} + . + \text{dem})$ denotes annual variation with detectability constant for all surveys within a year and higher at demography-study sites. Local extinction (ϵ) and colonization (γ) were held in their most parameterized form during selection of the detection model [$\epsilon(\text{year} + \text{fire}) \gamma(\text{year} + \text{fire})$]. Weight (sum = 1.0) gives the relative strength of evidence that a given model is the best model in the set. K is the number of parameters in the model.

Detection model ^a	ΔAIC^b	Weight	K
$p(\text{year} + T + \text{dem})$	0.00	0.34	39
$p(\text{year} + \text{dem})$	0.81	0.23	38
$p(\text{year} + \ln T + \text{dem})$	1.00	0.21	39
$p(\text{year} + T^2 + \text{dem})$	1.16	0.19	40
$p(\text{year} + \text{survey} + \text{dem})$	5.44	0.02	43
$p(\text{year} \times \text{survey} + \text{dem})$	22.95	0.00	81
$p(\text{year} \times T + \text{dem})$	30.07	0.00	50
$p(\text{year} \times \ln T + \text{dem})$	32.49	0.00	50
$p(\text{dem})$	36.53	0.00	27
$p(. + T + \text{dem})$	36.93	0.00	28
$p(. + \ln T + \text{dem})$	37.64	0.00	28
$p(\text{year})$	37.72	0.00	37
$p(. + T^2 + \text{dem})$	38.09	0.00	29
$p(\text{year} + \text{survey})$	39.14	0.00	42
$p(. + \text{survey} + \text{dem})$	42.32	0.00	32
$p(\text{year} \times T^2 + \text{dem})$	43.72	0.00	62
$p(.)$	67.26	0.00	26
$p(\text{year} \times \text{survey})$	99.40	0.00	80

^aYear = year-specific variation, . = constant, survey = survey-specific variation, T = linear trend, T^2 = quadratic trend, $\ln T$ = natural log trend, dem = effect of demography-study site, fire = fire effect.

^bMinimum AIC = 4284.5.

these sites differed. After we determined the most parsimonious form for p we examined temporal and fire effects in ϵ and γ while holding p in its most parsimonious form (Table 2).

We modeled temporal pattern in local extinction and colonization as all possible combinations of constant (.), a linear trend (T), and with year-specific probabilities (year) in each parameter for a total of nine models of temporal variation in local extinction and colonization. The top two models of temporal variation in local extinction and colonization had ΔAIC values ≤ 2 (Table 2), so in the next step we added fire effects to both models.

We modeled the intercept effect of fire on extirpation and colonization (fire) as a time-varying individual (site-specific) categorical covariate, coded 0 for unburned sites in all years, 0 for burned sites pre-fire, and 1 for burned sites post-fire. Thus models with fire effects had structure for a post-fire difference between burned and unburned sites in the mean estimates of probabilities of colonization and local extinction. We ranked a total of nine models of fire effects (Table 3).

Within a given season, sites are assumed to be closed to changes in occupancy; this assumption can be relaxed as long

TABLE 2. Model-selection results for temporal variation in probabilities of colonization (γ) and local extinction (ϵ) of the California Spotted Owl at sites in national forests of the Sierra Nevada, 1997–2007. Detection was held in its most parsimonious form during selection of the local extinction and colonization model [$p(\text{year} + T + \text{dem})$]. Weight (sum = 1.0) gives the relative strength of evidence that a given model is the best model in the set.

Colonization ^a	Local extinction ^a	ΔAIC^b	Weight	K
$\gamma(T)$	$\epsilon(\text{year})$	0	0.52	28
$\gamma(.)$	$\epsilon(\text{year})$	1.24	0.28	27
$\gamma(\text{year})$	$\epsilon(\text{year})$	2.08	0.18	37
$\gamma(T)$	$\epsilon(.)$	8.39	0.01	18
$\gamma(T)$	$\epsilon(T)$	9.71	0.00	19
$\gamma(.)$	$\epsilon(T)$	10.6	0.00	18
$\gamma(.)$	$\epsilon(.)$	12.83	0.00	17
$\gamma(\text{year})$	$\epsilon(.)$	14.11	0.00	27
$\gamma(\text{year})$	$\epsilon(T)$	15.08	0.00	28

^aYear = year-specific variation, . = constant, T = linear trend.

^bMinimum AIC = 4280.1.

TABLE 3. Model-selection results for fire effects in probabilities of colonization (γ) and local extinction (ϵ) of the California Spotted Owl at sites in Sierra Nevada national forests, 1997–2007. Detection was held in its most parsimonious form during selection of the local extinction and colonization model [$p(\text{year} + T + \text{dem})$]. Weight (sum = 1.0) gives the relative strength of evidence that a given model is the best model in the set.

Colonization ^a	Local extinction ^a	ΔAIC^b	Weight	K
$\gamma(T)$	$\epsilon(\text{year} + \text{fire})$	0	0.25	29
$\gamma(T)$	$\epsilon(\text{year})$	0.23	0.22	28
$\gamma(.)$	$\epsilon(\text{year})$	1.47	0.12	27
$\gamma(.)$	$\epsilon(\text{year} + \text{fire})$	1.63	0.11	28
$\gamma(T + \text{fire})$	$\epsilon(\text{year} + \text{fire})$	1.82	0.10	30
$\gamma(T + \text{fire})$	$\epsilon(\text{year})$	2.23	0.08	29
$\gamma(\text{fire})$	$\epsilon(\text{year})$	3.46	0.04	28
$\gamma(\text{fire})$	$\epsilon(\text{year} + \text{fire})$	3.52	0.04	29
$\gamma(\text{year} + \text{fire})$	$\epsilon(\text{year} + \text{fire})$	4.60	0.03	39

^aYear = year-specific variation, . = constant, T = linear trend, fire = fire effect.

^bMinimum AIC = 4279.9.

as changes occur at random (MacKenzie et al. 2006). All fires began after 28 August, so all surveys within a given year were in identical pre- or post-fire condition and fire did not affect conditions within a season.

Vegetation changes. Sierran mixed-conifer forests are characterized by mixed-severity fire regimes resulting in a mosaic of lightly to severely burned patches at intermediate scales (Weatherspoon et al. 1992, Sierra Nevada Ecosystem Project 1996). The USFS defines fire severity according to vegetation effects by the following criteria: low severity = areas of surface fire with little change in cover and little mortality of the dominant vegetation; high severity = areas

where the dominant vegetation experienced great to complete mortality due to the fire; moderate severity = areas between low- and high-severity classes and representing a mixture of effects on the dominant vegetation (USFS Region 5 Remote Sensing Lab, McClellan, CA). Fires in Sierran mixed-conifer forests typically generate a mix of areas burned at low, moderate, and high severity (Odion and Hanson 2006, Miller et al. 2009), but at owl sites we described only the portions burned at high severity because this level most concerns managers as being a threat to California Spotted Owls (USFS 2004).

To qualitatively describe how high-severity fire affected suitable vegetation at burned Spotted Owl sites, we used the GIS extension FRAGSTATS (McGarigal et al. 2002). We defined suitable vegetation as conifer, mixed conifer–hardwood, or hardwood, the types the Spotted Owl typically uses (Gutiérrez et al. 1992). We calculated the area of pre-fire suitable vegetation and the proportion of suitable vegetation that burned at high-severity within a circle of radius 1128 m (400 ha) around the best detection location at each site.

Cover types and fire severity were derived from vegetation maps based on Landsat Thematic Mapper imagery developed by the USFS Pacific Southwest Region's Remote Sensing Lab and available from the GIS Clearinghouse (<http://www.fs.fed.us/r5/rsl/clearinghouse/>). Fire severity was estimated from relative difference normalized burn ratios (RdNBR), which are calibrated with the composite burn index and provide data on a fire's severity to vegetation (see Miller and Thode 2007, Miller et al. 2009).

Simulation analyses. We used the program GENPRES (Bailey et al. 2007) to investigate how different allocations of survey effort affect estimability and bias of parameters of local extinction and colonization. We also wanted to determine the power to detect differences in probabilities of local extinction and colonization between groups of sites under various scenarios of survey-effort allocation. We simulated 3 years of data for two groups (i.e., burned and unburned sites) with realistic values of underlying parameters derived from our data and other Spotted Owl studies (MacKenzie et al. 2009, Dugger et al. 2011). Initial occupancy was set at 0.95 in both groups. Detection probabilities varied annually ($p = 0.50, 0.60, 0.40$). Colonization rates were 0.30 for affected sites, 0.40 for unaffected sites. Local extinction rates were 0.05 for unaffected sites, 0.10 for affected sites. Thus, the effect sizes we examined were 0.10 for colonization ($\Delta\gamma$, a 25% proportional change and more than double our observed effect size), 0.05 for local extinction ($\Delta\epsilon$, a 100% proportional change and similar to our observed effect size).

Our simulated effect sizes were much smaller than the documented effect of the Barred Owl (*S. varia*) on colonization ($\Delta\gamma \approx 0.42$) and local extinction ($\Delta\epsilon \approx 0.27$) of the Northern Spotted Owl (*S. o. caurina*) from its sites (Dugger et al. 2011). However, if a group of sites were affected by some disturbance that lowered colonization and raised local extinction

probabilities in the manner we simulated, the consequence would be occupancy of affected sites 10.4% lower after 3 years. Clearly, our simulations emulate biologically significant effects and a realistic trigger for management.

We simulated 3 years of surveys where all surveys were completed with no missing data. We assumed the two groups of sites were identical in every way except the effect of interest. We varied the number of sites surveyed in each group (50, 100, 200) and the number of surveys per year (2, 3, 5). We created 100 simulated data sets under each of the nine sets of conditions (number of sites and number of surveys) and analyzed them by the appropriate model, $\epsilon(g) \gamma(g) p(\text{year}, \cdot)$. In this model local extinction and colonization differ by group (affected versus unaffected) with detection different in each year but constant within a given year.

We analyzed each of our simulated datasets with the appropriate model and determined estimability, bias, and power. We computed failure of estimability as the number of simulations with one or more parameters whose β coefficient standard errors equal zero and excluded simulations with estimability failures from subsequent analyses. Bias was calculated as the mean difference between the true generating parameter value and the estimate from each simulation. Power was calculated as the proportion of simulated data sets that successfully determined the true group differences in ϵ and γ were significant.

The values reported under Results are means $\pm$ SD.

RESULTS

We analyzed data from 186 California Spotted Owl sites (41 burned and 145 unburned) from 1997 to 2007 with up to five surveys in each year. Sites in demography-study areas made up 27% of the burned sites (11/41) and 81% of the unburned sites (117/145). Out of 10 230 total possible instances of sampling, 6649 (65%) were missing data (no survey done). For sites that were surveyed at least once in a year, the median number of surveys was four at demography-study sites, three at other sites. The mean number of unburned sites surveyed each year was 71 ± 39 (1997–2007), of burned sites 21 ± 3 (2001–2007 because the first fires burned in fall 2000). In the last 7 years of the study (the years when burned sites were available), the proportion of surveyed sites that were in the burned group each year was 0.20 ± 0.06 .

DETECTION, LOCAL EXTINCTION, AND COLONIZATION

The best model of detection probability in our set included variation by year and an effect of demography-study area (Fig. 2). Within a given year, we found evidence that the probability of detection changed over time, with the highest-ranked model of survey-specific detection probability within a year being a positive linear trend (Table 1). We used the most

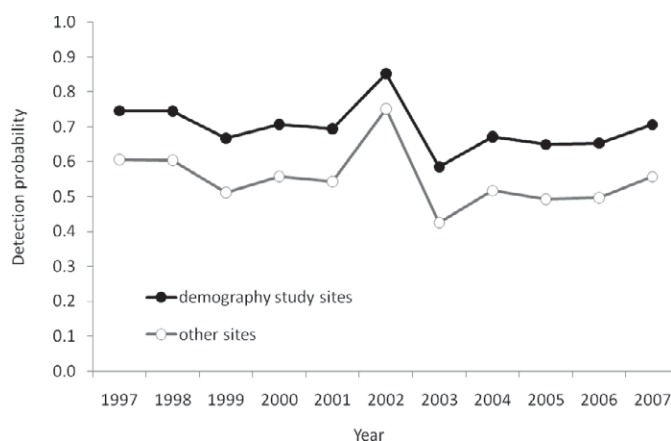


FIGURE 2. Annual probability of detection (p) of the California Spotted Owl at sites of demography studies (filled circles) and other sites (open circles) in national forests in the Sierra Nevada, California. Estimates are from the model $[\gamma(T) \varepsilon(\text{year} + \text{fire}) p(\text{year} + T + \text{dem})]$.

parsimonious form of the detection model for all subsequent model-ranking and estimation procedures. The mean annual probability of detection was 0.698 ± 0.069 at demography-study sites and 0.551 ± 0.084 at all other sites.

Temporal variation in probabilities of colonization and local extinction had two models with ΔAIC values < 2 (Table 2). Both top-ranked models had year-specific probabilities of local extinction, and probability of colonization was a negative linear trend or constant (Table 2). We added fire effects to both of these models in the next step of the analysis (Table 3).

We found no significant differences between burned and unburned sites in probabilities of colonization ($\chi^2_1 = 0.18$, $P = 0.86$) or local extinction ($\chi^2_1 = 2.23$, $P = 0.09$) (Fig. 3). Local extinction parameters for 1999 and 2001 were unestimable so we substituted mean values of each group for those years.

The model-averaged mean probability of colonization of unburned sites was 0.425 ± 0.073 , of burned sites 0.381 ± 0.051 , an effect size of 0.044 lower probability of colonization of burned sites. The model-averaged mean probability of local extinction from unburned sites was 0.137 ± 0.053 , from burned sites 0.094 ± 0.042 , an effect size of 0.043 lower probability of local extinction from burned sites. Model-averaged probabilities of colonization and local extinction resulted in derived site-occupancy probabilities that were slightly higher for burned sites than for unburned sites (Fig. 4). Mean occupancy from 2001–2007 was 0.761 ± 0.045 at unburned sites, 0.802 ± 0.035 at burned sites.

VEGETATION CHANGES

In our sample of 41 burned Spotted Owl sites, the area of pre-fire suitable vegetation (conifer, mixed conifer-hardwood, and hardwood types) within a 400-ha circle around the best pre-fire detection location was $280.2 \text{ ha} \pm 110.3$, range 28.2–398.8. The average proportion of suitable vegetation that burned at

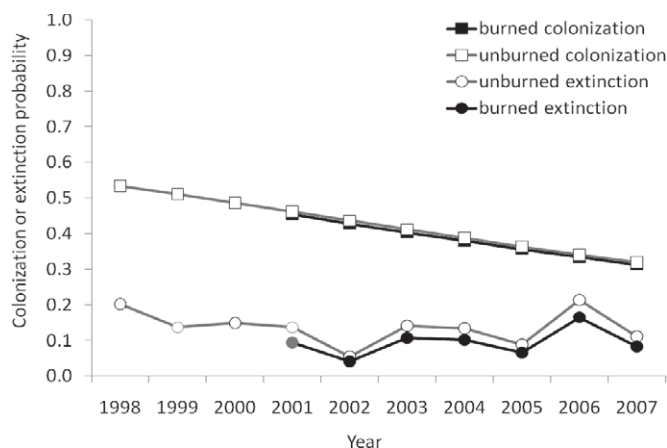


FIGURE 3. Model-averaged probabilities of colonization (squares) and local extinction (circles) of the California Spotted Owl at unburned control sites (unfilled) and sites burned by fires (filled) from 2001 to 2007 in national forests in the Sierra Nevada, California. Local extinction parameters for 1999 and 2001 were unestimable, so values for those years are the mean of all years.

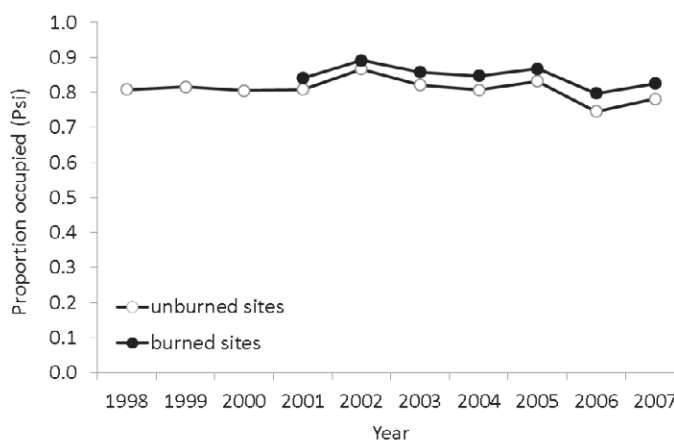


FIGURE 4. Mean annual probabilities of occupancy (ψ) of the California Spotted Owl at unburned sites (unfilled) from 1998 to 2007 and sites burned by fires (filled) from 2001 to 2007 in national forests in the Sierra Nevada, California. Mean annual probabilities of occupancy were derived from model-average estimates of colonization and local extinction.

high severity in the circle was 0.319 ± 0.234 , range 0.001–0.932. Over 50% of suitable vegetation was burned at high severity at 9 of 41 sites. Eight of these sites were surveyed after the fire, with Spotted Owls detected at 5 (63%).

SIMULATIONS

Our simulation results indicate that the number of sites surveyed and the number of surveys per season both had large effects on estimability, bias, and power. The failure rate of

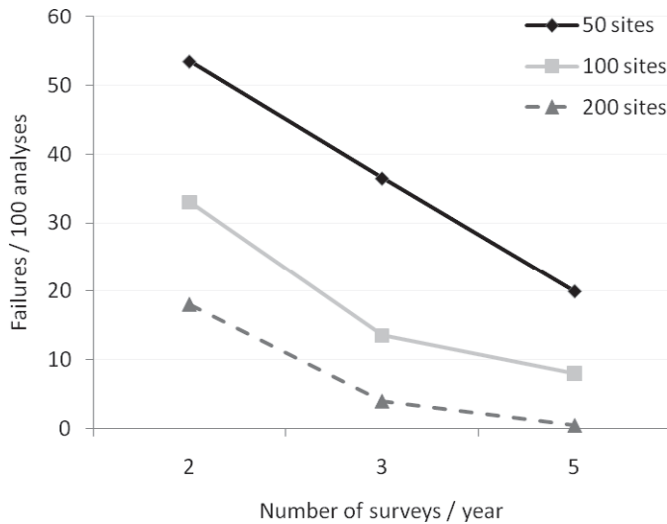


FIGURE 5. Failure rate of estimability under differing scenarios of spatial and temporal effort during 3 years of simulated Spotted Owl surveys. Failure is defined as any parameter SE = 0.

estimability was 54% under the lowest-effort scenario (50 sites, two surveys per year), but this was reduced by effort increased spatially or temporally (Fig. 5). Biases in parameter estimates were minimal in scenarios with ≥ 100 sites per group and ≥ 3 surveys per year (Fig. 6). Below this threshold of effort, estimates of initial occupancy tended to be biased low and estimates of colonization and local extinction rates were generally biased high (Fig. 6). Power to distinguish between groups with known differences was very low for colonization rate in all scenarios (Table 4). Power approximations for local

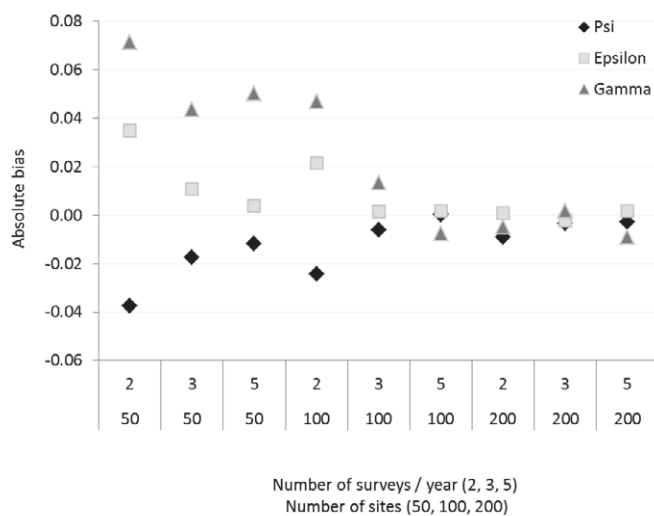


FIGURE 6. Bias of parameter estimates (0 = no bias) under differing scenarios of spatial (number of sites in each of two groups) and temporal (number of surveys per year) effort during 3 years of simulated Spotted Owl surveys. Psi = initial occupancy, epsilon = local extinction probability, gamma = colonization probability.

TABLE 4. Power to detect differences in local extinction ($\Delta\epsilon = 0.05$; $\epsilon = 0.05$ vs. 0.10) and colonization ($\Delta\gamma = 0.10$; $\gamma = 0.30$ vs. 0.40) between two groups of sites under differing scenarios of spatial (number of sites) and temporal (number of surveys per year) effort during 3 years of simulated surveys of Spotted Owl occupancy.

No. sites	No. surveys		
	2	3	5
$\Delta\epsilon = 0.05$			
50	16%	10%	22%
100	6%	40%	55%
200	27%	48%	80%
$\Delta\gamma = 0.10$			
50	16%	12%	22%
100	7%	12%	15%
200	22%	19%	29%

extinction rate were reasonable in scenarios with ≥ 100 sites per group and ≥ 3 surveys per year and good in the highest-effort scenario (Table 4).

DISCUSSION

Forest fire, particularly high-severity fire, is generally presumed to reduce occupancy by California Spotted Owls, on the basis of modifications to the forest canopy, basal area of live trees, and other vegetation and habitat elements. Our results do not support this presumption and instead corroborate and elaborate on previous studies of the Spotted Owl that found occupancy not diminished by forest fires of varying severities (Bond et al. 2002, Jenness et al. 2004, Roberts et al. 2011). We found no significant effect of fire on occupancy dynamics for up to 7 years post-fire and for the vegetation conditions of the sites in our study.

Bond et al. (2002) quantified post-fire site fidelity of all three subspecies of the Spotted Owl and found that 16 of 18 banded owls resighted after fire were at the same sites where they bred previously (89%); these rates were the same as those at unburned sites. Jenness et al. (2004) found rates of post-fire occupancy of the Mexican Spotted Owl (*S. o. lucida*) at 33 burned and 31 unburned sites were not significantly different and did not differ with time since fire. Moreover, the percentage of high-severity fire at a burned site had no significant influence on whether the site was occupied.

Roberts et al. (2011) were the first to model the effects of fire on rates of California Spotted Owl occupancy by incorporating detectability. They obtained unbiased estimates of single-season occupancy in Yosemite National Park at randomly selected burned and unburned areas and demonstrated no effect of fire on site occupancy.

At our burned sites, an average of 32% of suitable vegetation burned at high severity, yet rates of colonization of and local extinction from these sites were not significantly different from those at unburned sites. Thus owls continued to occupy sites where nearly one third of their suitable habitat burned severely. Existing data for habitat selection in burned landscapes show that within fire-affected landscapes California Spotted Owls typically nest and roost in unburned, lightly burned, or moderately burned patches, while patches burned at high severity provide preferred foraging habitat (Bond et al. 2009). Fires in mixed-conifer forests of the Sierra Nevada typically result in 11–26% of vegetation burned at high severity (Odion and Hanson 2006, Miller et al. 2009). Our results indicate that fire, even fire that burns on average 32% of suitable habitat within a California Spotted Owl site at high severity, does not threaten the persistence of the subspecies on the landscape.

However, it is conceivable that there may be a critical threshold proportion of a site that, if burned at high severity, could adversely affect the owl's occupancy rates. Seamans and Gutiérrez (2007) identified just such a threshold in their examination of 66 California Spotted Owl sites, of which 36 were logged and 2 were burned at high severity over 15 years. They found that logging of ≥ 20 ha of mature conifer forest ($>70\%$ canopy cover dominated by trees >30.4 cm in diameter at breast height) within a 400-ha circle surrounding an owl site resulted in lower rates of colonization and higher rates of local extinction. Seamans and Gutiérrez (2007) did not report the mean area of mature forest in their 400-ha circles, but the range was 0–257 ha. In addition, dispersal of marked breeding birds of both sexes increased dramatically when $\geq 20\%$ of mature conifer habitat in the 400-ha circle was logged.

Thus logging of $\sim 20\%$ of mature conifer forest within the 400-ha circle surrounding a site appears to be a threshold beyond which California Spotted Owl occupancy declines and dispersal of breeding birds increases significantly, whereas when an average of 32% of suitable vegetation within the 400-ha circle burns at high severity, no such negative effect on occupancy is apparent. On the contrary, we found some evidence for a positive effect of high-severity fire in probabilities of local extinction from burned sites lower than from unburned sites, resulting in overall higher occupancy of burned sites. This disparity between the effects fire and logging suggests that “legacy” snags or other habitat components generally not left from logging (Swanson et al. 2011) may play an important role in maintaining habitat suitability for the Spotted Owl and is an issue that deserves further study.

Post-fire logging (e.g., salvage logging) may have affected rates of occupancy of the burned sites we studied. We did not have spatially explicit data on post-fire logging, but it occurred within 2 years after the fire near at least eight of our 41 burned sites. Seven of the eight sites that were later logged were occupied by California Spotted Owls after the fire but

none of the eight sites was occupied after logging. Thus post-fire logging may have adversely affected rates of occupancy of the burned sites, but our sample size was too small for this effect to be included as a covariate. We suggest that future studies examine the effects of fire on rates of occupancy of Spotted Owl sites without the confounding factor of post-fire logging.

Our 3-year simulations provide guidance to land managers and researchers designing population-monitoring programs or experimental systems. The power of survey data to detect a change in colonization and/or local extinction rates is related to survey effort and the proportional difference in rates between groups (Bailey et al. 2007). When a species' detectability is ~ 0.5 it is clear that parameter estimates that are useful for informing management require surveys at a minimum of 100 sites in each group and a minimum of 3 surveys per year. This survey effort is sufficient if the expected proportional effect size is $\sim 100\%$, as in our simulated effect of local extinction. Smaller proportional effect sizes will require more sites and more surveys (as evident in our proportional effect of simulated colonization of $\sim 25\%$) or studies of longer duration if groups and effect sizes are stable over long periods. The power to detect effects of the size and proportion we simulated in 3 years is achieved only with large numbers of sites in each group (≥ 200) and many surveys per year (≥ 5). These recommendations are for historically occupied sites, not randomly selected sites, in which case the number of required sites would be larger and related to occupancy rate.

On the basis of our simulations, and given our mean annual sample sizes (71 unburned and 21 burned sites per year), the failure rate for 3 years of data similar to our survey data was a $\sim 20\%$ chance of unestimable parameters. Additionally, the power of 3 years of data to detect simulated differences between groups in rates of colonization and local extinction was low, $\sim 22\%$. However, Olson et al. (2005) completed six analyses of historical Northern Spotted Owl sites in three study areas where $\leq 25\%$ of 146 surveyed sites were affected by Barred Owls, and the proportional effect sizes during a 13-year study were 7–37%. The authors were able to detect effects of the Barred Owl on occupancy probabilities in five out of six analyses (83%). Also, Seamans and Gutiérrez (2007) observed significant deleterious effects of habitat alteration in a study of 66 California Spotted Owl sites of which 38 were altered during a 15-year study. Thus smaller proportional effects can be detected with low numbers of sites over a longer time.

However, most efforts at management would benefit from more immediate feedback. More than 1470 known historically occupied Spotted Owl sites have been identified in the Sierra Nevada (USFS Region 5 Remote Sensing Lab, McClellan, CA), but management and natural disturbances will only affect a small subset of this total each year. Obtaining data from numbers of affected sites sufficient for meaningful

comparison with controls is possible in 3 years if enough survey effort is expended.

Our simulations suggest that historically occupied California Spotted Owl sites in the Sierra Nevada should be surveyed more frequently, preferably every year, if the effects of fire or management on occupancy are to be distinguished. Efforts should be made to compile all survey data in a regional database for ease of analysis. To further assess the effects of fire on local Spotted Owl persistence, managers should strive to survey ≥ 200 burned sites (or as many as exist) throughout the Sierra Nevada annually as well as ≥ 200 historically occupied unburned sites from among the > 1470 known sites. Furthermore, given low detectability rates, we recommend more than one year of surveys be used to determine site occupancy before management that may be detrimental to the Spotted Owl is undertaken in potentially occupied habitat. When detectability is 0.55, as it was at sites not part of demography studies, almost half of all occupied sites would be misclassified as unoccupied by a single season of surveys. To inform management, all sites should be surveyed with a minimum of three visits per year to determine occupancy; five visits per year would provide a significant improvement in estimability and accuracy of parameters and power to detect effects. Meeting these recommendations would require a significant increase in survey effort in national forest lands outside demography-study areas but would provide a robust framework for inference about fire and other management effects throughout the Sierra Nevada.

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Influence of Fire and Salvage Logging on Site Occupancy of Spotted Owls in the San Bernardino and San Jacinto Mountains of Southern California

DEREK E. LEE,¹ Wild Nature Institute, P.O. Box 165, Hanover, NH 03755, USA

MONICA L. BOND, Wild Nature Institute, P.O. Box 165, Hanover, NH 03755, USA

MARK I. BORCHERT, U.S.D.A. Forest Service, San Bernardino National Forest, 602 S. Tippecanoe Ave., San Bernardino, CA 92408, USA

RICHARD TANNER, Tanner Environmental Services, P.O. Box 6132, Ventura, CA 93001, USA

ABSTRACT Fire over the past decade has affected forests in the San Bernardino Mountains of southern California, providing an excellent opportunity to examine how this disturbance, and subsequent post-fire salvage logging, influenced California spotted owl (*Strix occidentalis occidentalis*) breeding-season site occupancy dynamics there and in the nearby San Jacinto Mountains. Using occupancy survey data from 2003 to 2011 for all-detections and pairs-only data, we estimated annual extinction and colonization probabilities at 71 burned and 97 unburned breeding-season sites before and after fire, while controlling for confounding effects of non-fire-related temporal variation and among-site differences in habitat characteristics. We found no statistically significant effects of fire or salvage logging on occupancy dynamics of spotted owls of southern California. However, we found some evidence that fire and logging effects could be biologically meaningful. For pairs data, the model-averaged mean of fire-related effects on colonization and extinction probabilities resulted in a 0.062 lesser site-occupancy probability in burned sites 1-year post-fire relative to unburned sites. Post-fire salvage logging reduced occupancy an additional 0.046 relative to sites that only burned. We documented a threshold-type relationship between extinction and colonization probabilities and the amount of forested habitat (conifer or hardwood tree cover types) that burned at high severity within a 203-ha core area around spotted owl nests and roost centroids. Sites where approximately 0–50 ha of forested habitat within the core area burned at high severity had extinction probabilities similar to unburned sites, but where more than approximately 50 ha of forested habitat burned severely, extinction probability increased approximately 0.003 for every additional hectare severely burned. The majority (75%) of sites burned below this threshold. Sites where high-severity fire affected >50 ha of forested habitat could still support spotted owls, so all burned sites should be monitored for occupancy before management actions such as salvage logging are undertaken that could be detrimental to the subspecies. We also recommend that managers strive to reduce human-caused ignitions along the wildland–urban interface, particularly at lower elevations where owl sites are at higher risk of extinction from fire. © 2013 The Wildlife Society.

KEY WORDS California spotted owl, fire severity, forest structure, occupancy modeling, population dynamics, *Strix occidentalis*.

Natural disturbances influence the structure and function of forested ecosystems and create spatial and temporal heterogeneity of wildlife habitats. Habitat alterations by fire have the potential to affect population dynamics of animals, particularly territorial species that demonstrate high breeding-site fidelity, such as the California spotted owl (*Strix occidentalis occidentalis*; Blakesley et al. 2006, Seamans and Gutiérrez 2007). Post-fire salvage logging is widespread

in burned spotted owl habitats, and this additional alteration may also affect this species.

The California spotted owl is an iconic subspecies of management concern because it is strongly associated with late-seral coniferous forests for nesting, roosting, and foraging (Bias and Gutiérrez 1992, Call et al. 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Blakesley et al. 2005). Modifications of older forest habitat from timber harvest and fire are believed to be primarily responsible for habitat-driven changes in spotted owl populations (Verner et al. 1992) although under certain circumstances, spotted owls may benefit from some degree of forest heterogeneity, for example, when openings of different seral stages were interspersed with older forest (sensu

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¹E-mail: derek@wildnatureinstitute.org

California spotted owl: Bond et al. 2009b; northern spotted owl [*S. o. caurina*]: Franklin et al. 2000, Olson et al. 2004). Understanding how habitat disturbances affect site-occupancy rates is essential for developing appropriate pre- and post-fire forest management practices to conserve spotted owls. Modeling of site-occupancy dynamics allows biologists to quantify the influence of site-specific habitat variables on site occupancy and local rates of site extinction and colonization while accounting for imperfect detectability (MacKenzie et al. 2003, 2006, 2009, 2010; Nichols et al. 2007; Seamans and Gutiérrez 2007).

Populations of California spotted owls in southern California are at the southern edge of their range, are highly insular, and are substantially smaller compared to those in the Sierra Nevada (Gutiérrez and Pritchard 1990; LaHaye et al. 1994, 2001). In southern California, spotted owls occur within forested islands located at upper elevations along a series of mountain ranges surrounded by extensive desert and semi-desert communities (LaHaye et al. 1994). Twenty-two isolated populations have been identified in central-coastal and southern California with the number of breeding-season sites per population ranging from 3 to 133 (Verner et al. 1992, LaHaye et al. 1994), the largest of which is in the San Bernardino Mountains (SBM). Spotted owl populations in the SBM and nearby San Jacinto Mountains (SJM) declined precipitously during demographic studies conducted from 1987 to 1998 (LaHaye et al. 2004), prompting serious concerns about the future of the subspecies in southern California (Loe and Beyers 2004). LaHaye and Gutiérrez (2005) proposed an array of possible causes for the declines, including fire, drought, recreational activities, air pollution, urbanization, and water diversions, but occupancy of sites was not quantitatively linked to any of these factors. Previous studies examining the effects of fire on occupancy of spotted owl breeding-season sites in the Sierra Nevada found no differences between burned and unburned sites in occupancy (Roberts et al. 2011) or in colonization and extinction rates (Lee et al. 2012). However, Lee et al. (2012) hypothesized that there may be a critical threshold proportion of habitat within a site that, if burned at high-severity, could adversely affect occupancy rates.

In the period 2003–2007, California spotted owl breeding-season sites in the SBM were more heavily affected by fire than during any time since the commencement of spotted owl studies in the region. After historically low rainfall and high temperatures beginning in 1998, wildfires burned 5,800 ha of conifer forests in 2003 (Bond et al. 2009a). In 2007, additional fires burned another 11,200 ha of conifer types (Keeley et al. 2009). These and other smaller fires in forested habitat during the period 2003–2007 constituted a widespread impact that occurred across many regularly monitored spotted owl territories.

Our objectives were to investigate if recent fires were associated with occupancy dynamics of southern California spotted owl breeding-season sites (hereafter sites) from 2003 to 2011, and to identify if occupancy is affected by a critical threshold of vegetation change due to high-severity fire and salvage logging within a site. We used a natural impact

assessment where a subset of all the owl sites surveyed annually from 2003 to 2011 were burned during that same time period, and a subset of those burned owl sites were subsequently salvage logged. We estimated local extinction and colonization probabilities at burned, burned and logged, and unburned sites both before and after fire, while including the possibly confounding effects of non-fire-related temporal variation and among-site differences in habitat characteristics, thus providing strong inference that observed changes in occupancy dynamics were likely due to fire and/or logging (Burnham and Anderson 2002, Stephens et al. 2005, Mundry 2011).

STUDY AREA

The San Bernardino and San Jacinto Mountains rise above the surrounding lowlands approximately 140–150 km east of Los Angeles, California. The SBM are in the Transverse Mountain Range and trend east–west, whereas the SJM are the northernmost terminus of the north–south trending Peninsular Ranges (Stephenson and Calcarone 1999). Climate of the study area was Mediterranean with most precipitation falling during the winter as rain at lower elevations and rain and snow at higher elevations. Average annual precipitation ranged from 500 to 1,000 mm with substantial local variability due to aspect, elevation, topography, rain-shadow patterns, and seasonal storm patterns (Minnich 1988).

In southern California, spotted owls inhabit lower montane forests, montane coniferous forests, and occasionally desert forests and woodlands (Gutiérrez et al. 1992, LaHaye et al. 1997). Lower montane forests ranged from 915 to 1,525 m (Stephenson and Calcarone 1999). Chaparral was the dominant vegetation over most of this landscape, although stands of bigcone Douglas-fir (*Pseudotsuga macrocarpa*) with an understory of canyon live oak (*Quercus chrysolepis*) often occurred in the steep, dissected drainages. Knobcone pine (*Pinus attenuata*) and sometimes Coulter pine (*P. coulteri*) formed open woodlands with dense chaparral in the understory. Montane coniferous forests ranged from 1,525 to 2,440 m and were dominated by Jeffrey pine (*P. jeffreyi*) or ponderosa pine (*P. ponderosa*). California black oak (*Q. kelloggii*) was a common understory tree in these forests. Mixed-conifer forests were prevalent in more mesic settings between 1,920 and 2,690 m and included combinations of Jeffrey and ponderosa pines, white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), and sugar pine (*P. lambertiana*; Stephenson and Calcarone 1999). The eastern, interior desert portions of the mountains were covered by pinyon pine (*P. monophylla*) and western juniper (*Juniperus occidentalis*) forests and woodlands. Spotted owl sites occurred on both private and public (San Bernardino National Forest, U.S. Forest Service) lands.

Historical fire regimes in southern California's forests likely created a heterogeneous landscape that produced mixed patches of unburned, low-, moderate-, and high-severity burned forest (Weatherspoon et al. 1992). A century of intensive resource extraction, fire suppression, domestic

livestock grazing, and other management activities has led to changes in the structure and species composition of these forests (McKelvey and Johnston 1992, Minnich et al. 1995), but managers do not know whether or how this has altered pattern, frequency, and intensity of current fires.

The SBM and SJM ranges were isolated from each other by urban areas, deserts, and chaparral, all of which were unsuitable to spotted owls (LaHaye et al. 1994). Thus, dispersal of owls between mountain ranges was limited (LaHaye et al. 2001).

METHODS

Spotted Owl Surveys

All California spotted owl sites within the boundaries of the San Bernardino National Forest in the SBM and SJM were identified beginning in 1989 by annually surveying all forested stands (LaHaye et al. 2004). We defined an owl site as a distinct area within our geographic survey boundaries that was determined to be occupied prior to 2003 by seeing or hearing a single or pair of territorial spotted owls. Our population of interest consisted of previously identified owl sites that were subsequently burned (or not burned) by fire; therefore, using data from sites where occupancy status had been previously established is appropriate, rather than from randomly selected sites where previous occupancy status was unknown (MacKenzie and Royle 2005). Each year from 2003 through 2011, we attempted occupancy and reproductive surveys in all known spotted owl sites from 1 March to 31 August, following standardized methods described by Forsman (1983) and Franklin et al. (1996). Every year, the same experienced project manager (R. Tanner) trained field biologists in spotted owl survey and detection methods, and many of the biologists worked for multiple years on the project, thereby minimizing observer bias. Budgetary and safety constraints sometimes limited the number of sites surveyed in a given year. If the annual budget was insufficient to survey all sites, we prioritized sites potentially affected by management projects, but there was no systematic bias in selecting sites to survey in a given year. In other words, sites were neither included nor excluded from annual surveys based on prior occupancy history; sites with long periods of no detections continued to be surveyed as often as continuously occupied sites. The purposeful exclusion of a site from surveys in a given year was usually due to safety issues such as presence of a nearby marijuana (*Cannabis* spp.) plantation. We included in our analysis survey data from all known spotted owl sites in the SBM and SJM study areas that were surveyed for ≥ 2 consecutive years from 2003 to 2011 ($n = 168$).

Within a year, we used 2 types of surveys: 1) presence-absence surveys to initially locate owls in an area; and 2) reproductive surveys to locate roosts and nests and to assess the reproductive status of owls previously detected by presence-absence surveys. All survey visits were separated by >48 hours. We conducted presence-absence surveys to determine if spotted owls currently occupied previously identified sites by imitating spotted owl vocalizations while

thoroughly surveying designated areas between dusk and dawn. We accomplished survey coverage by calling from a series of fixed calling stations along roads and trails or by walking survey routes while calling continuously. We conducted up to 6 nighttime presence-absence surveys at each spotted owl site every year. If a spotted owl responded during a nighttime survey, we began conducting crepuscular (dusk and dawn) reproductive surveys. We conducted a maximum of 4 reproductive surveys to confirm occupancy and to assess reproductive status and success. We sexed owls based on their calls and behavior (Forsman 1983, Franklin et al. 1996). If we detected spotted owls at 1 site but then followed them back to an adjacent site during the same survey, we did not consider the first site to be occupied during that survey because owls were attracted to the surveyor's calls. We surveyed each site a maximum of 8 times (presence-absence and reproductive surveys combined), but both the median and mode number of visits across all sites each year was 6, so we truncated all within-year survey histories at 6 surveys for this analysis to reduce the number of missing observations. This was comparable to the average maximum number of visits rule used by Olson et al. (2005) and the unspecified rule used by Kroll et al. (2010) to truncate their survey data.

Site-Specific Habitat Characteristics and Burned Vegetation Changes

To define which sites were burned, and to characterize habitat variation among all sites, we evaluated vegetation and physical attributes in a 203-ha circle around the most recently used nest tree location or roost centroid (as of 2003) in all spotted owl sites in 2003, and again post-fire in sites that burned between 2003 and 2007 (the last year that fires affected the owl sites in our dataset). Previous studies on spotted owls elsewhere in the species' range also have examined the effects of habitat variables on occupancy and vital rates in an approximately 200-ha circle surrounding nests and core roosts (Blakesley et al. 2005, Stralberg et al. 2008, Manley et al. 2009, Lee et al. 2012). This area is intended to represent regions of concentrated use by spotted owls and are described here as core areas. Average breeding-season home-range size previously was reported as 439 ha for California spotted owls in the SBM (fixed-kernel method; Zimmerman et al. 2001).

The United States Forest Service's Adaptive Management Services Enterprise Team (AMSET; Tahoe National Forest, Nevada City, CA) developed an attributed, landscape Geographic Information System (GIS) data set in 2003 that we supplemented with elevation and fire-related habitat covariates for our analysis. On a base map constructed from ortho-rectified, 1-m resolution infrared aerial photographs of the SBM and SJM taken in September 2003, AMSET plotted the most recent (as of 2003) nest locations or centroids of roost locations of 136 owl pairs in the SBM and 32 in the SJM. Within each 203-ha core area surrounding the nest or roost locations, AMSET delineated polygons of similar vegetation using on-screen infrared photographs and stereo pairs of color aerial photographs (at a scale of

1:15,840) over a background of black-and-white orthophotos. Mapping was carried out in ArcMap (ESRI, Inc., Redlands, CA). A new polygon was added whenever there was a minimum 10% change in vegetation composition or structure from the surrounding vegetation. On-screen templates assisted in standardizing some attributes. In each 203-ha core area, AMSET estimated hectares of each cover type: conifers, hardwoods, shrubs, herbs (grasslands and meadows), riparian, and non-vegetation. For each site, we also recorded elevation at the nest tree or geometric mean of the roost centroids.

We defined burned spotted owl sites as those where the 203-ha core area was inside or included the perimeter of one of the fires that occurred from 2003 to 2007. Using National Agricultural Imager Program (NAIP) imagery taken for the San Bernardino National Forest in October 2009, we re-attributed vegetation in core areas that burned between October 2003 and October 2007. Fires in southern California forests typically burn in a mosaic of severities (Weatherspoon et al. 1992, Stephenson and Calcarone 1999), but we only analyzed the owl habitat burned at high-severity within owl sites because this fire severity most concerns managers as being a threat to spotted owls (Loe and Beyers 2004). We defined owl habitat as conifer and hardwood tree cover types, and determined the hectares of habitat that burned at high severity between 2003 and 2007 by overlaying burn severity and vegetation maps and quantifying change in tree cover due to fire. High-severity fire resulted in areas where dominant vegetation had high to complete mortality due to fire. Post-fire tree removal occurred on private inholdings and on United States Forest Service lands adjacent to roads, which affected 21 of the core areas. We used aerial photographs obtained from Google Earth to impose a grid of 1-ha cells in a 203-ha circle around the nests or roost centroids and estimate the amount of the circle affected by extensive (i.e., clearcut) post-fire tree removal.

Statistical Analysis

We used raw survey data to compile occupancy histories for 168 California spotted owl sites. We found no substantial or systematic differences in average elevation or habitat values between the owl sites in SBM ($n = 136$) versus those in SJM ($n = 32$), and preliminary analysis revealed no difference in mean occupancy dynamics between SBM and SJM. Therefore, we pooled sites from both areas for analysis of fire effects on occupancy dynamics. Ninety-seven sites were not burned at any time, and 71 sites burned from 2003 to 2007. Twenty-one of the burned sites were subsequently salvage logged.

From the raw occupancy survey data, we created 2 datasets called all detections and pair, corresponding to different levels of site occupancy (Olson et al. 2005). We defined all-detections occupancy as any spotted owl detection at a site, regardless of pair or reproductive status (surveys with any spotted owl detection were coded as 1, no detection was coded as 0). The pair dataset only contained detections of pairs (surveys where we detected both members of a pair, an

adult of any sex with ≥ 1 juvenile, or ≥ 1 juvenile with no adult were coded as 1, all other surveys coded as 0). We analyzed all-detections and pair data in an identical procedure. Site occupancy in all-detections data represented the broadest definition of occupancy and indicated the use of a site by any spotted owl, whereas site occupancy by pairs represented a more conservative definition of occupancy and indicated the potential for a site to support breeding (Olson et al. 2005).

We used Program Presence 4.0 (USGS-Patuxent Wildlife Research Center, Laurel, MD 2006) to fit models and estimate survey-specific detection probabilities, initial occupancy, annual colonization probabilities, and annual extinction probabilities from occupancy survey histories following methods developed by MacKenzie et al. (2003) and MacKenzie and Royle (2005) for open populations. Detection (P) is the probability that an occupied site is correctly identified as such. Colonization (γ) is the probability that a site unoccupied in year $t - 1$ becomes occupied in year t . Extinction (ϵ) is the probability that a site occupied in year $t - 1$ is unoccupied in year t . We were most interested in the colonization and extinction processes that determine occupancy state in a given year, but the probability of occupancy (ψ) in year t can be calculated from occupancy in year $t - 1$, extinction, and colonization rates (MacKenzie et al. 2003).

We followed methods used by Olson et al. (2005), Kroll et al. (2010), Dugger et al. (2011), and Farber and Kroll (2012) to model spotted owl site-occupancy dynamics. We employed a multi-staged technique to rank models, and selected the best and competing models at each stage using an information theoretic approach (Burnham and Anderson 2002). First, we ranked models of detection probabilities to find the most parsimonious form of this parameter while holding colonization and extinction in their year-specific forms. We used the top-ranked model of detection from the first stage of the analysis in the second stage of ranking temporal models for local extinction and colonization probabilities. During the third stage of modeling, we ranked a set of pre-fire habitat covariate models for extinction and colonization probabilities. Finally, we ranked a set of fire and salvage-logging covariate models based on the best temporal and pre-fire habitat covariate models.

In this manner, we investigated the support for fire and logging effects while controlling for potentially confounding temporal variation as well as pre-fire site-specific (individual) vegetation and physical habitat variation. Our temporal and habitat covariates included effects previously reported to be associated with spotted owl detectability, habitat selection, or vital rates (Table 1). Annual temporal variation in all detection, colonization, and extinction parameters were modeled as year-specific (year), as well as a linear time trend (Y), quadratic time trend (Y^2), cubic trend (Y^3), and constant ($\cdot$). We expected that colonization and extinction probabilities could exhibit annual variation (year) due to variation in weather or prey populations (Franklin et al. 2000; Seamans et al. 2002; LaHaye et al. 2004; Glenn et al. 2010, 2011) and

Table 1. Definition of temporal and habitat covariates within a 203-ha circle around the nest tree or roost centroid for 168 California spotted owl sites in the San Bernardino and San Jacinto mountains of southern California from 2003 to 2011.

Covariate name	Type	Definition
year	Binomial	Annual variation coded as categorical dummy variables (8 variables in γ and ε , 9 in P)
Y	Continuous	Linear annual temporal trend
Y ²	Continuous	Quadratic annual temporal trend
Y ³	Continuous	Cubic annual temporal trend
altyr	Binomial	Alternate year temporal pattern, every other year coded 1, 0, 1, 0, etc.
fire	Binomial	Intercept effect of fire between 2003 and 2011 coded 0 in unburned sites for all years, 0 for burned sites in fire years before fire, and 1 for burned sites in years after fire
hisev	Continuous	Hectares of owl habitat vegetation in 203-ha core area burned at high severity between 2003 and 2011 coded as a site-specific continuous covariate (mean = 24, range = 0.2–119)
hisev ²	Continuous	The square of hisev, used to model extinction as a quadratic function of the amount of owl habitat vegetation burned at high severity between 2003 and 2011
log	Continuous	Hectares of post-fire salvage logging in 203-ha core area (mean = 63, range = 0–150)
elev	Continuous	Site elevation standardized as (elevation – mean)/SD (raw mean = 5,686, range = 2,620–8,820)
rip	Continuous	Index of riparian vegetation cover (mean = 13, range = 0–96)
tree	Continuous	Hectares of pre-fire owl habitat in 203-ha core area (mean = 106, range = 44–149)
survey	Binomial	Survey-specific variation coded as 6 categorical dummy variables per year
S	Continuous	Linear within-year temporal trend
S ²	Continuous	Quadratic within-year temporal trend
S ³	Continuous	Cubic within-year temporal trend

detection probability could vary because of survey-specific (survey) or annual (year) differences in survey staff, weather conditions such as wind, or other unmeasured factors. We also included alternate year structure (altyr) in annual temporal covariate models of colonization and extinction of pairs data because previous studies found patterns of alternate-year oscillations in reproductive output for California and northern spotted owls (LaHaye et al. 2004, Blakesley et al. 2010, Forsman et al. 2011). Breeding dispersal of California spotted owls is more prevalent after breeding failures (Blakesley et al. 2006, Gutiérrez et al. 2011), so an alternate-year reproduction cycle could mediate an alternate-year territory extinction pattern. An alternate-year pattern is also evident for long periods in year-specific survival rates of California spotted owls, although the authors did not test this model structure (Blakesley et al. 2010).

We modeled temporal variation in detection probabilities for within-year surveys as survey-specific (survey), as well as a linear time trend (S), quadratic time trend (S²), cubic trend (S³), and constant (.). Within each year, survey crews made efforts to survey all sites completely before beginning another iteration of surveys. Therefore, the first, second, third, etc., survey for all sites were close together in time and represented a seasonal continuum making temporal trends representative of seasonal variation in detectability. We did not include more detailed covariates of survey-specific variation such as observer, date- and site-specific weather conditions, or time of night because these covariates were not available.

In unburned landscapes, habitat selection of California spotted owls typically is associated with large trees and high canopy cover (Gutiérrez et al. 1992, Blakesley et al. 2005, Seamans 2005), so we predicted colonization would be positively, and extinction negatively, correlated with tree cover within 203 ha of the nest or roost centroid (tree). Spotted owls seek cool roosting sites during periods of warm

weather as an adaptation to heat stress (Barrows 1981), and radio-marked northern spotted owls in dry forests of southwestern Oregon selected foraging locations closer to perennial streams (Clark 2007); therefore, we predicted colonization would be positively, and extinction negatively, correlated with amount of riparian habitat (rip). We expected elevation-related gradients in vegetation type, prey biomass (Smith et al. 1999), and climate (LaHaye et al. 2004) to affect colonization and/or extinction probability (elev). The raw elev covariate consisted of large numbers, so we standardized this covariate to units of standard deviation (Table 1).

Our model set included year- and site-specific fire effects in detection, colonization, and extinction probabilities. We modeled detection, colonization, and extinction with and without an intercept effect (fire) for whether the site burned between 2003 and 2011. We modeled the intercept effect of fire between 2003 and 2011 as a time-varying, site-specific, categorical covariate that was coded 0 for unburned sites in all years, 0 for burned sites in years before the fire, and 1 for burned sites in years after the fire. Within a given season, sites are assumed to be closed to changes in occupancy; this assumption can be relaxed as long as changes occur at random (MacKenzie et al. 2006). All fires burned after surveys ended for the year, so fire did not affect within-season conditions in this study.

In colonization and extinction, we modeled covariates of vegetation changes due to high-severity fire as linear (hisev) and quadratic (hisev²) functions of the hectares of trees killed by fire within the 203-ha core area. We included quadratic covariates because we believed the relationship between the amount of habitat burned and occupancy dynamics could be nonlinear. Spotted owls may require a threshold amount of habitat in their core area that abruptly affects colonization or extinction probabilities rather than a smooth linear relationship. We modeled a site-specific colonization and extinction covariate of post-fire salvage logging (log) as a

linear function of the hectares of clearcut within the 203-ha core area.

To minimize potential biases, for both datasets (all detections and pair), within each stage of model selection, we ranked all possible combinations of covariates (Doherty et al. 2010). In detection, we examined every combination of temporal covariate for year- and survey-specific variation with and without fire effects (28 models). When modeling temporal variation in colonization and extinction, we examined every combination of annual variation covariates (22 models), pre-fire habitat covariates (19 models), and fire and salvage-logging effects (49 models).

To protect against spurious conclusions based only upon a single top model, and to account for model selection uncertainty, we present all results as the model-averaged parameter estimates (Burnham and Anderson 2002, Doherty et al. 2010). We calculated model-averaged parameter estimates by summing the individual model estimates multiplied by the associated Akaike's Information Criterion (AIC) model weight (Burnham and Anderson 2002). Model averaging produces real parameter estimates that account for the weight of evidence from our data for each model in the set, and these weighted averages result in real parameter estimates that are conservative and adjusted according to the amount of weight of evidence behind each model. Thus, even though the 95% confidence interval of point estimates of beta coefficients includes zero, the model-averaged real parameter estimates of burn or logging effects should be viewed as a conservative effect size that accounts for uncertainty and inference can be based on that model-averaged effect size. We used mean values of all individual covariates when computing mean model-averaged parameter estimates (Burnham and Anderson 2002). When presenting effects of a given covariate across its full range, we held all other covariates at their mean values. We computed unconditional estimates of variance, standard errors, and 95% confidence intervals (Buckland et al. 1997, Burnham and Anderson 2002). We determined specific covariate effects were statistically significant when the 95% confidence interval of the beta coefficient did not include zero. We calculated relative importance of variables by summing the weights from all models in a set that contained a variable of interest (Burnham and Anderson 2002). We ascertained potential biological significance by examining effect sizes among the 3 treatment groups (unburned, burned, burned and salvage logged) using model-averaged real parameters. Model averaging inherently presents parameter estimates based on the weight of evidence in the data for a given effect.

RESULTS

We analyzed 9,558 possible sampling events; 3,143 surveys (33%) were missing data (no survey done). Missing data were mostly the result of some sites not being surveyed in a given year because of budget or safety constraints (see the Methods Section). The mean number of California spotted owl sites surveyed each year (2003–2011) was 78 (SD = 23, minimum = 39) for unburned sites and 58 (SD = 13,

minimum = 38) for burned sites from 2004 to 2011 because the first fires burned in fall 2003. The mean number of sites surveyed each year that had been surveyed in the previous year (consecutive annual site surveys) was 76 (SD = 24, minimum = 39) for unburned sites and 52 (SD = 16, minimum = 31) for burned sites. In the last 8 years of the study (the years when burned sites were available), the mean annual proportion of surveyed sites that were in the burned group was 0.37 (SD = 0.09).

Vegetation Change and Site-Specific Covariates

The mean amount of pre-fire owl habitat (sum of conifer and hardwood types) within a 203-ha core area around the nest location or roost centroid in all 168 sites was 106 ha (SD = 24, range = 44–149). In our sample of 71 spotted owl sites burned from 2003 to 2007, the amount of owl habitat that burned at high severity within the core area around the pre-fire nest location or roost centroid was 24 ha (SD = 31, range = 0–119). Salvage logging was only detected when more than 20 ha of habitat burned at high severity in the core area, and occurred on 21 burned sites. Mean amount of salvage logging in burned sites was 63 ha (SD = 53, range = 0–150). Sites at higher elevations tended to support a greater amount of owl habitat pre-fire ($t = 2.77$, $P = 0.006$), but among burned sites the amount of owl habitat burned at high-severity within a core area was similar at all elevations ($t = -1.19$, $P = 0.23$).

Detection, Extinction, and Colonization

Top-ranked models for all detections and pairs data indicated evidence for time- and fire-related effects on colonization; time-, fire-, and logging-related effects on extinction (Table 2); and time- and fire-related effects on detection (for complete model selection results see Table S1, available online at www.onlinelibrary.wiley.com). Beta coefficients (β) and their standard errors from the highest-ranked models indicated that all parameters were estimable and reasonable. The 95% confidence intervals of beta coefficients for all fire and logging effects overlapped zero indicating these effects were not statistically significant (Tables 3 and 4), and the relative importance (cumulative AIC weights) of fire and logging variables was low (0.01) to moderate (0.42). Model-averaged real parameter effect sizes for mean detection, colonization, and extinction values indicated some evidence for potentially biologically significant effects, if we assume point estimates of beta coefficients are accurate (Fig. 1).

All detections.—The mean annual detection probability was 0.072 greater in burned sites versus unburned sites (burned $\bar{p} = 0.667$; unburned $\bar{p} = 0.595$). At unburned sites, mean colonization probability was 0.158 (SE = 0.041), and mean extinction probability was 0.172 (SE = 0.061). At burned sites, mean colonization probability was 0.067 (SE = 0.013), and mean extinction probability was 0.229 (SE = 0.004). Mean annual colonization probability was 0.090 lesser in burned sites relative to unburned sites, but colonization was unaffected by salvage logging (Fig. 1B). Mean annual extinction probability was 0.057 greater in burned sites relative to unburned sites, and 0.065 greater in salvage logged

Table 2. Top-ranked models of fire and logging effects on colonization and extinction probabilities for California spotted owl sites in the San Bernardino and San Jacinto mountains of southern California from 2003 to 2011. In all-detections data models, minimum Akaike's Information Criterion (AIC) was 3,618.68, and detection was modeled as $P(Y^3 + S^3 + \text{fire})$. In pairs data models, minimum AIC was 2,557.75, and detection was modeled as $P(\text{year} + S^3 + \text{fire})$. We included lower-ranked models with no fire effects for comparison.

Colonization ^a	Extinction ^a	ΔAIC	w_i^b	Model likelihood	K^c
All detections data					
(Y ² + tree + fire + hisev)	(Y ² + tree + elev + fire + log)	0	0.11	1	21
(Y ² + tree + fire + hisev)	(Y ² + tree + elev + fire + hisev ² + log)	0.81	0.07	0.67	23
(Y ² + tree + fire + hisev ²)	(Y ² + tree + elev + fire + log)	1.06	0.06	0.59	22
(Y ² + tree + fire + hisev)	(Y ² + tree + elev + fire)	1.21	0.06	0.55	20
(Y ² + tree + fire + hisev)	(Y ² + tree + elev + fire + hisev)	1.23	0.06	0.54	21
(Y ² + tree + fire + hisev)	(Y ² + tree + elev + fire + hisev + log)	1.60	0.05	0.45	22
(Y ² + tree + fire + hisev)	(Y ² + tree + elev + fire + hisev ²)	1.65	0.05	0.44	22
(Y ² + tree + fire + hisev + log)	(Y ² + tree + elev + fire + log)	1.98	0.04	0.37	22
(Y ² + tree + fire + hisev ²)	(Y ² + tree + elev + fire + hisev ² + log)	2.03	0.04	0.36	24
(Y ² + tree + fire + hisev)	(Y ² + tree + elev)	2.24	0.03	0.33	19
(Y ² + tree)	(Y ² + tree + elev + fire + log)	11.84	0	0	19
Pairs only data					
(tree + fire)	(Y + altyr + tree + elev + fire + hisev)	0	0.06	1	24
(tree)	(Y + altyr + tree + elev + fire + hisev)	0.08	0.06	0.96	23
(tree + fire)	(Y + altyr + tree + elev + fire + hisev + log)	0.16	0.06	0.92	25
(tree)	(Y + altyr + tree + elev + fire + hisev + log)	0.27	0.05	0.87	24
(tree + fire + hisev)	(Y + altyr + tree + elev + fire + hisev + log)	0.38	0.05	0.83	26
(tree + fire + hisev)	(Y + altyr + tree + elev + fire + log)	0.39	0.05	0.82	25
(tree + fire + hisev)	(Y + altyr + tree + elev + fire + hisev)	0.48	0.05	0.79	25
(tree + fire + hisev)	(Y + altyr + tree + elev + fire + hisev ² + log)	0.53	0.05	0.77	27
(tree + fire + hisev ²)	(Y + altyr + tree + elev + fire + hisev ² + log)	0.55	0.05	0.76	28
(tree + fire)	(Y + altyr + tree + elev + fire + hisev ² + log)	0.61	0.04	0.74	26
(tree)	(Y + altyr + tree + elev + fire + hisev ² + log)	0.63	0.04	0.73	25
(tree + fire + log)	(Y + altyr + tree + elev + fire + hisev)	0.67	0.04	0.72	25
(tree + fire + hisev ² + log)	(Y + altyr + tree + elev + fire + hisev ² + log)	1.45	0.03	0.48	29
(tree + fire + log)	(Y + altyr + tree + elev + fire + hisev + log)	1.48	0.03	0.48	26
(tree + fire)	(Y + altyr + tree + elev + fire + hisev ²)	1.53	0.03	0.47	25
(tree)	(Y + altyr + tree + elev + fire + hisev ²)	1.60	0.03	0.45	24
(tree + fire + hisev + log)	(Y + altyr + tree + elev + fire + hisev)	1.83	0.02	0.40	26
(tree + fire + log)	(Y + altyr + tree + elev + fire + hisev ² + log)	1.84	0.02	0.40	27
(tree + fire + hisev)	(Y + altyr + tree + elev + fire + hisev ²)	1.91	0.02	0.38	26
(tree + fire + log)	(Y + altyr + tree + elev + fire + hisev ²)	1.91	0.02	0.38	26
(tree + fire + hisev ² + log)	(Y + altyr + tree + elev + fire + hisev ²)	1.95	0.02	0.38	28
(tree)	(Y + altyr + tree + elev + fire + log)	2.01	0.02	0.37	23
(tree + fire)	(Y + altyr + tree + elev)	8.59	0	0.01	22

^a Y = year effect, tree = hectares of tree cover (owl habitat) in core area, fire = binomial fire effect, hisev = hectares of owl habitat in core area burned with high severity, log = binomial post-fire salvage logging effect, elev = standardized site elevation, altyr = alternative year temporal pattern.

^b Akaike weights.

^c Number of parameters.

versus unlogged sites (Fig. 1C). Extinction probability increased, and colonization probability decreased as a function of the amount of owl habitat that burned at high-severity (Fig. 2A). When >30 ha of owl habitat burned at high severity, colonization probability was significantly lesser than in unburned sites (Fig. 2A); when >110 ha of owl habitat burned at high severity, extinction probability was significantly greater than in unburned sites (Fig. 2A). Colonization and extinction parameters were correlated with amount of owl habitat in the 203-ha core area (Fig. 4A), and extinction probability was negatively correlated with elevation (Table 3).

Initial occupancy for all sites was 0.625. The difference between unburned and burned sites was small in the first year post-fire, but because occupancy is calculated using annual colonization and extinction rates combined with the previous year's occupancy, the difference between burned and unburned sites grows over time (Fig. 3A). Thus, the mean annual site occupancy probability from 2004 to 2011 of

unburned sites was 0.477, for sites burned in 2003 mean occupancy was 0.306, and logged sites was 0.255. The relationships between the amount of habitat burned at high severity and the probabilities of colonization and extinction resulted in significant differences (no overlap of standard errors) in site occupancy probabilities when >50 ha of owl habitat burned at high severity in the 203-ha core area. Salvage logging reduced burned site occupancy probability an additional 0.051.

Pair data.—The mean annual detection probability was slightly greater in burned sites versus unburned sites (burned $\bar{p} = 0.151$; unburned $\bar{p} = 0.144$), but detection increased during the study period from 0.063 to 0.312. At unburned sites, mean colonization probability was 0.071 (SE = 0.041), and mean extinction probability was 0.138 (SE = 0.061). At burned sites, mean colonization probability was 0.055 (SE = 0.004), and mean extinction probability was 0.238 (SE = 0.033). Mean annual colonization probability was 0.015 lesser in burned sites relative to unburned sites, but

Table 3. All-detections data model-averaged beta coefficients (β), their unconditional standard errors (SE) and 95% confidence intervals (95% CI) for temporal, habitat, and fire-related covariates of occupancy dynamics at burned and unburned California spotted owls sites in the San Bernardino and San Jacinto mountains from 2003 to 2011.

Covariate ^a	β	SE	95% CI	
Initial occupancy	0.510	0.239	0.041	0.978
Colonization				
intercept	-2.459	0.771	-3.969	-0.948
Y	-0.722	0.000	-0.722	-0.722
Y ²	0.073	0.000	0.073	0.073
tree (pre-fire owl habitat)	0.039	0.014	0.011	0.067
fire	-0.529	0.399	-1.311	0.253
hisev	-0.029	0.019	-0.066	0.008
hisev ²	-0.00017	0.00007	-0.00030	-0.00004
log	0.00014	0.00101	-0.00184	0.00212
Extinction				
intercept	0.816	0.263	0.300	1.331
Y	0.426	0.000	0.426	0.426
Y ²	-0.061	0.000	-0.061	-0.061
tree (pre-fire owl habitat)	-0.052	0.013	-0.078	-0.026
elev	-0.131	0.150	-0.425	0.163
fire	0.379	0.304	-0.217	0.975
hisev	-0.007	0.005	-0.018	0.004
hisev ²	0.00033	0.00010	0.00013	0.00053
log	0.010	0.006	-0.001	0.022
Detection				
intercept	-1.224	0.197	-1.610	-0.838
S	1.249	0.099	1.055	1.444
S ²	-0.425	0.016	-0.455	-0.394
S ³	0.040	0.001	0.038	0.042
Y	0.179	0.049	0.084	0.275
Y ²	-0.007	0.005	-0.016	0.002

^a Y = year effect, tree = hectares of tree cover (owl habitat) in core area, fire = binomial fire effect, hisev = hectares of owl habitat in core area burned with high severity, log = binomial post-fire salvage logging effect, elev = standardized site elevation, S = within year temporal trend.

colonization was unaffected by logging (Fig. 1E). Mean annual extinction probability was 0.100 greater in burned relative to unburned sites, and 0.110 greater in logged versus unlogged sites (Fig. 1F). Extinction probability increased as a function of the amount of owl habitat that burned at high-severity (Fig. 2B). When >50 ha of owl habitat burned at high severity, extinction probability was significantly greater than in unburned sites (Fig. 2B). Colonization and extinction parameters were correlated with amount of owl habitat in the 203-ha core area (Fig. 4B), and extinction probability was negatively correlated with elevation (Table 4).

Initial occupancy for all sites was 0.403. Mean annual site occupancy probability from 2004 to 2011 of unburned sites was 0.346, of burned sites was 0.239, and logged sites was 0.185 (Fig. 3B). The relationships between the amount of habitat burned at high severity and the probabilities of colonization and extinction resulted in significant differences (no overlap of standard errors) in site occupancy probabilities where >50 ha of owl habitat burned at high severity in the 203-ha core area. Salvage logging reduced burned site occupancy probability an additional 0.054.

DISCUSSION

We found no statistically significant effects of fire or salvage logging on occupancy dynamics of spotted owls in the San Bernardino and San Jacinto mountains of southern

California. However, we found some weak to moderate evidence that fire and logging impacts could be biologically meaningful. Uncertainty in model selection and parameter estimation does not mean the effects are not real, only that they were difficult to detect in this study. If we assume the model-averaged effect sizes were accurate, compared to unburned sites, sites affected by fires had lesser colonization probabilities and greater extinction probabilities, resulting in lesser site occupancy. Furthermore, compared with unlogged burned sites, salvage-logged sites had greater extinction probabilities which further reduced site occupancy. We also quantified the relationship between colonization and extinction probabilities and the amount of habitat that burned at high severity in the 203-ha circular core area around the nest or roost centroid. When 0–50 ha of forested habitat burned at high severity, colonization and extinction probabilities—and thus site occupancy probabilities—were similar to unburned sites. However, when >50 ha of forested habitat burned severely, site occupancy probability decreased approximately 0.003 for every additional ha of forested habitat severely burned. The 50-ha threshold should be considered approximate, because error bars for the modeled relationship were large (Fig. 2A,B). The majority of sites (75%) burned below the 50-ha threshold. Post-fire salvage logging exacerbated the lesser site occupancy of burned versus unburned sites by decreasing occupancy probability an additional 0.05.

Table 4. Pairs data model-averaged beta coefficients (β), their unconditional standard errors (SE), and 95% confidence intervals (95% CI) for temporal, habitat, and fire-related covariates of occupancy dynamics at burned and unburned California spotted owls sites in the San Bernardino and San Jacinto mountains from 2003 to 2011.

Covariate ^a	β	SE	95% CI	
Initial occupancy	-0.393	0.268	-0.918	0.131
Colonization				
intercept	-5.139	0.810	-6.727	-3.552
tree (pre-fire owl habitat)	0.048	0.015	0.019	0.078
fire	-0.133	0.414	-0.945	0.678
hisev	-0.005	0.021	-0.046	0.035
hisev ²	-0.00022	0.00007	-0.00035	-0.00009
Extinction				
intercept	1.790	0.263	1.274	2.306
Y	-0.097	0.099	-0.290	0.096
altyr	0.715	0.413	-0.095	1.525
tree (pre-fire owl habitat)	-0.068	0.042	-0.149	0.014
elev	-0.124	0.198	-0.512	0.264
fire	0.359	0.398	-0.422	1.139
hisev	0.014	0.015	-0.015	0.044
hisev ²	0.0004	0.0006	-0.0007	0.0015
log	0.015	0.012	-0.008	0.039
Detection				
intercept	-2.705	0.295	-3.282	-2.127
2004	0.087	0.304	-0.510	0.684
2005	-0.125	0.304	-0.722	0.472
2006	0.475	0.279	-0.072	1.022
2007	0.177	0.282	-0.375	0.730
2008	1.363	0.292	0.790	1.936
2009	1.223	0.277	0.680	1.767
2010	1.907	0.292	1.334	2.479
2011	1.490	0.289	0.923	2.057
S	1.734	0.135	1.470	1.999
S ²	-0.443	0.023	-0.487	-0.399
S ³	0.035	0.002	0.032	0.039
fire	0.076	0.158	-0.234	0.387

^a tree = hectares of tree cover (owl habitat) in core area, fire = binomial fire effect, hisev = hectares of owl habitat in core area burned with high severity, Y = year effect, altyr = alternative year temporal pattern, elev = standardized site elevation, log = binomial post-fire salvage logging effect, S = within year temporal trend.

We found that spotted owl sites in the SBM and SJM that burned tended to occur at lower elevations than sites that did not burn. The increase in fires at lower elevations in the SBM and SJM over the past decade was almost entirely a result of human-caused ignitions (Halsey 2005), compounded by drier conditions and warmer-than-average temperatures. Owl sites at lower elevations often are found in patchily distributed bigcone Douglas-fir-canyon live oak forests (Smith 1995). Because this forest type typically intergrades with chaparral along its margins, it is particularly vulnerable to high-severity fires (Lombardo et al. 2009).

Our results for fire-related effects on occupancy contrast with similar studies of the same subspecies in the Sierra Nevada (Roberts et al. 2011, Lee et al. 2012). Lee et al. (2012) used 11 years of breeding-season survey data from 41 burned California spotted owl sites (1997–2007) in the Sierra Nevada where on average 32% of owl habitat in a 200-ha circle around core areas burned at high severity (D. Lee, unpublished data), and found no significant effects of fire on extinction or colonization probabilities. In southern California, an average of 23% of owl habitat in a 203-ha circle around core areas burned severely, which was less than in the Sierra Nevada, yet some evidence for fire and logging effects was documented. Many of the spotted owl sites in the Sierra

Nevada differ from sites in southern California with respect to vegetation, elevation, climate, and fire regime, thus fire effects likely differ as well. The Sierra Nevada are farther north, higher in elevation, hold massive snowpack that irrigates lower elevations throughout the dry summer (Kattelmann 1996), and support a larger, more contiguous population of spotted owls relative to southern California's meta-populations (LaHaye et al. 1994). Furthermore, spotted owl surveys in the Sierra Nevada study were primarily associated with timber-harvest projects in mixed-conifer habitats, whereas the southern California study areas incorporated sites in all forested habitats within the SBM and SJM (Gutiérrez and Pritchard 1990, LaHaye et al. 1994), including vegetation types not typically monitored for spotted owls in the Sierra Nevada, such as pure hardwoods and conifer-hardwood forests associated with chaparral (Smith 1995). Moreover, southern California owl sites associated with vegetation such as bigcone Douglas-fir-canyon live oak forests have no corollary in the Sierra Nevada.

Effects of fire on occupancy dynamics in the Sierra Nevada compared with southern California may also be related to extent of pre-fire forested habitat within core areas. Colonization and extinction parameters in this study were

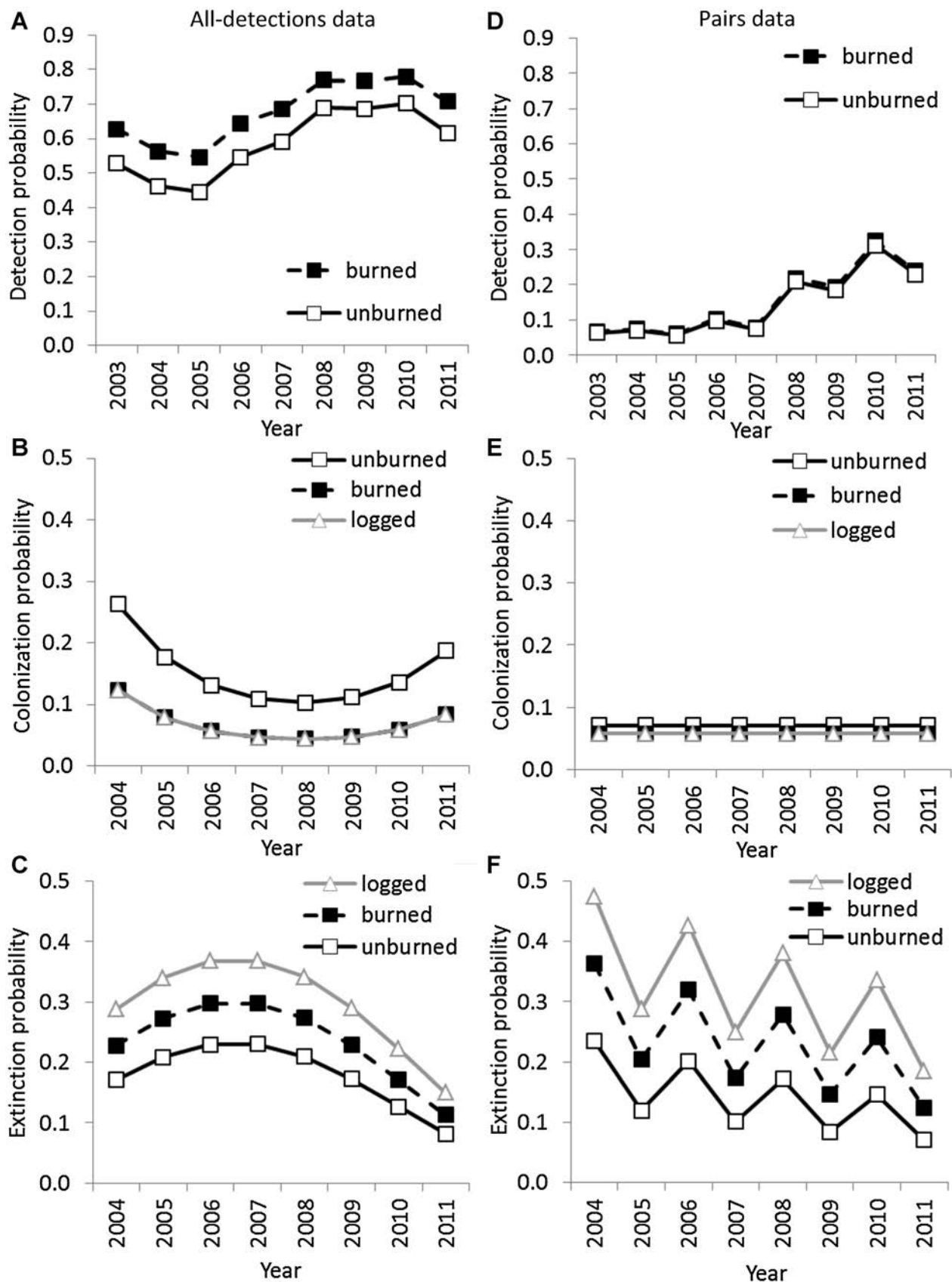


Figure 1. Annual modeled estimates of detection (A and D), colonization (B and E), and extinction (C and F) probabilities from all-detection (A–C) and pairs-only (D–F) data for burned and unburned California spotted owl sites in the San Bernardino and San Jacinto mountains from 2003 to 2011 as calculated from model-averaged beta parameters. We calculated burned sites as having burned in 2002 (detection) or 2003 (colonization and extinction). We set individual (site-specific) covariate values to the mean for each covariate.

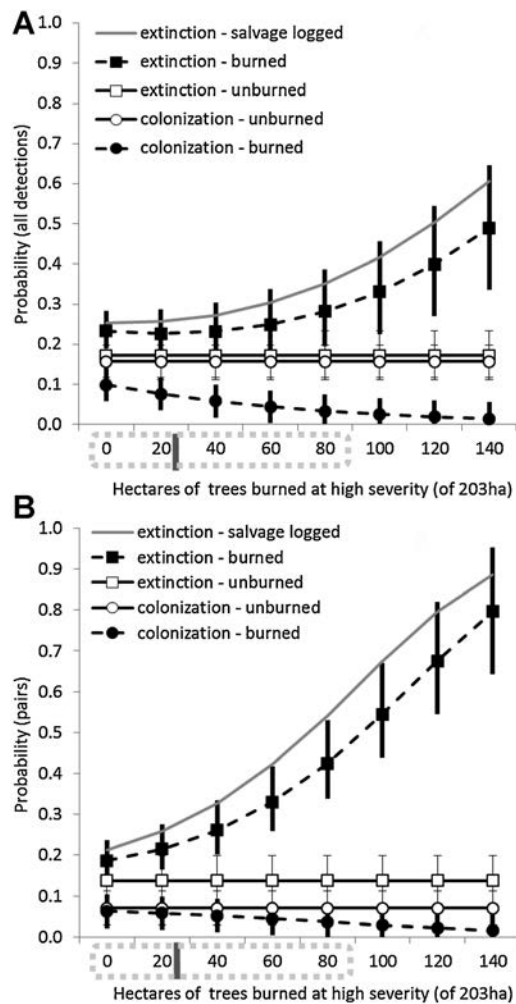


Figure 2. Model-averaged relationship between site colonization and extinction probability and the hectares of owl habitat that burned at high severity within a 203-ha circle around the nest or roost centroid of 71 California spotted owl sites in the San Bernardino and San Jacinto mountains from 2003 to 2011 from all-detection (A) and pairs-only (B) data as calculated from model-averaged beta parameters. Filled symbols and dashed lines are burned owl sites ($\pm$ SE), open symbols and solid lines are unburned sites ($\pm$ SE), and solid gray lines represent burned and salvage-logged site extinction probabilities. Vertical gray line in x -axis indicates the mean amount of owl habitat that burned at high severity in all burned sites. Dotted gray rectangle in x -axis indicates 95% confidence interval of amount of owl habitat that burned at high severity in all burned sites. We set individual (site-specific) covariate values to the mean for each covariate.

correlated with amount of forested habitat within the core area. The amount of pre-fire forested habitat in the core area averaged 180 ha ($SD = 20$) in the Sierra Nevada (D. E. Lee, Wild Nature Institute, unpublished data), but only 106 ha ($SD = 24$) in southern California. Core areas of southern California sites also had a greater proportion of hardwoods compared with Sierra Nevada core areas (D. E. Lee, unpublished data), which tend to burn at higher severities than conifer types (Bond et al. 2009a). The smaller amount of pre-fire forested habitat within spotted owl core areas in southern California translated into fewer hectares remaining unburned or lightly burned post-fire compared with the Sierra Nevada, perhaps explaining the potential impacts of

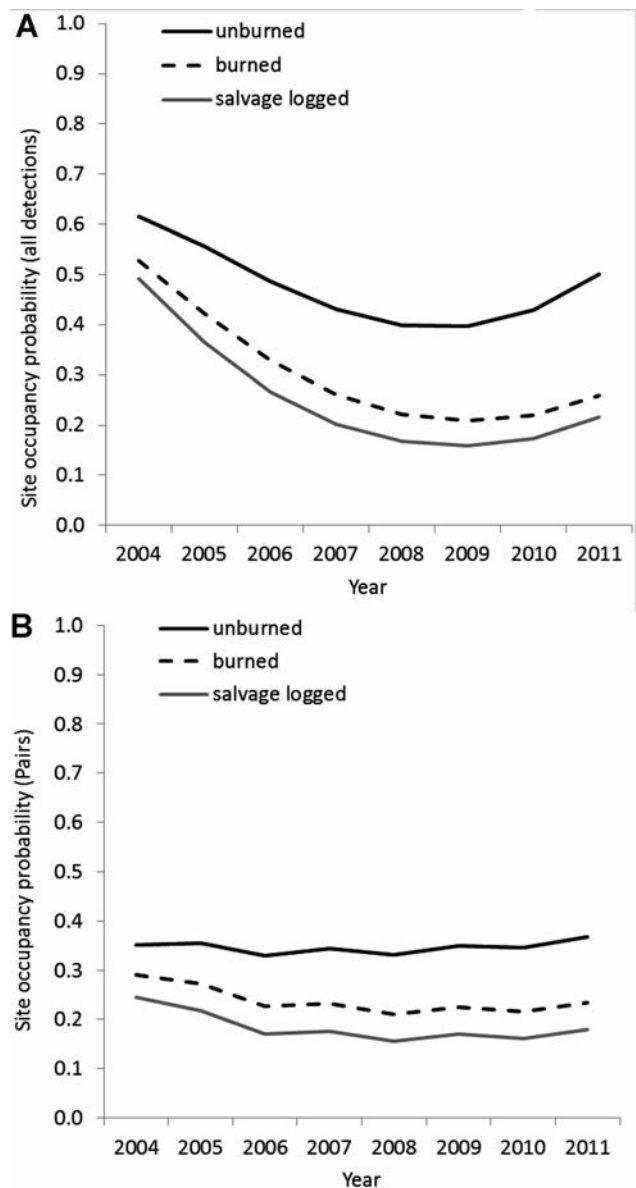


Figure 3. Annual estimates of southern California spotted owl site occupancy probability in unburned sites, sites that burned, and sites that were burned and salvage logged in San Bernardino and San Jacinto mountains. We computed estimates from estimates of initial occupancy, and annual colonization and extinction probabilities from the model-averaged parameters for all-detection (A) and pairs-only (B) data. We calculated burned sites as having burned in 2003. We set individual (site-specific) covariate values to the mean for each covariate.

severe fire on site occupancy we observed in southern California.

Post-fire salvage logging is a widespread practice that affects spotted owl habitat. Few studies have specifically examined this effect, but those that did reported adverse effects on foraging and occupancy rates of spotted owls elsewhere in the range of the species. In the Klamath Province in Oregon, northern spotted owls selected stands for foraging that were lightly or moderately burned and used severely burned stands in proportion to their availability, but avoided areas that were salvage logged after the fire

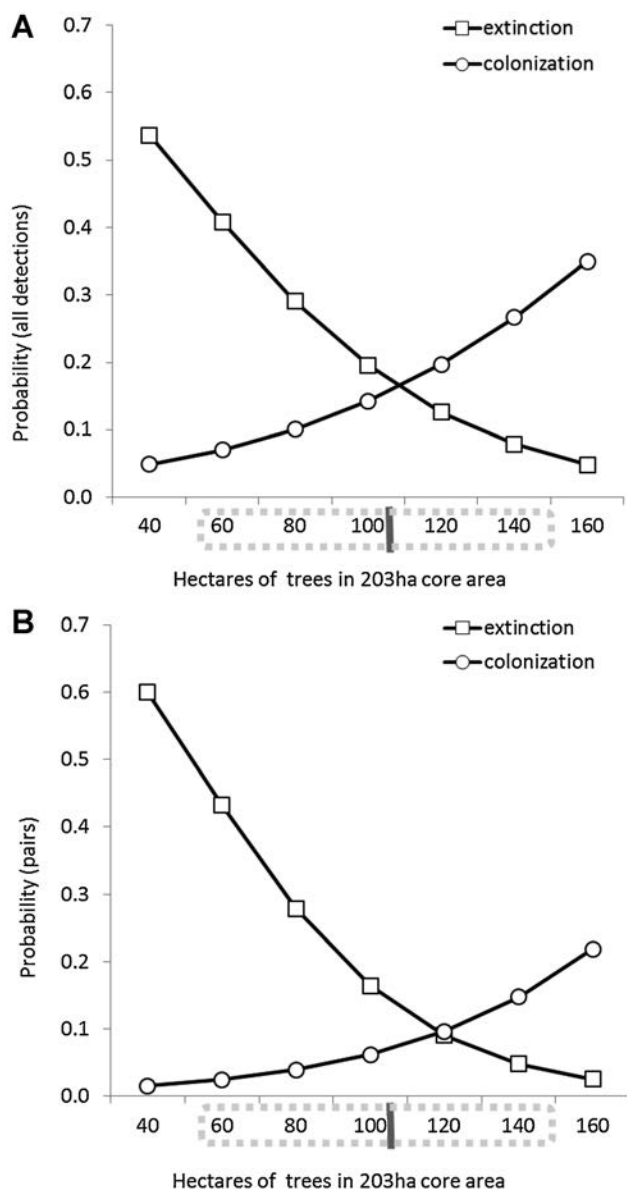


Figure 4. Model-averaged relationship between site colonization (circles) and extinction (squares) probabilities and the hectares of owl habitat (trees) within a 203-ha circle around the nest or roost centroid of California spotted owl sites in the San Bernardino and San Jacinto mountains from 2003 to 2011 from all-detection (A) and pairs-only (B) data. Vertical gray line in x -axis indicates the mean amount of owl habitat in all sites. Dotted gray rectangle in x -axis indicates 95% confidence interval of amount of owl habitat in all sites.

(Clark 2007). In a sample of 8 burned California spotted owl sites in the Sierra Nevada that were subsequently logged, 7 were occupied post-fire, but none were occupied after logging (Lee et al. 2012).

This study is the first to examine the discrete effects of severe fire and salvage logging on occupancy dynamics of spotted owls. Salvage logging in our southern California study area occurred mainly on private inholdings and as fuel wood cutting and hazard-tree removal along roads on United States Forest Service lands, rather than within the larger commercial salvage-logging projects typically conducted in the Sierra Nevada or the Pacific Northwest. Yet, even in the

absence of large-scale salvage-logging projects in southern California, post-fire tree removal in spotted owl cores was extensive enough to increase extinction probabilities and reduce occupancy relative to unlogged burned sites. Clark et al. (2013) examined effects of fire and logging on occupancy dynamics of northern spotted owls, but their analysis did not differentiate between the 2 disturbances.

Temporal factors also influence occupancy dynamics of California spotted owls. Weather conditions, particularly cold, wet conditions during winters (Nov–Mar) and nesting seasons (Mar–Apr), heavily influence annual variation in demographic rates of this species (Franklin et al. 2000; LaHaye et al. 2004; Olson et al. 2004; Glenn et al. 2010, 2011; Peery et al. 2011). Our annual estimates indicated that both burned and unburned sites experienced a drastic increase in extinction and decrease in colonization during the 2006 breeding season when snowfall in March and April was significantly greater than in any other year from 2003 to 2011 (>2.3 standard deviations above the mean). The elevated rate of extinction persisted through the 2007 breeding season for the all-detection data. We posit that this unusually extreme spring weather adversely affected demographic processes, which was reflected in greater site extinction and lesser colonization rates. LaHaye et al. (1994) documented a precipitous decline in site occupancy in the SBM, from more than 0.90 in 1987 to approximately 0.60 in 1992, among sites that were mostly unaffected by fire. Our all-detections estimate of unburned site occupancy from 2003 to 2004 was 0.61, but occupancy declined sharply in 2005 to 2009 before rebounding to 0.501 in 2011 (Fig. 3A). Our estimate of pair site occupancy was nearly constant during the study period (Fig. 3B). The alternate-year pattern we found in pairs extinction probability could be related to the alternate-year patterns found in California spotted owl reproduction and survival (Blakesley et al. 2010). This pattern in spotted owl demographic rates has been hypothesized to be related to cyclic small mammal populations, or to 1 irruptive small mammal year after a poor year (or years) resulting in a synchronized boom in owl reproduction that sets in motion an alternate-year pattern because of costs of reproduction that mediate a 2-year breeding cycle (Forsman et al. 2011). The alternate-year pattern attenuates as new recruits and stochastic effects increase the number of non-synchronized breeders.

The smaller, insular populations of the spotted owl in southern California are likely more vulnerable to extinction (Noon and McKelvey 1992, LaHaye et al. 1994) and thus may be more adversely affected by fires than populations in the Sierra Nevada. Often, populations at the edge of a species' range exhibit more variable occupancy dynamics than populations near their biogeographic core (Gaston 2009). In southern California, lower-elevation spotted owl sites appear to be most at risk, but these also are considered some of the most productive owl habitats. LaHaye et al. (2001) documented breeding spotted owls in lower-elevation bigcone Douglas-fir-oak habitat in the SBM produced more fledglings per nest, and Smith (1995) estimated relatively high densities of owls in these habitats. The higher

incidence of fires and greater risk of extinction in these sites is cause for concern.

MANAGEMENT IMPLICATIONS

We found no statistically significant effects of fire or salvage logging on occupancy dynamics of spotted owls of southern California. However, we found some evidence that fire and logging impacts could be biologically meaningful. The potential effect of fire on spotted owl occupancy in our southern California study area was most evident where >50 ha of owl habitat burned at high severity in the 203-ha core area. However, the majority of sites (75%) burned below this threshold. Bond et al. (2009b) documented California spotted owls in the southern Sierra Nevada selectively foraged in severely burned stands over unburned when those habitats were available, suggesting a possible fitness benefit from smaller high-severity burns within a site. We caution that our results not lead to conclusions that all sites with >50 ha of high-severity fire can no longer be occupied by spotted owls, as occupancy is site-specific, probabilistic, and influenced by factors other than fire. Burned sites, even those subjected to large areas of high-severity fire, should continue to be monitored for occupancy before management actions such as salvage logging are undertaken that could be detrimental to spotted owls. Post-fire salvage logging has the potential to increase extinction rates relative to burned sites, therefore California spotted owls will benefit from retaining fire-killed trees within core areas unless non-occupancy has been confirmed by protocol-level surveys conducted over multiple years (Lee et al. 2012). In southern California, the amount of owl habitat within spotted owl site core areas was correlated with colonization and extinction. Thus, forested habitat should be safeguarded from human-caused alteration wherever possible. Conserving maximum amounts of owl habitat, including large trees and dense canopy cover, could provide resiliency to potential adverse effects of severe fire. Finally, higher-elevation owl sites had more owl habitat relative to lower-elevation sites, but owls at lower-elevation sites are known to produce comparatively more offspring. Therefore, the risk of severe fire and site extinction is greater at lower elevations. The most effective management action may be to increase efforts aimed at reducing the rate of human-caused ignition in southern California mountains, especially at lower elevations. Because of the myriad differences between southern California and the rest of the species' range, our inferences are not directly applicable to spotted owls or their habitats outside of southern California.

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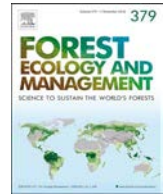
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Supporting Information

Additional supporting information can be found in the online version of this article at the publisher's web-site.



Cover of tall trees best predicts California spotted owl habitat



Malcolm P. North^{a,k,*}, Jonathan T. Kane^b, Van R. Kane^b, Gregory P. Asner^c, William Berigan^d, Derek J. Churchill^b, Scott Conway^e, R.J. Gutiérrez^{d,f}, Sean Jeronimo^b, John Keane^a, Alexander Koltunov^{e,j}, Tina Mark^g, Monika Moskal^b, Thomas Munton^h, Zachary Peery^d, Carlos Ramirez^e, Rahel Sollmannⁱ, Angela M. White^a, Sheila Whitmore^d

^a USFS PSW Research Station, Davis, CA 95618, United States

^b College of the Environment, University of Washington, Seattle, WA 98195, United States

^c Department of Global Ecology, Carnegie Institution for Science, Stanford, CA 94305, United States

^d Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI 53706, United States

^e US Forest Service Region 5 Remote Sensing Laboratory, McClellan, CA 95652, United States

^f Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, Minneapolis, MN 55455, United States

^g Tahoe National Forest, Nevada City, CA 95959, United States

^h USFS PSW Research Station, Fresno, CA 93710, United States

ⁱ Dept. of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA 95616, United States

^j Center for Spatial Technologies and Remote Sensing (CSTARS), University of California, Davis 95616, United States^k John Muir Institute, University of California, Davis, CA 95616, United States

^k John Muir Institute, University of California, Davis, CA 95616, United States

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ABSTRACT

Restoration of western dry forests in the USA often focuses on reducing fuel loads. In the range of the spotted owl, these treatments may reduce canopy cover and tree density, which could reduce preferred habitat conditions for the owl and other sensitive species. In particular, high canopy cover ($\geq 70\%$) has been widely reported to be an important feature of spotted owl habitat, but averages of stand-level forest cover do not provide important information on foliage height and gap structure. To provide better quantification of canopy structure, we used airborne LiDAR imagery to identify canopy cover in different height strata and the size and frequency of gaps that were associated with owl nest sites, protected activity centers (PACs), and territories within four study areas and 316 owl territories. Although total canopy cover was high in nest stands and PAC areas, the cover in tall (> 48 m) trees was the canopy structure most highly selected for, while cover in lower strata (2–16 m) was avoided compared to availability in the surrounding landscape. Tall tree cover gradually decreased and lower strata cover increased as distance increased from the nest. Large (> 1000 m²) gaps were not found near nests, but otherwise there was no difference in gap frequencies and sizes between PACs and territories and the surrounding landscape. Using cluster analysis we classified canopy conditions into 5 structural classes and 4 levels of canopy cover to assess the relationship between total canopy cover and tree size within nest sites, PACs, and territories. High canopy cover ($\geq 70\%$) mostly occurs when large tree cover is high, indicating the two variables are often confounded. Our results suggest that the cover of tall trees may be a better predictor of owl habitat than total canopy cover because the latter can include cover in the 2–16 m strata – conditions that owls actually avoid. Management strategies designed to preserve and facilitate the growth of tall trees while reducing the cover and density of understory trees may improve forest resilience to drought and wildfire while also maintaining or promoting the characteristics of owl habitat.

1. Introduction

Historically dry western forests, on average, had lower tree densities, canopy cover and fuel loads than forests today largely due to the absence of frequent, low-severity fire for much of the 20th century

(Knapp et al., 2013; Collins et al., 2015; Stephens et al., 2015; North et al., 2016). To increase resistance and resilience to current high-intensity wildfire and increasingly frequent and severe drought conditions (Graumlich, 1993; Asner et al., 2016; Margulis et al., 2016), managers often use mechanical thinning and managed fire to create

* Corresponding author at: USFS PSW Research Station, Davis, CA 95618, United States.
E-mail address: mnorth@ucdavis.edu (M.P. North).

some semblance of these historic stand conditions (Agee et al., 2000; Agee and Skinner, 2005; North et al., 2009). Such treated forests, however, often lack some of the structural features that have been linked with old-growth associated species such as the spotted owl (*Strix occidentalis*), fisher (*Martes pennanti*) and northern goshawk (*Accipiter gentilis*) (McClaren et al., 2002; Lee and Irwin, 2005; Purcell et al., 2009; North et al., 2010; Truex and Zielinski, 2013; Tempel et al., 2014; Sweitzer et al., 2016). In particular, throughout much of the western U.S., managing for the high canopy cover and tree density conditions of preferred spotted owl habitat may conflict with reducing ladder and canopy bulk density fuels, and stem density to improve a forest's fire and drought resilience (Zabel et al., 1995; North et al., 1999; Stephens et al., 2014; Jones et al., 2016; Stephens et al., 2016). The uncertainty about the effect of forest treatments on owls has often led to forest plans that separate landscapes into distinct restoration (i.e., managed to reduce fuels and stand density) and owl habitat zones (managed to preserve and increase high canopy cover) (Ager et al., 2007; Carroll and Johnson, 2008).

High ($\geq 70\%$) levels of canopy cover within both owl territories and their core use areas (120 ha management designated Protected Activity Centers [PACs]) have been associated with greater owl occupancy and survival (Tempel et al., 2014; Tempel et al., 2015), and higher reproduction at nest sites (North et al., 2000). High canopy cover is commonly used to identify potential habitat areas and determine management options. Yet, canopy cover can be a difficult management target because estimates significantly vary depending on how many measurements are taken, the observer's viewing angle (i.e., closure vs. cover sensu Jennings et al., (1999)) and whether estimates are derived from direct field measurements (ex. spherical densiometer, densiometer, or 'moosehorn'), indirect interpretation (i.e., using aerial photographs or Landsat imagery) or modeled from non-spatial plot data (i.e., such as the Forest Service's estimates using the Forest Vegetation Simulator) (Fiala et al., 2006; Korhonen et al., 2006; Christopher and Goodburn, 2008; Paletto and Tosi, 2009). Field plots are used to record tree size and foliage characteristics, but sample size is often small, which makes it difficult to extrapolate across the large, diverse forest conditions used by owls.

Canopy cover estimates using Landsat imagery or interpreted aerial photographs can sample larger areas, but neither method can be used to identify the tree size or height of foliage cover, and must be categorized (e.g., 0–39%, 40–69% and $\geq 70\%$) to meet the wide variety of ages and structures of forests (Tempel et al., 2016). Given the challenges of measuring canopy cover, both managers and researchers have often resorted to coarse classifications such as the widely used California Wildlife Habitat Relationships (CWHR) classes (Tempel et al., 2014) that are known to simplify and only roughly correlate with patterns of actual animal use (Purcell et al., 1992; Block et al., 1994; Howell and Barrett, 1998). Regardless of how it is estimated as a stand-level characteristic, canopy cover does not provide information on the height and distribution of foliage or the size and frequency of forest gaps (Jennings et al., 1999). Consequently, it is unclear how foliage and gaps are either distributed within owl use areas, or how best to assess and then establish management objectives for sustaining and enhancing owl habitat.

In this study we use airborne LiDAR data to measure canopy structure both intensively and accurately within all owl territories ($n = 316$ territories within a cumulative 420,478 ha) found in four large study areas having a variety of management histories in the central and southern Sierra Nevada. Three of these locations are long-term owl demographic study areas, and include an area in Sequoia/Kings Canyon National Park (SEKI) where the only logging occurred 75–120 years ago in localized, limited areas. SEKI includes forests with restored fire regimes, and has the only known non-declining population of spotted owls that have been studied in California. The fourth site, Tahoe National Forest, while not a demographic study area, did survey owl occupancy and reproduction over an extensive area for which

LiDAR data was collected. The LiDAR data allowed us to map forests in high fidelity, measuring total canopy cover, the distribution of cover by height strata, and opening sizes and frequencies. We analyzed habitat at three scales for each owl pair: nesting area (~ 4 ha), the surrounding Protected Activity Center (~ 120 ha), and the encompassing territory (~ 400 ha). Using the data on tree cover in different height strata and how they are associated, we used cluster analysis to identify common forest structural conditions. We then compared structural conditions between owl use areas and the surrounding forest with a complete LiDAR sampling of the landscape within a 5 km radius.

The goal of this study was to use our large sample size and high fidelity measurements over large areas to examine which attributes of forest structure are most strongly associated with California spotted owl habitat. Using LiDAR measures of forest structure, we examined the following specific questions:

- Which canopy structures are most strongly associated with different scales of owl habitat use, focusing on the nest, PAC and territory?
- How does the percentage of overstory tree canopy area in different height strata and gap sizes compare between owl use areas and across study areas?
- How strongly selected are different canopy attributes at nests compared to the available landscape and how does that change with distance from the nest?
- How are structure classes distributed between different owl use areas and what is the relationship between these structure classes and total canopy cover?

2. Methods

2.1. Study areas

The four study areas are located on the western slopes of California's Sierra Nevada Mountains in predominantly ponderosa pine (*Pinus ponderosa*) and mixed-conifer forests, and extend over a range of 3° latitude or about 320 km (Fig. 1). The Tahoe study area (311,930 ha) encompasses most of the Tahoe National Forest and is dominated by ponderosa pine, incense cedar (*Calocedrus decurrens*) and black oak (*Quercus kelloggii*) on drier, lower elevation locations, and a combination of ponderosa and sugar pine (*P. lambertiana*), incense cedar, Douglas-fir (*Pseudotsuga menziesii*) and white and red fir (*Abies concolor* and *A. magnifica*) generally above 1300 m in more mesic conditions. At higher elevations (generally > 2000 m) and in the eastern-most portion of the owl use area, red and white fir and Jeffrey pine (*P. jeffreyi*) dominate forest composition. Areas of the Tahoe NF are checkerboarded with private ownership and much of the forest has been heavily selectively logged over the last century, resulting in scattered large individual trees and small pockets of old growth (Taylor, 2004). Since about the 1930s almost all fires have been suppressed leaving forests often in a fuel-loaded condition with high stem density and canopy cover.

The Eldorado Study Area (40,549 ha) includes an owl demographic study area on the Eldorado National Forest (Tempel et al., 2016). It is located east of Georgetown on steep terrain surrounding the Rubicon and middle Fork of the American rivers between 300 and 2500 m elevation. It is primarily mixed conifer with occasional black and canyon live oaks (*Quercus chrysolepis*), tanoak (*Notholithocarpus densiflorus*) and bigleaf maple (*Acer macrophyllum*). At higher elevations some of the study area includes red fir and lodgepole pine (*Pinus contorta*). The Eldorado National Forest was logged selectively, often removing the largest trees, and fire suppressed through much of the last century (Darr, 1990). Portions of the demographic study area have a checkerboard of private land ownership, much of which is owned by SIMORG Forests LLC. About 50% of the owl study area burned, much of it at high severity, in the 2014 King Fire (Jones et al., 2016). The LiDAR data we use is from an acquisition completed before 2014.

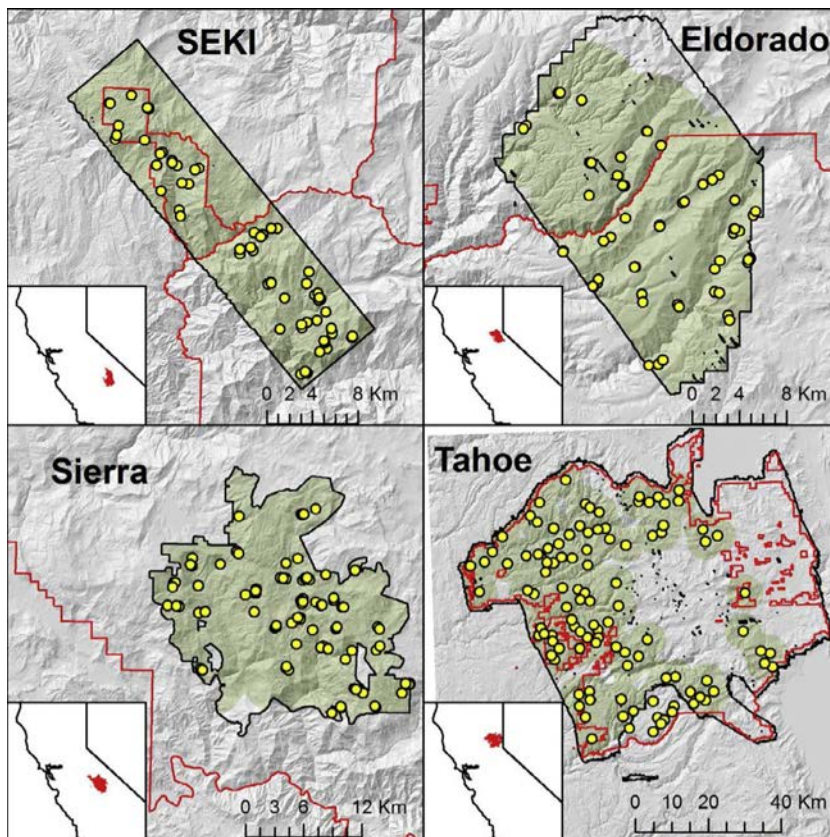


Fig. 1. The location in California (inset) of each of the four study areas. The black line shows the area of the LiDAR acquisition, circles indicate owl nest sites and green shading indicates the study area analyzed (i.e., within a 5 km radius of the PAC nests centroid). The background grey shading indicates the topography of the area. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The Sierra Study Area (41,080 ha) is on the Sierra National Forest, east of Fresno between 300 and 2900 m elevation. Both the Sierra study area and the nearby Sequoia-Kings Canyon study area (SEKI) are drier than the Tahoe and Eldorado areas (North et al., 2016). The Sierra study area is dominated by mixed-conifer forests, but on lower and drier sites includes ponderosa pine, interior live (*Quercus wislizeni*) and canyon oaks. Higher elevations include red fir, lodgepole pine and western white pine (*Pinus monticola*) (North et al., 2002). Most wildfire has been suppressed on the Sierra National Forest for decades but the forest was not as extensively logged as the more northern study areas (North et al., 2005). Many large, old trees remain in stands that were selectively logged and areas of old growth remain on steeper slopes because topography limited access for mechanical logging (North et al., 2015).

The Sequoia/King Canyon (SEKI) area (26,919 ha) is located on the western side of the two national parks of the same name and is mostly comprised of ponderosa pine and mixed-conifer forest types between 425 and 3050 m in elevation. Within the mixed-conifer zone there are several giant sequoia (*Sequoiadendron giganteum*) groves. With the exception of localized hazard tree removal and small areas of late 19th century logging (Stohlgren, 1992), these forests have not been logged (Vankat and Major, 1978). In addition, although many fires were suppressed in the first half of the 20th century, fire has been restored throughout much of the study area beginning in the 1970s (Parsons et al., 1986). Of California's four demographic study areas, SEKI is the only owl population that has been stable to expanding (Franklin et al., 2004; Blakesley et al., 2010; Conner et al., 2013; Tempel et al., 2014; Tempel et al., 2016). Therefore in our analyses we often compare SEKI forest structure to the three other study areas because it may provide more favorable habitat relative to the more heavily logged and fire-suppressed areas on the national forests.

2.2. Spotted owl data

The three study areas (Eldorado, Sierra, and SEKI) that encompass

California spotted owl demographic studies had similar survey methods (Blakesley et al., 2010), whereas slightly different owl survey methods were used in the Tahoe study area. For the three demographic areas, owls were annually surveyed from at least 1993 to the present (Tempel et al., 2016). All three areas contained a core zone that was completely surveyed (i.e., known territories as well as areas not containing owls). Some individual owl territories were added over time that surrounded core areas to increase sample size for demographic analysis, while a portion of SEKI was deleted in 2006 due to funding limitations. Surveys were conducted from April 1 to August 31 in the Eldorado study area and from March 1 to September 30 in the Sierra and SEKI study areas. SEKI was not surveyed in 2005 due to budget limitations that year. Spotted owl vocalizations were used as vocal lures and broadcast at designated survey stations or while walking survey routes. The sex of owls was initially determined by the pitch of territorial 4-note calls (Forsman et al., 1984). If owls were detected during nocturnal surveys, diurnal surveys were conducted as a follow up to band unmarked birds, re-sight marked birds, assess reproduction, locate nesting/roosting areas, and band fledglings (Franklin et al., 1996).

Owl surveys in the Tahoe National Forest were conducted for at least two years before and two years after in areas where management treatments (e.g., thinning to reduce fuel loads) were conducted. As such the Tahoe area did not have a core study area that was continually sampled but instead had focal surveys that shifted with management activities. However, owl survey methods were similar to those used on the owl demographic study areas.

In each study area, our analysis focused on confirmed owl pair nest sites that were occupied for at least one year. To insure that the LiDAR assessed forest conditions relevant to owl use, we only used 2001–2013 owl nest sites. We conducted our analysis at four different scales related to owl use and management. The nest site was considered a four-hectare area immediately surrounding each nest tree or snag. The size of the area around a nest that may influence owl selection has not been assessed but several studies have suggested canopy cover and

microclimate conditions may be factors in nest site selection (LaHaye et al., 1997; LaHaye and Gutierrez, 1999; North et al., 2000). We used four hectares as a conservative estimate for the area over which forest structure might influence microclimate (Ma et al., 2010). The protected activity center (120 ha or 300 ac) has been a forest management construct designed to approximate a core area that receives heavy use (Verner et al., 1992). In practice, agencies define these areas as a polygon of the best available habitat (often related to tree size and disturbance history) around a nest location (Verner et al., 1992; Tempel and Gutierrez, 2013) that often approximates a circle. Without knowing the exact shape of each PAC, for our analysis we defined this area as a circle of 120 ha (300 ac) immediately around the centroid of all nests belonging to an individual owl (Berigan et al., 2012). To estimate forest characteristics within a territory, we used territory sizes within the three study areas that were delineated as 400 ha, 302 ha and 254 ha for the Eldorado, Sierra and SEKI studies, respectively (Tempel et al., 2016). We did not have similar information for the Tahoe study area. Thus we fitted a regression line of territory size against latitude using the three demographic studies areas, as well as a fourth demographic study area on the Lassen NF (639 ha), which resulted in an approximated territory size of 437 ha for the Tahoe study area.

To estimate availability in the surrounding landscape, we used a circle 5 km in radius from the calculated activity center of each territory. To evaluate how forest conditions may differ with potentially different owl uses (e.g., nesting vs foraging and the influence of a central place forager), we removed the PAC area from territory calculations. In contrast, we did not remove the nest areas from each PAC, because studies have shown that owls select multiple nest and roost locations throughout a PAC (LeHaye et al., 1997).

2.3. Analysis of canopy structure

LiDAR data was acquired over our study areas between 2010 and 2015 (Table 1). We used the digital terrain models prepared by the acquiring vendor or organization. We processed the LiDAR data using the USDA Forest Service's Fusion software package (version 3.60, <http://forsys.cfr.washington.edu/fusion/fusionlatest.html>) (McGaughey, 2016) to produce metrics describing the canopy structure. In the processing, we normalized all laser returns to height above the digital terrain models. There were no major disturbances such as large high severity fire on our study areas between the time of the collection of the owl field data and the acquisition of the LiDAR data.

We used several strategies to generate the widest possible range of canopy structure measurements. We used the FUSION gridmetrics utility to produce 30 m resolution rasters of statistical measures of the vertical distribution of LiDAR return heights. This provided measurements of percentile return heights (e.g., 95th percentile height is the height at which 95% of returns fall below), standard deviation of return heights, and skew and kurtosis of return heights. These quantify canopy structures that have been associated with owl use: tall tree height, the variability in tree heights and how evenly or skewed tree heights are,

respectively. We calculated these statistical descriptors excluding returns < 2 m to exclude returns representing the ground, shrubs, and saplings. The gridmetrics utility also produced a measurement of canopy cover calculated as the count of returns above 2 m divided by the count of all returns.

Researchers are beginning to analyze forests as clumps of trees and openings (e.g., Larson and Churchill, 2012). We developed methods for this study to do this using the LiDAR data. Several studies have found that characteristic tree clump and opening patterns emerge at scales of 0.5–1 ha (Harrod et al., 1999; Larson and Churchill, 2012; Knapp et al., 2012; Lydersen et al., 2013). We therefore analyzed these patterns at a 90 m (0.81 ha) scale. We created a canopy surface model with a grid cell size of 0.75 m² and assigned the height above the digital terrain model of the highest return to each grid cell. We used the canopy surface model to identify tree approximate objects (TAOs) using the watershed segmentation algorithm implemented in the TREESEG utility in the FUSION package (Fig. 2). The TREESEG utility provided a raster map of the modeled canopy area of each TAO with the maximum height of each TAO assigned to the entire canopy area for that TAO (Fig. 3a). We then reclassified each TAO into the following height strata: 2–16 m, 16–32 m, 32–48 m, and > 48 m so that clumps of overstory trees with similar heights could be identified. Areas with no canopy > 2 m were considered openings. We measured the area in each strata using a moving 90 by 90 m window with measurements centered at 30 m spacing to match the raster cells of the statistical and canopy cover measurements (Fig. 3b). The use of an overlapping moving window had the practical effect of smoothing the measurements of tree clump and opening areas. We report metrics as the area in each stratum for each grid cell.

We also investigated whether the presence and density of larger gaps that might affect microclimate and protective cover conditions for the owls, as well as providing foraging opportunities for the owl, were negatively associated with owl habitat. We defined gaps following methods (Lydersen et al., 2013) that set a minimum size of 112 m², the approximate crown area of a dominant tree. We binned gaps larger than this minimum size into categories suggested by research on forests that have frequent fire regimes (Harrod et al., 1999; Larson and Churchill, 2012) and operational sizes often used by managers in thinning prescriptions (Knapp et al., 2012; North and Rojas, 2012; Stine and Conway, 2012). We reported the percentage of area and frequency for gaps in the categories 112–1000 m², 1000–5000 m², 5000–10,000 m², and > 10,000 m² (Fig. 3c).

2.4. Statistical analysis

To identify canopy variables most strongly associated with owl use, we initially used three statistical approaches to compare structures at nest sites against the surrounding landscape: niche overlap modeling, general linear models and random forest. All three approaches produced similar results and hereafter we base inference on niche overlap modeling because it provides a quantitative measurement of distinction

Table 1
Attributes of owl territories and LiDAR data used for the four study areas.

Owl data	Tahoe	Eldorado	Sierra	SEKI
No. of nests	64	58	63	131
Area (ha) of coverage within 5 km of a nest	311,930	40,549	41,080	26,919
Elevation range within 5 km of a nest	292–2673	711–2190	390–2961	835–2643
Year(s) data acquired	2013 & 2014	2012	2010 & 2012	2015
Acquirer	NCALM ^a	NCALM ^a	Watershed Sciences ^b	Carnegie Institution for Science
Instrument family	Optech	Optech	Leica	CAO ^c /Optech
# of returns/m ²	10.3	8.1	12.3	14

^a National Center for Airborne LiDAR Mapping.

^b Now part of Quantum Spatial.

^c Carnegie Airborne Observatory modification of Optech (see Asner et al., 2012).

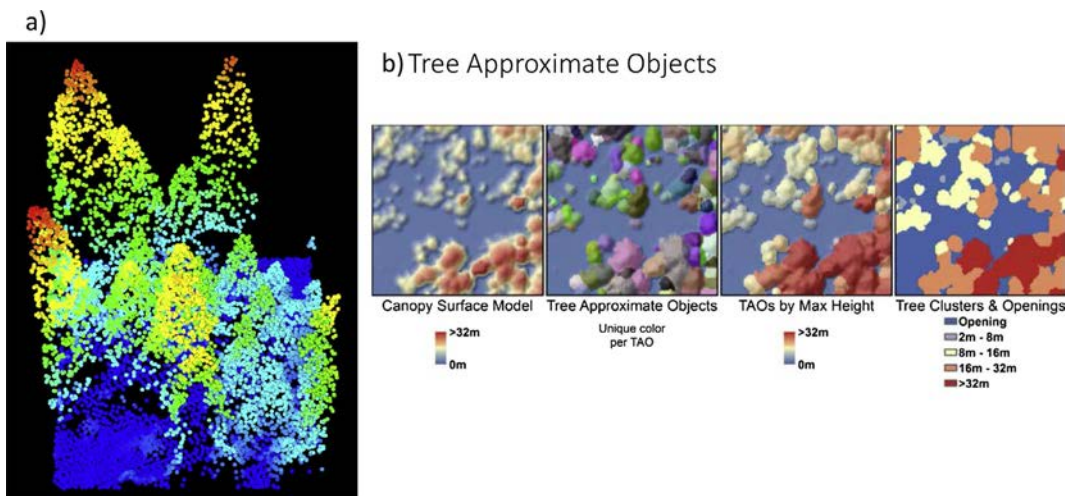


Fig. 2. Example of (a) a LiDAR point cloud where returns are color-coded by height; and (b) how tree approximate objects (TAOs) and gaps are derived from the point cloud data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

between two distributions (Mouillot et al., 2005; Broennimann et al., 2012). Niche overlap compared the distribution of values of a structural variable across a landscape (‘availability’) relative to a specific location (‘selection’). Smaller overlaps indicated that areas used by owls were more distinct from what was available across the landscape and by inference was selected by the owls (Fig. 4a).

Focusing on the canopy and gap attributes with the highest niche model ranks (Supplemental Table 1), we calculated the median, and standard deviation of each attribute as four different scales; nest sites, PACs, territories and the surrounding landscape within each study area. We then tested for significant differences between study areas using Student’s post hoc ANOVA.

Spotted owls are central place foragers (Carey and Peeler, 1995),

suggesting that canopy structure may change with distance from core locations (i.e., nesting and roosting sites). To evaluate changes in canopy conditions with distance from the nest, we assessed the niche decay function using annuli that expanded by 30 m per step. For highly ranked niche model variables, we plotted the percentage of niche overlap as a function of distance from owl nests for each of the four study areas.

Forests are often a complex assemblage of foliage in different strata. To quantify and describe how multiple canopy structures may commonly occur together, we created structure classes combining three core attributes of forest structure: tree height distribution, total canopy cover, and cover in different strata. These variables were analyzed using hierarchical clustering with the Ward method and the hclust

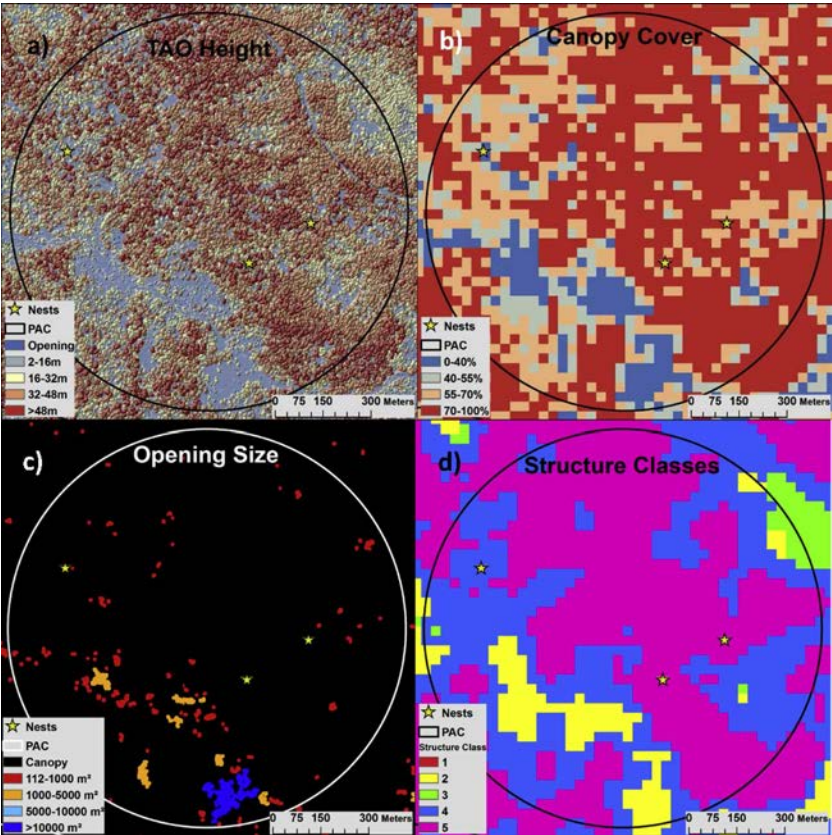


Fig. 3. Example of the distribution of (a) TAOs by height class; (b) total canopy cover; (c) opening size; and (d) structure class for the same PAC area (black circle) in the Eldorado study area. Stars indicate nest locations.

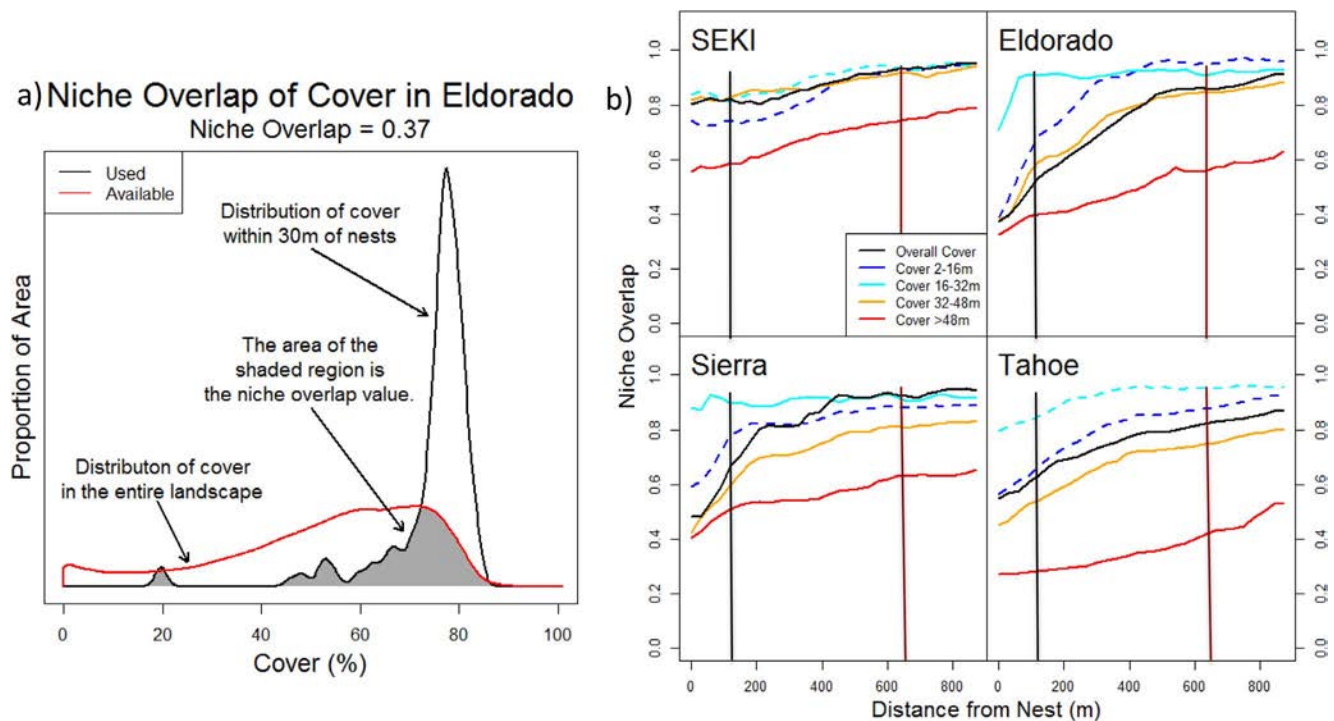


Fig. 4. (a) An annotated example of how niche overlap is calculated; and (b) graphs of niche overlap for total canopy cover and cover in four different height strata in each of the four study areas with distance (m) from the owl nest. Dashed lines are canopy structures that have lower values near the nest than in the surrounding landscape. Vertical lines indicate the distance defining the nest (black) and PAC (brown) areas.

function of the R statistical package (Team, 2013). Using dendrograms derived from 30,000 samples and structural characteristics of trial classes, we parsed conditions into five canopy structure classes that was the most parsimonious grouping that retained most (> 70%) of the original information (McCune and Mefford, 1999) (Supplemental Fig. 1). Within each of the five structure classes, we divided samples into four different canopy cover classes that previous research has suggested may be important thresholds to spotted owls; 0–39%, 40–54%, 55–69% and ≥70% canopy cover (Tempel et al., 2015, 2016). Therefore, we derived the percent area of each combination of canopy structure and canopy cover classes for nest, PAC, territory, and landscape areas.

3. Results

3.1. Canopy attributes associated with owl use

To determine which forest conditions were most distinct in areas used by owls versus the surrounding landscape, we evaluated 75 canopy structural attributes (Supplemental Table 1). The area of TAO canopy > 48 m was the most distinct metric for all study areas. The strongest nest and PAC selection for tall tree cover was in the Eldorado and Tahoe study areas presumably because both National Forests have been extensively logged and large, tall trees are rarer (Table 2). Area of TAO canopy 32–48 m, canopy cover, and measures of canopy height from LiDAR returns were moderately distinct from the surrounding landscape. Total area in gaps and gaps in different size ranges were among the least distinct. However, in the Tahoe study area, there were fewer small gaps (112–1000 m²) within PACs compared to the surrounding landscape (Table 2).

Across all four study areas, median values for total canopy cover and cover in trees > 48 m were highest at nest sites, and consistently decreased as area expanded to PACs, territories and then the surrounding landscape (Table 3). We also found a similar trend of decreasing values from nest sites to landscape for the 32–48 m strata on the three National Forest study areas but not at SEKI. We found a

reverse trend for cover in the 2–16 height strata with the lowest cover values near nest sites and increasing through larger scales. We did not find a consistent trend with changes in scale for cover values for the 16–32 m strata.

Across the entire study area, 20–40% of LiDAR returns were penetrating below 2 m indicating substantial area in openings. However, few of these openings were aggregated enough to reach the 112 m² threshold we used to define a ‘functional’ gap (an opening approximately equal to the canopy space occupied by a dominant tree). Gaps 112–1000 m² were rare within nest areas, and only accounted for 0.17–1.45% of the area in PACs and territories. Larger gaps were not found in nest areas. The area in gaps of 1000–5000 m² within PACs and territories ranged from 0.05 to 1.21% and we only found gaps > 5000 m² in the Sierra and Tahoe study areas (Table 3).

We found differences in canopy and gap conditions among the four study areas (Table 3). SEKI had lower canopy cover at nest sites, higher cover of tall trees (> 48 m) within nest sites, PACs and territories, and higher cover in the 32–48 m strata in territories. The Eldorado had greater cover than other areas in the 2–16 m cover in PACs and territories. The Sierra had lower total canopy cover in PACs and territories, and more gaps of all sizes, particularly those > 1 ha, in PACs and territories. The Tahoe had no distinguishing canopy cover conditions but did have high cover in gaps of all sizes at the territory scale (Table 3).

3.2. Changes in canopy structure with habitat scale

We examined spatially-explicit relationships by evaluating how niche overlap values changed with distance from the owl nest using a moving window and comparing each canopy attribute to its abundance in the surrounding (5 km) landscape (Fig. 4b). For all four study areas, the cover in tall (> 48 m) trees was the most distinct canopy attribute (i.e., the least niche overlap) starting at the nest site (the y intercept) and remained the most distinct over the 1000 m distance evaluated. The slope of the line for the cover of trees > 48 m continued to rise over 1000 m from the nest, suggesting that selection for tall trees may continue beyond the bounds of the PAC (618 m radius). Total canopy

Table 2

Niche values for different canopy structure attributes in four study areas and their overall mean comparing PAC and landscape habitat conditions. Bold values have low niche overlap (≤ 0.6) suggesting a structure selected for within PACs compared to the landscape. Metrics in *italics* are negative (i.e., have lower values in PACs compared to landscape). Metric type indicates the data used to calculate the structure value and pixel size indicates the dimension of the pixel used in the calculation. Canopy cover was calculated as the proportion of LiDAR returns greater than 2 m in height above the ground divided by all returns. Gap area was calculated as the area of the 0.75–2 m canopy surface model with no returns > 2 m.

Metric	Eldorado	SEKI	Sierra	Tahoe	Mean	Metric type/Pixel size
Canopy area TAO's > 48 m	0.49	0.66	0.6	0.37	0.53	TAO/90 m
Canopy area TAO's > 32 –48 m	0.75	0.87	0.75	0.71	0.77	TAO/90 m
95th percentile lidar return height	0.81	0.75	0.79	0.76	0.78	Returns/30 m
75th percentile lidar return height	0.81	0.75	0.8	0.76	0.78	Returns/30 m
50th percentile lidar return height	0.81	0.75	0.81	0.77	0.78	Returns/30 m
Std Dev. of lidar return heights	0.83	0.79	0.8	0.77	0.8	Returns/30 m
25th percentile lidar return height	0.81	0.76	0.83	0.79	0.8	Returns/30 m
Canopy area TAO's 2–16 m	0.8	0.76	0.84	0.82	0.81	TAO/90 m
Canopy cover from lidar returns	0.75	0.88	0.87	0.78	0.82	Cover/30 m
Total gap area	0.75	0.89	0.88	0.77	0.82	TAO/90 m
Area in gaps 112–1000 m ²	0.91	0.91	0.94	0.56	0.83	Gap/90 m
Area in gaps 5000–10,000 m ²	0.9	0.77	0.88	0.88	0.86	Gap/90 m
Area in gaps $> 10,000$ m ²	0.81	0.88	0.86	0.89	0.86	Gap/90 m
Area in gaps 1000–5000 m ²	0.96	0.89	0.86	0.85	0.89	Gap/90 m
Canopy area TAO's 16–32 m	0.93	0.81	0.91	0.94	0.9	TAO/90 m

Table 3

Median percent cover of total canopy cover, cover by height strata and cover of different gaps by size class in owl nests, PACs, territories and the surrounding landscape in four study areas. Comparing values within the same scale (ex. all nests), **bold** values are significantly higher and *italic bold* values significantly lower than the values in the other three study areas ($p < 0.05$, post hoc ANOVA). Landscape values are medians calculated from the whole landscape area and as single values are not included in the ANOVA analysis.

Area	Scale	Total and by Stratum Canopy Cover (%)					Cover (%) in Gaps by Size Class			
		Total CC	> 48 m	32–48 m	16–32 m	2–16 m	112–1000 m ²	1000–5000 m ²	5000–10,000 m ²	$> 10,000$ m ²
SEKI	Nest	67.9	23.7	26.6	19.4	6.7	0.02	0	0	0
	PAC	66.8	20.6	29.3	20.8	9.3	0.46	0.2	0	0
	Terr	63.9	16.6	30.5	23.3	11.6	0.59	0.31	0	0
	Land	65.9	3.2	24.1	26.4	11.7	0.82	0.54	0.18	0.42
Eldo.	Nest	76	14.7	38.1	31.8	5.1	0	0	0	0
	PAC	67.6	8.3	25.6	35.8	16.9^b	0.17	0.05	0	0
	Terr	61.8	4.8	20.8	36.7	25.7^b	0.39	0.26	0	0
	Land	55.8	0	9.9	32.4	22.2	0.73	0.57	0.22	1.7
Sierra	Nest	75.9	9.4	30.4	24.2	6.2	0.20	0^a	0	0
	PAC	59.6	9.2	27.4	24.8	7.7	0.88	1.03	0	0.60
	Terr	52.3	5.5	22.6	25.2	9.1	1.45	1.21	0.3	1.57
	Land	55.7	0	14.9	22.8	9.4	1.51	1.28	0.55	4.18
Tahoe	Nest	73.7	12.5	41.5	25.6	3.6	0.01	0	0	0
	PAC	67.2	6.9	31.6	32.7	9.9	0.72	0.51	0	0
	Terr	62.2	4.3	22.6	35.4	12.1	1.16	0.81	0.21	0.71
	Land	46.2	0	2.4	26.9	10.1	1.93	1.43	0.51	4.07

^a Although all the cover values for gaps 1000–5000 m² at nest locations are zero due to rounding, the Sierra value is significantly higher than the values at the other three study areas.

^b The high percentage of cover in the 2–16 m stratum on the Eldorado is influenced by a checkerboard of private ownership lands, many of which contain young plantations in this height class.

cover continued to rise across the 1000 m measured, but had the lowest niche overlap values between 0 to approximately 500 m on the Eldorado, Sierra and Tahoe study areas. In contrast, canopy cover at SEKI was not a selected canopy attribute except right at the nest site (Table 3).

3.3. Structure classes and canopy cover

Using the percent cover of TAOs in different height strata within over 30,000 pixels (each 30 by 30 m), hierarchical cluster analysis produced a dendrogram that had five structure classes retaining $> 70\%$ of the information (McCune and Mefford, 1999) (Supplemental Fig. 1). Understory (class 1) is dominated by tree cover in the 2–16 m strata, Openings (class 2) has low total canopy cover and more large gaps, Ladders (class 3) by cover in the 16–32 m strata, Co-dominants (class 4) by cover in the 32–48 m strata and Tall Trees (class 5) by cover in the > 48 m strata (Fig. 5).

Taking each of the classes and subdividing them into four canopy

cover classes (0–39%, 40–54%, 55–69% and $\geq 70\%$), we examined how the percentage of total area of each structure/canopy cover class changed between nest sites, PACs, territories, and landscapes in each of the four areas (Fig. 6). Canopy cover conditions $\geq 70\%$ (right slant hatching in Fig. 6) was dominated by the Tall Tree structure class (purple bars in Fig. 6) indicating that tall trees and high canopy cover co-vary. The Co-dominant structure class was dominated by canopy cover categories $\geq 55\%$, as the Understory and Ladders structure classes had fairly equal canopy cover distributions, while the Openings structure was dominated by 0–40% canopy cover. Nest sites and PAC areas were dominated by the Tall Tree and Co-dominant structure classes with high canopy cover (i.e., $> 55\%$), but territories and landscapes had a much more even distribution of structure classes suggesting greater heterogeneity of forest conditions at these larger scales. Trees > 32 m, and especially > 48 m, were almost always associated with high canopy cover in large part because the large canopy area of these trees created high canopy cover. Locations with high canopy cover but without tall trees were not associated with owl nest sites or PACs.

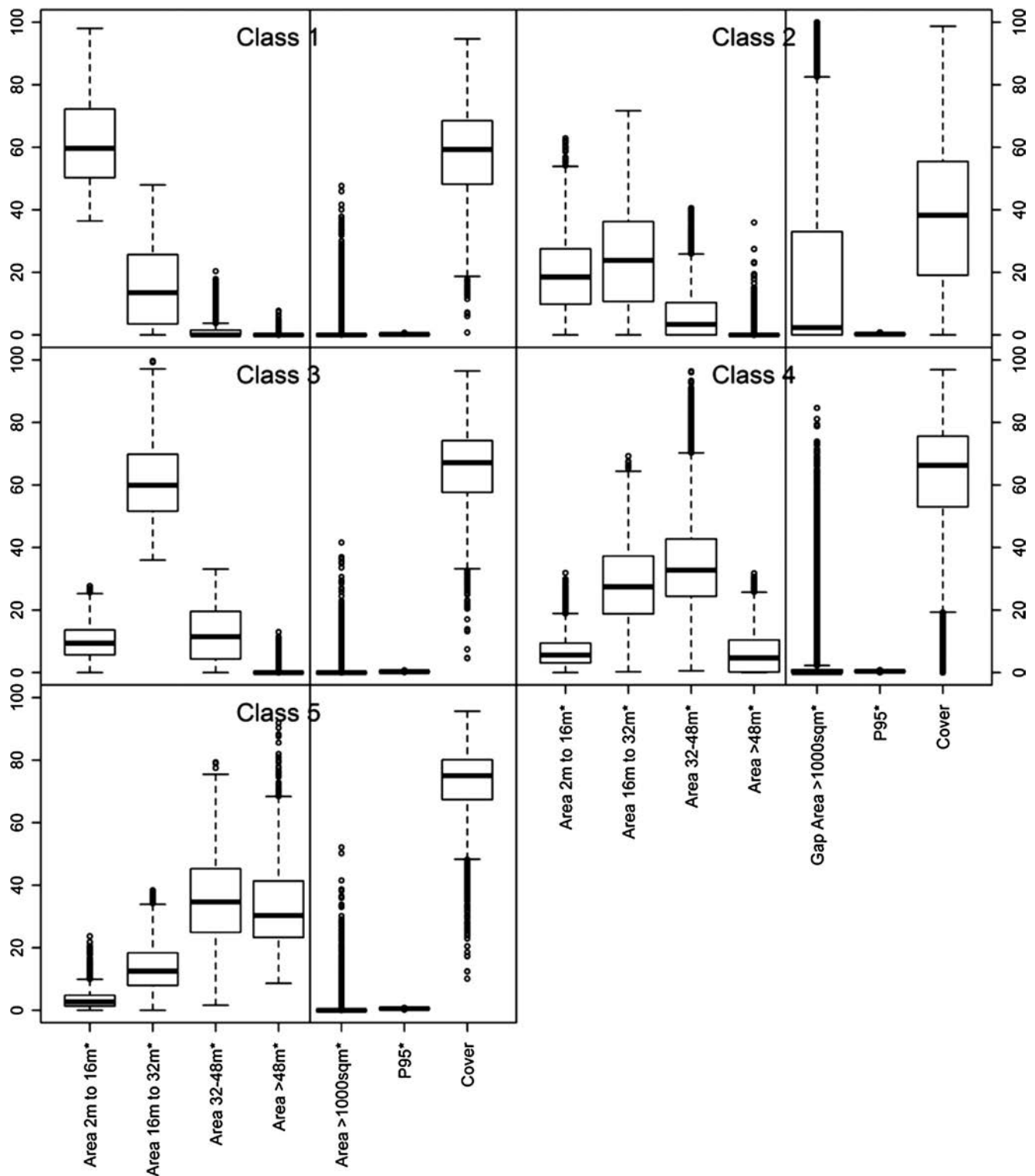


Fig. 5. Boxplots of canopy attribute values for each of the five identified structure classes. The boxplot contains the 25–75% range of values and the interior line is the median value. Whiskers show the range from 10 to 90% and dots are outliers. Gap area > 10,000 m², P95 (maximum height recorded from 95% of returns) and canopy cover are shown for reference but were not used in the cluster analysis to determine the structure classes.

4. Discussion

We found that the height of canopy cover matters, and the retention and promotion of large trees and the cover they provide may more directly benefit owl habitat than high levels of total cover from any canopy strata. Median values of total canopy cover were higher in nest and PAC areas than territories and the surrounding landscape, but the

most distinct niche selection was cover of trees > 48 m. Tall tree cover is rarer on national forest lands (Table 3), and yet what is available is consistently found in nest and PAC areas. Our structure class analysis indicated that > 70% total canopy cover rarely occurred except when cover of Tall Trees and Co-dominants was high (classes 4 and 5 in Fig. 6), suggesting these two variables were often confounded. This covariance may explain why canopy cover, which is easier to measure

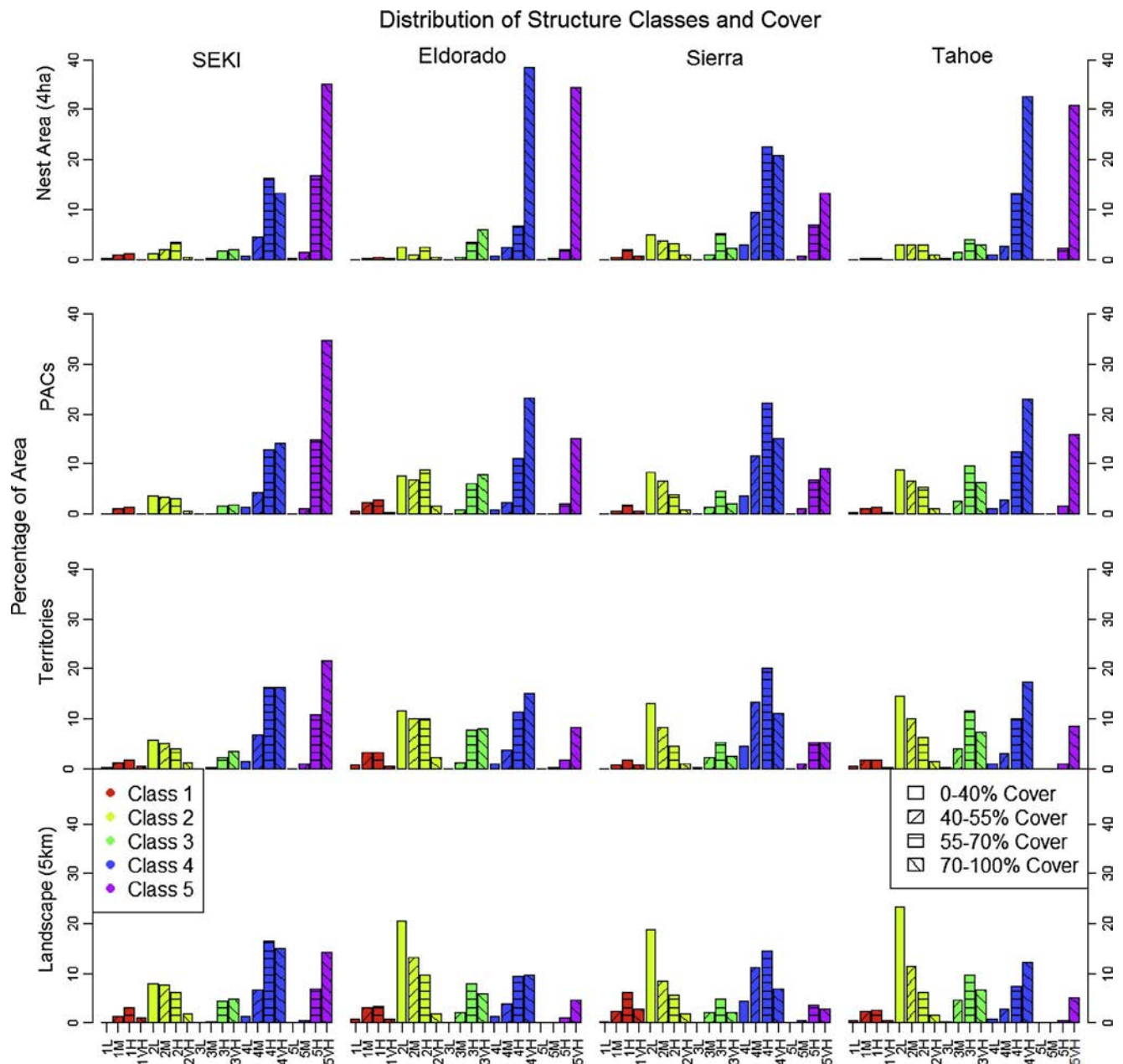


Fig. 6. Frequency distribution (% of total area) for each of the structure classes by nest, PAC, territory and surrounding landscape for each of the study areas.

and often recorded, has been reported as the forest condition associated with spotted owls rather than the cover in tall trees. Furthermore, although cover in the 2–16 strata can contribute to total canopy cover values, our analysis indicates nest sites and PACs actually have less cover in this stratum than is present in territories and the surrounding landscape, suggesting owls avoid this condition.

4.1. Large trees and canopy cover

Spotted owl research has consistently shown that owls are associated with large trees and total canopy cover (Call et al., 1992; Verner et al., 1992; North et al., 2000; Tempel et al., 2014; Tempel et al., 2016), but research has rarely parsed canopy structure into different height strata or assessed gap conditions. Our results confirm some widely reported owl habitat characteristics (Hunsaker et al., 2002; Blakesley et al., 2005; Seamans and Gutierrez, 2007), using larger sample sizes and a more quantitative measure of canopy structure than previous ground-based plot sampling and aerial photograph

interpretation (although see Garcia-Feced et al., (2011)). Owl nest sites are in areas of high canopy cover that are dominated by a high percentage of cover in tall trees and few canopy gaps. Several studies of California spotted owl nest stands have also reported a selection for areas with high levels of canopy cover and groups of large (> 75 cm dbh) trees (LaHaye et al., 1997; Blakesley et al., 2005).

The high canopy cover levels associated with spotted owl use areas has suggested that gaps were generally avoided or might reduce habitat quality. We found that gaps of any size, even as small as those in our 112–1000 m² category were rare in nest sites. Few studies have measured or discussed gap size and their frequency near nests, although one paper reported that owls generally avoided nesting in gap areas in fire-restored forests in Yosemite (Roberts, 2008; Roberts et al., 2011). At larger scales (PACs and territories) gaps were still rare in the SEKI and Eldorado study areas (Table 3), and sparse in the Sierra and Tahoe areas, but we did not find any pattern suggesting their abundance or size class distribution was significantly different from conditions in the surrounding landscape. Owl tolerance of gaps is difficult to infer from

our data because gaps of at least a dominant tree crown area or larger are rare in our study areas. Since spotted owls persisted in historic forests that had much lower canopy cover and more gaps than modern forests, a better understanding of owl response to gaps may require telemetry location data.

We found the cover in tall trees was the most important canopy feature in PACs from the surrounding landscape (Table 2). In contrast, several studies have found the percentage of moderately high (> 50%) and high (> 70%) levels of canopy cover were most associated with owl occupancy and reproduction (Berigan et al., 2012; Tempel and Gutierrez, 2013; Tempel et al., 2014; Tempel et al., 2015; Tempel et al., 2016). Across our four study areas, PAC canopy cover averaged 67.6% (Table 2), and on the three national forest study areas PAC canopy cover ranged from 3.9% (Sierra) to 21% (Tahoe) higher than the surrounding landscape (Table 3). However, our niche overlap analysis showed that the canopy structure that was most distinct (i.e., lowest niche overlap scores of 0.49–0.68) was the cover in tall trees (Table 2). Canopy cover had much higher niche overlap values (0.75–0.88) than other attributes. The confounding of high-levels of canopy cover with the cover of tall trees may explain why other studies that did not account for tree height have generally reported total canopy cover as the most significant feature of PAC habitat.

4.2. Variation in canopy conditions from nest site to landscape

While we found that total canopy cover was generally higher within about 500 m of nests (Fig. 4b) compared to the surrounding landscape, the area in tall trees continued to be the most distinct canopy structure (lowest niche overlap) as distance from the nest sites increased over the 1000 m from nests we assessed. This suggests that the cover in tall trees could also be beneficial to owls when foraging because they often travel away from the nest to forage (Irwin et al., 2007; Williams et al., 2011). However, without telemetry we were unable to assess how owls used different forest conditions for foraging. Several studies have suggested heterogeneous forest conditions, particularly edges between cover types, may influence foraging behavior or reproductive success (Franklin et al., 2000; Eyes et al., 2017). Some degree of vertical structure seems to be important for owl foraging (Call et al., 1992) but it's unclear whether owls respond to canopy layering produced by adjacent forest patches of contrasting height or multi-layer foliage within the same stand. New technologies such as lightweight GPS tracking devices could be used to pinpoint foraging locations and improve our analysis of vertical layering.

4.3. Study area differences in large tree abundance

We found that > 70% canopy cover was usually only achieved when there were tall trees present. Canopy cover in modern Sierra Nevada forests typically averages between 40 and 60% depending on several factors including forest type, site productivity and disturbance history (Lydersen and North, 2012; Miller and Safford, 2017). Forests with canopy cover > 70% are not rare, but they usually occur in mixed-conifer forest types and require a combination of high site productivity and/or a long period of fire suppression (Collins et al., 2011). The owl's documented association with high canopy cover conditions has raised one hypothesis that owls have benefited from fire suppression and may presently have more high-quality habitat than would have been present under active-fire forest conditions (North et al., 2017; Peery et al., 2017). However, if the preferred canopy characteristic of nest and PAC conditions is an abundance of tall trees, then large tree harvest, such as National Forests have experienced, may have reduced the quality and/or extent of favorable habitat on Forest Service lands.

We did not find significantly higher canopy cover levels in SEKI, the only owl study population that is not declining, but we did find significantly higher cover of tall trees. The covariance of many structural attributes in forests (i.e., old forests often have large trees, big snags and

logs, etc.) makes it difficult to partition individual attributes as the most significant habitat variable. Cover of tall trees may directly benefit owls by providing overhead predator protection or microclimate modification or indirectly by being associated with other age, size, and dead wood structural attributes that often occur when tall trees are present (Gutiérrez et al., 1995). Our research shows that tall tree cover is correlated with owl habitat, but identifying the particular benefits will require further study.

4.4. Implications for future research

We acknowledge several limitations of our research that constrain our understanding of California spotted owl habitat but that might be addressed with future research. While our LiDAR analysis provides a large sample size and precise quantification of the forest canopy, it cannot provide information on snags and logs, either of which may influence habitat selection (Call et al., 1992; Verner et al., 1992; LaHaye et al., 1997). Methods are being developed to accurately assess snags using LiDAR, and understory conditions, including coarse woody debris, can be measured with ground-based LiDAR (Hopkinson et al., 2004). Ground-based methods will have smaller sample sizes than aerial LiDAR, however, stratified sampling of different structure classes may overcome these limitations.

We focused on partitioning elements of canopy conditions that usually co-vary. This required a large dataset of owl locations and their delineated PACs. A next step building upon our analysis would be to weight these locations either by their frequency of use (accounting for years of observation) or reproductive output. We also did not have spatially-explicit data of owl habitat use such as that derived from radio telemetry and therefore, beyond the nest site, we used general scales of PAC and territory. However, as a central place forager and as several telemetry studies have shown, owl use decreases with distance from nests or roost (Call et al., 1992; Carey and Peeler, 1995; Rosenberg and McKelvey, 1999; Blakesley et al., 2005; Irwin et al., 2007; Williams et al., 2011; Williams et al., 2014). We hypothesize that telemetry would likely show that owls typically have many areas within their territories that are lightly used or completely avoided (Carey et al., 1992). This would greatly refine an analysis of forest structural conditions associated with owl territories, which are predominantly used for foraging. The structural heterogeneity of forests that some studies have suggested may benefit owl foraging (Eyes et al., 2017) could be examined with a much better understanding of which parts of the territory areas are most heavily used. Better insight into owl territory use would also greatly benefit from a spatially-explicit sampling of small mammal abundance, particularly common prey species such as the dusky-footed woodrat (*Neotoma fuscipes*) and northern flying squirrel (*Glaucomys sabrinus*) (Ward et al., 1998; Smith et al., 1999; Meyer et al., 2005a; Innes et al., 2007; Meyer et al., 2007a) and how these prey species are affected by common forest treatments (Meyer et al., 2005b).

Finally, we do not infer what may constitute 'optimal' owl habitat. In three of our four study areas, forests have been extensively altered by past timber management and fire suppression. We have attempted to identify favorable habitat using areas in SEKI without timber harvest and having recently (i.e., since the 1970s) restored fire regimes. However, even these forests have higher density and canopy cover from pre-1970 tree ingrowth that is now large enough to survive re-introduced surface fire (Lydersen and North, 2012; Collins et al., in press). Our analyses may help identify favorable habitat under current conditions but this may be different from historical forests.

4.5. Management implications

Research on characterizing the structure of owl habitat has been constrained by both technological (aerial photography and landsat imagery) and logistical (ground-based vegetation measurement) issues. Early remote sensing efforts in owl studies has been limited to

estimation of area, spatial configuration, and canopy cover whereas ground-based sampling provided limited estimates of density and sizes of habitat attributes at small spatial scales. All this previous research has linked spotted owls to a combination of high canopy cover and large trees at both nest and roost sites (Verner et al., 1992; Gutiérrez et al., 1995; Tempel et al., 2014, 2016). One consequence of these studies has been that managers have tended to focus on canopy cover as the metric of interest for conserving spotted owl habitat.

Two lines of evidence, one historical and one derived from our findings in this study, suggest that a focus on preserving patches of large trees rather than canopy cover per se may be more effective. Historical data sets and forest reconstruction studies from the Sierra Nevada consistently suggest active-fire forests on average were dominated by large trees and stands generally had low canopy cover (17–41%) and tree densities (60–328 trees/ha or 24–133 tree/ac) (Lydersen et al., 2013; Collins et al., 2015; Stephens et al., 2015). The range in these values suggests forest conditions likely varied with topography and disturbance history (North et al., 2009; Lydersen and North, 2012; Kane et al., 2014; Kane et al., 2015). More mesic sites likely burned less frequently and intensely, and higher productivity resulted in bigger trees in larger patches than more xeric sites. Fuels were able to accumulate more rapidly on more productive sites, especially when fires “skipped an area”, making them more prone to patchy crown fire (Innes et al., 2006). Variability in topography and soils combined with the inherent variability of fire created and maintained high levels of heterogeneity at small to large spatial scales in historical frequent fire landscapes (Meyer et al., 2007b; Kane et al., 2015).

Management based on canopy cover targets creates significant challenges in restoring this multi-scale heterogeneity. Canopy cover is generally used as a stand average measurement of forest conditions and as such does not account for the group/gap horizontal distribution of trees that is a defining characteristic of frequent-fire forests (Larson and Churchill, 2012). Furthermore, because high canopy cover can occur under a wide variety of stand ages, levels of productivity, and disturbance histories, it does not incorporate important habitat components such as vertical structure, snags, downed logs, and large trees. Forests with high canopy cover, particularly those with continuous cover over large areas, are at greater risk from high-severity wildfire and drought-induced mortality. An additional challenge is that while canopy cover estimates of forest conditions are widely available, their calculation from ground-based measurements, aerial photo interpretation or model estimates such as FVS, based on tree diameters and density, can be widely variable and inaccurate (Fiala et al., 2006; Korhonen et al., 2006; Christopher and Goodburn, 2008; Paletto and Tosi, 2009).

In contrast, the association of owl nests and PACs with the cover in tall trees has more tractable forest management implications. Managing for the protection and production of large trees can be accomplished while still reducing potential fire intensity (through surface and ladder fuel reduction) and drought stress (lowering overall leaf area by removing small trees). Furthermore, PACs in our study had low canopy cover in the 2–16 m strata suggesting treatment of these potential ladder fuels may not adversely affect owl habitat. Reduction of sub-canopy and intermediate-size trees may reduce water competition increasing large tree resilience to beetle attack while opening up more growing space to accelerate tree growth (Fettig et al., 2010a; Fettig et al., 2010b). Managing for landscapes that contain tall trees, which are more fire resilient, may reduce the loss of owl habitat that is increasingly occurring in an era of rising wildfire severity. In landscapes where patches of tall trees are rare, managers might identify the tallest tree areas and seek to reduce their vulnerability to drought and wildfire mortality through density reduction so the trees can grow to become anchors of more suitable habitat.

As a sensitive species with declining populations, forest managers should consider approaches to retain and improve California spotted owl habitat. Retaining current use areas is important to guard against

further population declines. In the long-term an effective strategy may be to focus management on cultivating tall trees in more productive areas (i.e., wetter areas, drainage bottoms, lower slopes) of the landscape (Underwood et al., 2010) that can better support large tree biomass and that may be more resistant to fire and drought stress. This may take several decades and will require strategies that maintain current owl areas until new, more resilient forest locations develop large tree cover through growth and succession. To maintain selected habitat in the near-term, management may need to take a more active role reducing stem density in the 2–16 m class and surface fuels in tall tree areas to make these stands more resistant and resilient to drought and high-severity wildfire that can significantly reduce local owl populations (Jones et al., 2016). With climate conditions changing, managing for the retention and creation of large trees may benefit both owls and forest resilience to increasingly common wildfire and drought events.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.09.019>.

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Effects of fire on spotted owl site occupancy in a late-successional forest

Susan L. Roberts^{a,*}, Jan W. van Wagtenonk^a, A. Keith Miles^b, Douglas A. Kelt^c

^a US Geological Survey, Western Ecological Research Center, Yosemite Field Station, El Portal, CA 95318, USA

^b US Geological Survey, Western Ecological Research Center, Davis Field Station, University of California, One Shields Avenue, Davis, CA 95616, USA

^c Wildlife, Fish, and Conservation Biology, University of California, One Shields Avenue, Davis, CA 95616, USA

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ABSTRACT

The spotted owl (*Strix occidentalis*) is a late-successional forest dependent species that is sensitive to forest management practices throughout its range. An increase in the frequency and spatial extent of stand-replacing fires in western North America has prompted concern for the persistence of spotted owls and other sensitive late-successional forest associated species. However, there is sparse information on the effects of fire on spotted owls to guide conservation policies. In 2004–2005, we surveyed for California spotted owls during the breeding season at 32 random sites (16 burned, 16 unburned) throughout late-successional montane forest in Yosemite National Park, California. Our burned areas burned at all severities, but predominately involved low to moderate fire severity. Based on an information theoretic approach, spotted owl detection and occupancy rates were similar between burned and unburned sites. Nest and roost site occupancy was best explained by a model that combined total tree basal area (positive effect) with cover by coarse woody debris (negative effect). The density estimates of California spotted owl pairs were similar in burned and unburned forests, and the overall mean density estimate for Yosemite was higher than previously reported for montane forests. Our results indicate that low to moderate severity fires, historically common within montane forests of the Sierra Nevada, California, maintain habitat characteristics essential for spotted owl site occupancy. These results suggest that managed fires that emulate the historic fire regime of these forests may maintain spotted owl habitat and protect this species from the effects of future catastrophic fires.

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1. Introduction

Fire is an essential and dynamic process in many terrestrial systems throughout the world (Dickman and Rollinger, 1998). Whether on a 5-year or 200-year return interval, fire structures and maintains ecosystems (Wright and Bailey, 1982; Minnich et al., 2000). In western North America, fire regimes are so strongly correlated with the habitats they shape that it is difficult to ascertain whether fire regimes drive patterns in vegetation or vice versa (Agee, 1993; van Wagtenonk and Fites-Kaufman, 2006). The severity of fire can be quantified as a function of changes in vegetation after an area burned (van Wagtenonk, 2006). Attempts to exclude fire from these systems through a century of suppression have not been completely successful because continuing fuel accumulation (Kilgore, 1973; Vankat and Major, 1978; Agee et al., 2000) has led to more extensive high-severity fires (Skinner and Chang, 1996). While it is clear that unchecked wildfires in these forests are not an acceptable management option (Weatherspoon

et al., 1992), van Wagtenonk (1996) suggested the best tool for restoring and protecting these forests is carefully planned prescribed fire.

One species that is dependent on old-growth and late-successional forests is the spotted owl (*Strix occidentalis*) (Forsman et al., 1984; Gutiérrez and Carey, 1985; Gutiérrez et al., 1992; Verner et al., 1992a). Spotted owls are strongly associated with old forests, but are threatened by habitat loss and fragmentation (Bart and Forsman, 1992; Noon and Blakesley, 2006), the recent expansion of barred owls (*Strix varia*) into the range of spotted owls (Olson et al., 2005), and climate change (Glenn et al., 2010; Carroll, 2010). The old, and often dense, forests favored by spotted owls are economically desirable (Thomas et al., 1990; Verner et al., 1992a), but are at risk to stand-replacing fires due to heavy fuel loading (Agee et al., 2000). A century of fire exclusion and various management activities has transformed much of this forest into even-aged, early-successional forests that often contain large amounts of understory fuels (Husari et al., 2006; Stevens and Sugihara, 2006). This accumulated dead and down woody debris acts not only as fuel to carry the fire horizontally through the forest, but also vertically into the upper canopy (Weatherspoon and Skinner, 1995; Tappeiner and McDonald, 1996). Such high fuel loading and spatially continuous ladder fuels place adjacent

* Corresponding author. Tel.: +1 209 375 9557.

E-mail addresses: susan_roberts@usgs.gov (S.L. Roberts), jan_van_wagtenonk@usgs.gov (J.W. van Wagtenonk), keith_miles@usgs.gov (A.K. Miles), dakelt@ucdavis.edu (D.A. Kelt).

old-growth forests at greater risk of catastrophic fire (Weatherspoon et al., 1992; Agee, 1993; Wright and Agee, 2004). The combination of logging and large-scale conversion of forests to human communities has resulted in dramatic declines in the extent and continuity of old-growth forests throughout western North America, causing concern for the persistence of spotted owls (Thomas et al., 1990; McKelvey and Weatherspoon, 1992). In the fire-adapted forests of the Sierra Nevada where California spotted owls (*S. o. occidentalis*) live and reproduce, habitat loss from wildfire also is a concern as the risk of catastrophic fire steadily increases in the absence of periodic low to moderate severity fire (Miller et al., 2009). Skinner and Chang (1996) estimated that prior to Euro-American settlement, montane forests in the Sierra Nevada experienced low to moderate severity fires every 2–20 years.

In montane forests of the Sierra Nevada, California spotted owls typically nest and roost in stands with high canopy cover ($\geq 75\%$) and forage in stands with moderate ($\geq 40\%$) to high canopy cover (Call et al., 1992; Zabel et al., 1992). These owls use stands for nesting and roosting that have multilayered canopies and an abundance of large trees (>60 cm diameter at breast height [dbh]) (Bias and Gutiérrez, 1992; Gutiérrez et al., 1992; Verner et al., 1992b; LaHaye et al., 1997; Moen and Gutiérrez, 1997). We wanted to determine if the low to moderate severity fires that reduce fuels would sustain functional spotted owl habitat by maintaining specific forest characteristics necessary for nesting and roosting. To do this, we investigated site occupancy patterns by California spotted owls within burned and unburned montane forests in Yosemite National Park. We had three primary objectives. First, we wanted to determine whether burned and unburned forests contained sufficient nesting and roosting habitat elements (e.g., canopy closure, basal tree area) for spotted owl site occupancy. We predicted that spotted owl occupancy would be positively influenced by canopy closure and tree basal area, and that these characteristics would be maintained in forests burned at low to moderate severity. Yosemite has a large area of relatively contiguous, mixed-conifer forest, leading us to predict that the density of spotted owl pairs would be higher in the park than in other mixed-conifer forest in the Sierra Nevada. Our second objective was to develop a model that land managers could use to accurately predict spotted owl site occupancy in a particular forest stand based on fire history and vegetation characteristics. Our final objective was to estimate spotted owl density within Yosemite. This was to provide baseline information in late-successional forests experiencing a frequent fire regime and not confounded by the effects of past forest management practices. To date, population estimation for this subspecies has been almost exclusively limited to National Forests in California that have experienced decades of fire exclusion and intensive timber harvest.

2. Methods

2.1. Study area

Located in the central Sierra Nevada, Yosemite National Park encompasses 3027 km², of which approximately 1580 km² was relatively contiguous montane forest (van Wagtendonk and Lutz, 2007) and potential habitat for spotted owls. This habitat occurred between 1000 m and 2500 m elevation on the western slope of the range and supports a diverse fauna (Graber, 1996). White fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), California black oak (*Quercus kelloggii*), incense-cedar (*Calocedrus decurrens*), and sugar pine (*P. lambertiana*) dominated the lower montane forests. Red fir (*Abies magnifica*), white fir, sugar pine, and Jeffrey pine (*Pinus jeffreyi*) dominated the upper montane forests. The most prevalent forest type in our study area consisted of white fir with a mix of

Jeffrey pine (at higher sites) or ponderosa pine (at lower sites). More than half of the precipitation occurred from January through March, primarily as snow (van Wagtendonk and Fites-Kaufman, 2006). Between 1989 and 2004, 466 km² of the 1580 km² montane forest burned at least once.

At the time of this research, managers recognized three types of wildland fires, prescribed, wilderness, and wildfire. Managers purposefully set prescribed fires in order to meet defined objectives. In 1970, Yosemite National Park developed a prescribed burning program to reduce fuels and lower the risk of stand-replacing fires while conserving the selection pressures that fire historically imposed on these ecosystems (van Wagtendonk et al., 2002). Wilderness fires were naturally occurring lightning fires and since 1972, the park's wildland fire use program managed them under prescribed conditions. Since 1972, as long as these conditions were met, wilderness fires were typically not suppressed in Yosemite. Yosemite's Fire Management Program suppressed all wildfires, including human caused fires and wildland fires that did not meet management objectives. Researchers dated, mapped, and digitized for use with geographic information system (GIS) software all fires that occurred within Yosemite since 1930 (van Wagtendonk et al., 2002). Yosemite Park personnel also developed a digital vegetation map consisting of polygons of dominant overstory and understory vegetation types with cover classes assigned to each vegetation type polygon (National Park Service, 1997). Although our study area experienced all three types of fire, we did not have a large enough sample size to perform separate analyses on each type. Therefore, a "burned" forest in our study could have experienced any of the three fire types.

2.2. Data collection

2.2.1. Plot selection

Spotted owls in the Sierra Nevada rarely use forests with $<40\%$ canopy cover (Call et al., 1992; Gutiérrez et al., 1992; Zabel et al., 1992); therefore, we used 40% canopy cover as our cutoff criterion for mapping potential owl habitat. We used ArcMap 9.1 (ESRI, Redlands, California) and the digital vegetation map to delineate montane forest stands with $>40\%$ canopy cover within the park. We overlaid the digital fire history map onto the vegetation map to delineate all fires in the montane forest zone that burned since 1989, and had post-fire canopy cover $>40\%$. By this method, we delineated 466 km² of burned forest and 1113 km² of unburned forest, and we focused our surveys within these forests. We restricted our efforts to areas burned between 1989 and 2004 because this 15-year interval falls within the range of historic fire return interval (2–20 years) for these forest types (Skinner and Chang, 1996). We then generated 200 random points across that defined landscape (100 in burned, 100 in unburned areas) and selected the first 16 points in each stratum (total of 32 survey areas) that met logistical constraints of accessibility (≤ 2 days travel, including driving and hiking) and crew safety (Fig. 1).

2.2.2. Owl surveys

We used acoustic-lure and live-lure surveys (Reid et al., 1999) and mark-recapture methods (Franklin et al., 1996) to survey owls during the breeding season (April–July) in 2004 and 2005. We sampled each survey area at night three times during the breeding season and separated surveys by at least two weeks. We surveyed each site for only 1 year; 16 survey areas in 2004 and 16 different survey areas in 2005. Because these owls exhibit extreme site fidelity, we assumed if owls were present at a site in 1 year, they would continue to occupy that site until their death. To support this assumption, we conducted follow up diurnal visits (to observe annual reproduction) at each occupied site we located in the previous year and found all sites occupied by both or one of the same owls in

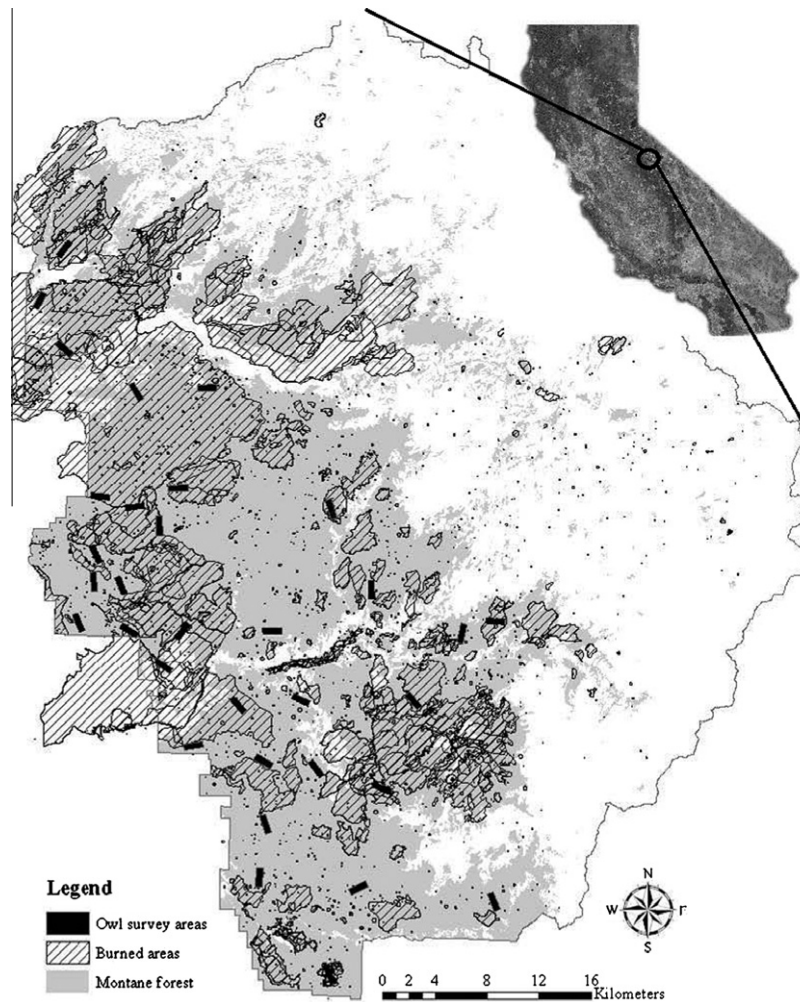


Fig. 1. Locations of 16 burned and 16 unburned California spotted owl survey areas (2004–2005) in Yosemite National Park, California. Burned areas experienced wildfires, managed wildland fires, or managed prescribed fires between 1989 and 2004.

repeated years (i.e., all sites occupied in 2004 were occupied in 2005). Therefore, we based our occupancy analyses on only the initial survey year and our results are not confounded by annual effects. Each survey area consisted of a rectangular grid with eight (four on each side) calling stations 500 m apart. We centered the grids on the 32 random points and thoroughly examined the entire survey area during grid establishment to ensure each survey area contained only one type of sampling strata (burned or unburned). We assumed that the effective sampling area was a 500 m wide buffer around each grid (Forsman, 1983) which converted to a sampling area of 3.75 km². In the rugged and remote terrain within the park, this was the largest area we could reasonably expect a field crew to survey in a single night. The combined area of the 32 transects we surveyed during the 2-year period was 120 km². We conducted systematic nocturnal surveys by vocally imitating spotted owl calls and listening for responses for 10 min at each station (Forsman, 1983; Franklin et al., 1996). Because spotted owls defend their territories by responding to “intruders” with hooting, we assumed owls responding to our vocally imitated calls were territorial (Forsman, 1983). We recorded the time, location (elevation and UTM [NAD27, Zone11 N]), sex, and species of all owl responses.

We identified, located, and captured spotted owls using the methods and protocols that were originally developed and published by Forsman (1983) and Franklin et al. (1996). When we detected spotted owls at night, we returned to the same locations the

next morning to try to determine the nest or roost location of each owl. We marked non-juvenile owls with a plastic colored leg band on one leg, and a numbered aluminum US Geological Survey Bird Banding Laboratory band on the other leg. To locate nests, we offered up to six live house mice (*Mus musculus*) to each pair and then observed what the owls did with each mouse. Reproductively active owls usually took mice to the nest or juvenile(s), allowing us to identify individual owls (band re-sighting), and locate nests or roosts (Reid et al., 1999). Through our diurnal band re-sighting, we were able to determine whether a particular owl pair’s territory overlapped >1 survey area. To avoid pseudoreplication, we only included one (chosen at random) of these overlapping survey areas. This situation occurred only once across the entire study area.

2.2.3. Habitat sampling

Following owl surveys each year, we measured spotted owl nesting and roosting habitat characteristics at all sites. We categorized owl activity sites as nests, roosts, or night survey observations (“night response”), and defined the geographic center for each site as the nest or roost tree used by the owls. Survey areas that did not yield spotted owl responses during nocturnal surveys we termed “no-response sites.” For no-response sites, we defined the geographic site center of the vegetation plot as the random point we used to locate the owl survey area during plot selection. At each site center, we recorded elevation (using Suunto wrist

altimeters) and location (UTM coordinates in NAD27 Zone 11 N). To characterize locations where we found owls, we compared the vegetation at those locations to vegetation at a random point at the no-response sites. We sampled vegetation at owl activity and no-response sites using nested circular plots oriented around the owl nest or roost tree (activity sites) or the largest tree closest to the random point (no-response sites). To measure the characteristics at the local stand level, we recorded tree species, diameter at breast height (dbh), and status (live tree or snag) in three concentric, nested, circular plots (0.05 ha, 0.1 ha, 0.2 ha) with the plot size expanding to quantify larger aspects of the habitat (i.e., larger trees) (Spies and Franklin, 1991; North et al., 1999, 2000). Within the plots, we measured all trees and snags in three size classes: 10–49 cm, 50–79 cm, and ≥ 80 cm dbh, respectively. We estimated the cover of downed coarse woody debris (CWD; logs ≥ 20 cm in diameter and ≥ 2 m long) using a 35.6 m line transect through the middle of the 0.1-ha plot. We measured shrub (>0.5 m tall) and sapling (<10 cm dbh and >0.5 m tall) ground cover using 8 m line transects at three locations: 2 m east, 8.6 m north, and 8.6 m south of the center tree. We estimated tree canopy closure using digital hemispherical photos taken 1 m above the ground surface at points 2 m north and south of the base of the center tree (Jennings et al., 1999). We used Gap Light Analyzer v 2.0 (Frazer et al., 1999) to estimate canopy closure from the photos.

Canopy closure is the proportion of the sky hemisphere obscured by vegetation when viewed from a single point, usually on the ground (Jennings et al., 1999). Closure is affected by tree heights and canopy widths and takes into account light interception and other factors that influence microhabitat. Canopy cover is a measure of the percent of ground covered by a vertical projection of the tree canopy (Jennings et al., 1999). Cover can be measured from multiple points on the ground or estimated from aerial photographs. We used remotely sensed canopy cover estimates to focus our survey efforts and used canopy closure estimates in the model estimations. We felt canopy closure was the best metric to use to measure the canopy for a particular nest or roost site in recent or current use by an owl.

2.3. Data analysis

We quantified fire severity for each of the 16 burned owl survey areas using the Relative differenced Normalized Burn Ratio (RdNBR) developed by Miller and Thode (2006). They used differential remote sensing imagery from before and after fire to create a map of polygons representing four levels of fire severity for all of the fires in Yosemite since 1973. Miller and Thode (2006) classified areas as unchanged if the severity was so low that a change could not be detected in the images one year post-fire. Low severity stands were generally lightly burned with only the fine fuels removed and some scorching of the understory trees. Moderate severity stands retained some fuels on the forest floor, but created some small tree mortality and scorching of the crowns of medium and large sized trees. High severity areas had near complete combustion of all of the litter, duff, and small logs, higher mortality of small to medium sized trees, and consumption of the crowns of large trees. Fire severity levels ranged from “1” (an unchanged area within the fire perimeter) to “4” (burned completely at high severity). We used ArcMap 9.1 (ESRI, Redlands, CA) to calculate the proportional area of each fire severity class within each of the 3.75 km² polygons that we surveyed for owls. If a survey area contained multiple fires with spatial overlap, we used the most recent fire for the overlapping areas. We then calculated the fire severity index for each survey polygon as the sum of the proportional area of each fire severity level within that survey polygon multiplied by the fire severity level (1–4) for that proportional area.

We calculated the total basal area (m² ha⁻¹) of live trees ≥ 10 cm dbh (BA_t), live trees ≥ 50 cm dbh (BA₅₀ cm), and dead trees (snags) ≥ 80 cm dbh (BA_s). We estimated CWD cover (%) based on the percent of the 35.6 m line transect that was covered by CWD. We estimated shrub cover (%) in each plot as the mean across the three 8 m line transects.

In our analyses of owl pair site occupancy, we used nest sites when possible ($n = 15$), roost sites ($n = 3$) when we did not observe nesting at a particular owl site, and night response sites ($n = 1$) when we were unable to locate nests or roosts. We calculated the mean of each habitat variable (canopy closure, BA_t, BA₅₀ cm, BA_s, shrub cover, CWD cover, and site elevation) within each owl activity type for sites where there was more than one nest ($n = 2$) or roost ($n = 2$) location for a territorial owl pair. In all analyses, we used only one site per owl pair to ensure independence among sites and followed established protocols when determining owl social status (G. Miller, Forest Service, unpublished paper).

We examined the correlation matrix for all of the habitat data to determine if any habitat variables were highly intercorrelated. To avoid collinearity in our models, we did not develop models that included highly correlated variables (e.g., correlation coefficient ≥ 0.70 ; Burnham and Anderson, 2002). Canopy closure and basal tree area tend to be highly correlated. To avoid including these two intercorrelated variables as separate variables in the same model (Burnham and Anderson, 2002), we standardized them using z-scores and summed them into a single derived variable (BA_tCan), which we believe provided an ecologically based (e.g., “owl-centric”) perception of forest density.

We defined spotted owl pair occupancy as the probability that a pair of territorial spotted owls will occupy a particular patch of habitat. Before conducting owl surveys, we developed a list of candidate models for predicting pair occupancy as a function of site burn history, all seven habitat variables, and survey year. We standardized habitat variables using z-scores because they were measured at different scales. We determined the model that best predicted spotted owl occupancy with program PRESENCE v 2.1 (Hines, 2006), which estimates site occupancy (Ψ) as a function of the probability of detection (ρ); therefore, ρ was included in each candidate model. By including habitat characteristics in the candidate models, we tested if Ψ varied as a function of habitat while also investigating if ρ varied as a function of survey time or fire history (burned vs. unburned). To include survey-specific detection rates, we employed the full identity function in PRESENCE and followed the procedures for single species, single season surveys detailed by MacKenzie et al. (2002). We considered only models with two to five parameters (including the intercept and probability of detection) to avoid the occurrence of spurious results by maintaining an approximate ratio of data to parameters >10 ($n = 32$ sites; maximum # parameters = $n/10$; Burnham and Anderson, 2002). We used Akaike's Information Criteria (AIC) corrected for low sample size (AIC_c; Akaike, 1973; Hurvich and Tsai, 1989) to quantifiably and simultaneously compare candidate models (Burnham and Anderson, 2002).

We selected the “best” model on the basis of AIC_c values, Akaike weights (w_i), and evidence ratios as defined by Burnham and Anderson (2002). The Akaike weight (w_i) represents the probability that a particular model provides the best explanation of the data given the tested set of models. The difference in AIC_c values of alternative models relative to the model with the lowest AIC_c (ΔAIC_c) reflects the level of support for the alternative models. Models with $\Delta\text{AIC}_c \leq 2$ have “substantial” support, whereas models with ΔAIC_c of 4–7 have “considerably less” support, and models with $\Delta\text{AIC}_c > 10$ have essentially no support. To compare an alternative model to the best model, we calculated evidence ratios as w_1/w_2 , where w_1 and w_2 refer to Akaike weights for the two models being compared, with our best model always being the numerator.

Evidence ratios ≤ 2.7 are equivalent to a $\Delta AIC_c \leq 2$ and indicate substantial support for the model being compared to the best model, whereas evidence ratios ≥ 3 provide “little evidence” in favor of the alternative model (Burnham and Anderson, p. 79).

We applied the logistic model in program PRESENCE to incorporate habitat variables in our candidate models and to calculate the maximum likelihood estimates required for AIC calculations (Donovan and Hines, 2007). The logistic model employed by PRESENCE is

$$\log e[\Psi/(1 - \Psi)] = X\beta, \quad (1)$$

where Ψ refers to the probability of owl pair occupancy, X is the row vector of the habitat variables, and β is the column vector of model coefficients.

We applied a closed population model because of the short survey period (2 years) relative to the life span of adult California spotted owls (14 years; Steger et al., 2002) and their high adult annual survival rates (83%; Blakesley et al., 2001). We estimated the total population size (N) of California spotted owls in Yosemite, as well as the population size within areas characterized by different burn histories (burned and unburned) following Lancia et al. (1996):

$$\hat{N} = O_{\text{park}}/(a\hat{\rho}) \text{ with } \text{var}(\hat{N}) = \hat{N}^2 \times [(\text{var}O_{\text{park}}/O_{\text{park}}^2) \times (1 - a) + (\text{var}\rho/\rho^2)] \quad (2)$$

where O_{park} is the total number of owl pairs observed in the field from the surveys from both years, a is the proportion of the total area surveyed, and ρ is the probability of detecting a spotted owl pair from the surveys. We calculated the density of owl pairs at each survey area as

$$\hat{D}_{\text{site}} = O_{\text{site}}/A \quad (3)$$

where O_{site} is the number of owl pairs observed from the surveys for that survey site, and A is the area of the survey site (3.75 km²). To estimate owl density for the entire park ($\hat{D}_{\text{park}}$), we determined the grand mean and variance across all survey sites ($n = 32$)

$$\hat{D}_{\text{park}} = (\sum \hat{D}_{\text{site}})/n \text{ with } \text{var}\hat{D}_{\text{park}} = (\text{SD}_{\text{site}})^2 \quad (4)$$

where SD is the standard deviation of owl pair density across all survey sites. For our population estimation, we only included individuals that we detected during the nocturnal surveys and if their nest or roost was inside the 3.75-km² survey area. We doubled our spotted owl density estimate to represent individual owls and compare it to other estimates in the Sierra Nevada, although owl pairs represent a more informative measure of owl density because pairs are the reproductive unit (Olson et al., 2005).

3. Results

3.1. Fire severity and habitat variability

The fire severity index of burned survey areas ranged from 0.4 to 3.1, with an overall mean (SE) of 2.0 (0.2). Across all burned survey areas, the mean (SE) proportion of area burned at unchanged, low, moderate, and high fire severity was 8% (2), 25% (4), 29% (4), and 14% (4), respectively. The maximum proportion of any given survey area that burned at high fire severity was 46%. Generally, survey areas burned at a low to moderate fire severity.

Canopy closure ranged from 28% to 94% ($\bar{x} = 77\%$) for burned sites and 63% to 96% ($\bar{x} = 87\%$) for unburned sites. The mean (SE) basal area of all trees (≥ 10 cm; BAT) was 42.8 (6.5) m² ha⁻¹ at burned sites and 56.3 (5.6) m² ha⁻¹ at unburned sites. In burned and unburned sites, the mean basal area for large snags (≥ 80 cm dbh) was 10.3 (2.0) m² ha⁻¹ and 9.0 (2.0) m² ha⁻¹, mean

coarse woody debris cover was 4.3% (1.2) and 6.6% (1.3), and mean shrub cover was 7.6% (2.2) and 12.9% (3.8), respectively.

The correlation matrix showed that BAT was highly correlated with BAT50 cm ($r = 0.89$) and canopy closure ($r = 0.70$). Consequently, neither of these appears as a separate variable together with BAT in the same model. The high correlation between BAT and BAT50 cm shows the BAT at our sites was driven by large trees and, on average, 74% of the BAT for any particular site comprised trees >50 cm dbh.

3.2. Spotted owl site occupancy

We detected 19 owl pairs and 2 single males (we did not include single owls in any analyses) after 116 h of nocturnal surveys confirmed by diurnal observations. Through the diurnal observations, we located 19 nests (9 in burned survey areas, 10 in unburned). We fitted 30 adults and 5 subadults with unique number and color leg bands. The unmodeled (naïve) site occupancy (Ψ) for owl pairs was 0.59 (SE = 0.09) across all site types and 0.50 (SE = 0.13) and 0.69 (SE = 0.12) for burned and unburned sites, respectively (Table 1). Detection rates at survey sites did not vary based on fire history.

The mean annual detection rates for spotted owl pairs (ρ) were consistently high, with $\rho = 0.47$ for 2004 and $\rho = 0.59$ for 2005 with the particular year in which we surveyed an area bearing no influence on site occupancy (Table 2). Within a year, owl pair detection rates (ρ) were similar across all sites within survey periods, but varied temporally, with $\rho = 0.52$ (SE = 0.11) in the first survey and 0.89 (SE = 0.05) thereafter. Because all pairs detected in the first survey were also detected in ≥ 1 subsequent survey within that survey year, we used only the second and third surveys in subsequent analyses (Table 1). We ran this same candidate model set using all three surveys and the results are exactly the same. Therefore, for brevity, we only present the most parsimonious model set (Table 2).

The best model for predicting the presence of owl pairs included basal area of trees >10 cm dbh and the ground cover of coarse woody debris in a model structured as:

$$\text{Logit}\hat{\Psi} = (3.92) + [41.81 \times \text{Zscore}(\text{BAT})] - [10.52 \times \text{Zscore}(\text{CWD})] + (2.13 \times \rho), \quad (5)$$

with an Akaike weight (w_i) of 0.40 (Table 2). The standard error of the parameter estimate for BAT was 84.29 and 24.94 for CWD. The second best model included the derived variable BATCan (Table 2), with structure as follows:

$$\text{Logit}\hat{\Psi} = (0.24) + 4.56 \times [\text{Zscore}(\text{BAT}) + \text{Zscore}(\text{canopyclosure})] + (2.12 \times \rho). \quad (6)$$

This model also had substantial support with w_i of 0.15 and an evidence ratio of 2.6 and ΔAIC_c of 1.90. The standard error (2.18) for the parameter estimate in this alternative model was much smaller than for either of the standard errors for the parameters in the “best” model. There was no support for a model that distinguished between burned and unburned sites ($w_i = 0.00$, $\Delta AIC_c = 35.09$) indicating that indirect complexities of post-fire effects on forest structure (e.g., changes in canopy closure) influence owl site occupancy rather than the direct effect of fire on the owls. Applying the best model, the mean and standard error (SE) of estimated occupancy rate was 0.46 (0.12) for burned sites 0.72 (0.11) for unburned sites, and 0.59 (0.08) across all sites. Total basal tree area (BAT) was higher both at burned and unburned sites with owls than at no-response sites (Fig. 2).

Table 1

Total counts^a and unmodeled mean (SE) occupancy and detection rate^b, population size^c, and density estimates of California spotted owls from random, systematic, nocturnal surveys in burned and unburned areas (April–July 2004–2005) in Yosemite National Park, California.

Burn treatment	Count of owl pairs ^a	Occupancy probability ^b	Detection probability ^b	Population size (pair) ^c	Density (owl pair km ⁻²)
Burned	8	0.50 (0.13)	0.89 (0.05)	123 (10)	0.15 (0.04)
Unburned	11	0.69 (0.12)	0.89 (0.05)	156 (13)	0.21 (0.04)
ALL	19	0.59 (0.09)	0.89 (0.05)	356 (20)	0.18 (0.03)

^a Count of owl pairs refers to the total number of pairs of owls observed in all survey areas within the burn treatment.

^b Occupancy and detection rates refer to the mean and standard error (SE) of the occupancy and detection rates for each owl survey areas calculated from program PRESENCE (Hines, 2006).

^c Population size refers to the total number of owl pairs calculated for each burn treatment with standard error representing the error rate in the estimate.

Table 2

Summary of model selection statistics^a from logistic model^b analysis of nesting and roosting habitat variables^c predicting the site occupancy of California spotted owl (*Strix occidentalis occidentalis*) pairs in Yosemite National Park, California, 2004 and 2005 ($n = 32$; 16 burned sites, 16 unburned sites).

Model description ^d	K	log (L) ^a	AIC _c	ΔAIC _c	w _i
Occupancy{BAT}{CWD}	5	-15.03	40.07	0.00	0.40
Occupancy{BATCan}	4	-16.99	41.97	1.90	0.15
Occupancy{BATCan}{Shrub}	5	-16.71	43.42	3.35	0.07
Occupancy{BAT}{Elevation}	5	-16.72	43.44	3.37	0.07
Occupancy{BATCan}{CWD}	5	-16.76	43.52	3.45	0.07
Occupancy{BAT}	4	-17.91	43.82	3.75	0.06
Occupancy{BATCan}{BAs}	5	-16.91	43.82	3.75	0.06
Occupancy{BATCan}{Elev}	5	-16.94	43.88	3.81	0.06
Occupancy{BAT}{Shrub}	5	-17.78	45.56	5.49	0.03
Occupancy{Canopy}{BAT50 cm}	5	-18.13	46.26	6.19	0.02
Occupancy{Canopy}	4	-22.63	53.26	13.19	0.00
Occupancy{Canopy}{Elevation}	5	-22.21	54.42	14.35	0.00
Occupancy{Canopy}{CWD}	5	-22.32	54.64	14.57	0.00
Occupancy{Canopy}{Shrub}	5	-22.47	54.93	14.86	0.00
Occupancy{Canopy}{BAs}	5	-22.59	55.18	15.11	0.00
Occupancy{BAT50 cm}	4	-24.52	57.04	16.97	0.00
Occupancy{Elevation}	4	-30.47	68.94	28.87	0.00
Occupancy{constant} (null model)	3	-34.17	74.33	34.26	0.00
Occupancy{Burned}	4	-33.58	75.16	35.09	0.00
Occupancy{Shrub}	4	-33.77	75.54	35.47	0.00
Occupancy{BAs}	4	-34.05	76.11	36.04	0.00
Occupancy{SurveyYear}	4	-34.10	76.20	36.13	0.00
Occupancy{CWD}	4	-34.15	76.30	36.23	0.00
Occupancy{constant}, detection rate{Burned}	2	-38.85	81.70	41.63	0.00

^a Statistics include: log_e likelihood (log(L)), Akaike's Information Criterion corrected for small sample size (AIC_c), relative AIC_c (ΔAIC_c), Akaike weights (w_i), and the number of parameters (K) in the model.

^b Logistic model used: $\log_e(\Psi/(1 - \Psi)) = X\beta$, where Ψ refers to the probability of owl pair occupancy, X is the row vector of habitat variables, and β is the column vector of coefficient values.

^c 'BAT' refers to basal area of all live trees >10 cm diameter at breast height (dbh), 'BAs' refers to basal area of snags ≥80 cm, 'BAT50 cm' refers to basal area of all live trees >49 cm, 'canopy' refers to canopy closure estimated from digital hemispherical photos, 'BATCan' refers to the sum of BAT and canopy closure at the owl site, shrub refers to mean shrub cover, and 'CWD' is the cover of coarse woody debris.

^d Detection rate was survey-specific ("full identity") in every model except the last one, in which it varied by burn treatment.

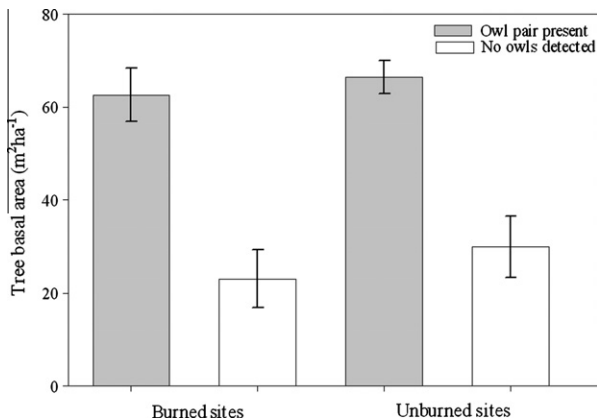


Fig. 2. Comparing the mean ± SE basal area of all live trees (≥ 10 cm) at burned and unburned sites with owls (nest and roost sites) and without (random points) between April–July, 2004–2006 at Yosemite National Park, California.

3.3. Population estimation

Eighty-four percent of all of the nests or roosts we located were within the boundary of our 3.75 km² survey areas. Using the detection rate (ρ) estimated by PRESENCE and extrapolating across all potential habitat, we estimated the population size (SE) for Yosemite as 280 (16) pairs of California spotted owls, with 70 (6) pairs in the burned montane forest and 228 (18) pairs in the unburned forest (Table 1). The mean (SE) density of owl pairs was 0.15 (0.04) pairs km⁻² in the burned forest and 0.21 (0.04) pairs km⁻² in the unburned for an overall average of 0.18 (0.03) pairs km⁻² across the entire park (Table 1), or 1 pair 6.25 km⁻². This is a conservative estimate because there were three pairs of owls we did not include in the estimate because their nests were 0.2 km, 0.7 km, and 1.3 km outside of the survey areas. We also omitted an additional pair that we detected only during the diurnal follow-up surveys (while looking for another pair) and not during our nocturnal surveys. The roost for this "consequential" pair were within the same survey area as the nest of another pair (<1.5 km apart).

4. Discussion

The relatively low mean fire severity index documented for our burned forests (2.0) suggests a fire history similar to what existed before Euro-American settlement (Skinner and Chang, 1996). Although we characterized individual survey areas with a single fire severity index value, burned areas contained a mosaic of different fire severities. This mosaic reflects heterogeneity among burned forest patches and creates a complex matrix of habitat characteristics at multiple scales (e.g., microhabitat, stand, and landscape). This post-fire heterogeneity may be one of the most important aspects of the burned landscape to spotted owls. Franklin et al. (2000) showed that owls with territories that contained a mosaic of vegetation types infused within old-growth conifer forest had higher fitness. Bond et al. (2009) found that California spotted owls use this mosaic for a variety of different activities such as low severity for nesting and roosting and higher severities for foraging.

4.1. Spotted owl occupancy

Based on our modeling results, California spotted owl nest and roost site occupancy in montane forests of Yosemite National Park was best predicted by combining the positive effect of total basal area (BA_T), and the negative effect of coarse woody debris (CWD). However, there was substantial support for the alternative model that used the derived variable combined canopy closure and tree basal area (BA_TCan). The abundance of large trees has a clear association with spotted owl nest and roost sites (Bias and Gutiérrez, 1992; Gutiérrez et al., 1992; Verner et al., 1992b; LaHaye et al., 1997; Moen and Gutiérrez, 1997). These results also indicate that fire does not reduce the probability of spotted owl occupancy, especially if numerous large trees remain after a fire. Clark (2007) showed northern spotted owl occupancy declined and local extinction increased immediately following fire. However, his results are confounded by post-fire salvage logging and large areas of early-seral forests in his study area. Also, the fire age of our study is variable (2–14 years) while his was only 1–2 years. However, it is important to note the disparity of these results with ours suggests that salvage logging may have detrimental effects on spotted owl occupancy. Jenness et al. (2002) found a weak negative association of fire to Mexican spotted owl occupancy. However, they collected no data on the habitat characteristics to allow investigation into the post-fire forest structure that potentially drove that association.

We included detection rates in our models because the California spotted owl home range is potentially larger than our survey area (MacKenzie, 2005). According to MacKenzie et al. (2002), however, high detection rates (e.g., >0.5), such as what we estimated from our nocturnal surveys ($\rho = 0.89$; Table 1), produce accurate and unbiased predictive models for occupancy.

In an earlier study on habitat associations of California spotted owls in northeastern California, site occupancy was positively associated with large trees (>61 cm dbh) and high canopy cover (>70%; Blakesley et al., 2005). However, the proportion of smaller trees (<60 cm dbh) around the nest, even with high canopy cover (>70%), was negatively associated with occupancy (Blakesley et al., 2005). By contrast, models incorporating only large trees (>50 cm dbh; BA_T50 cm) were not supported in our analyses (Table 2), indicating that a range of tree sizes influence site occupancy by spotted owls. Trees between 10 cm and 50 cm dbh contribute to a multilayered understory that presumably allows for efficient thermoregulation by owls (Barrows, 1981; Weathers et al., 2001). Large trees are important as nest sites for northern flying squirrels (*Glaucomys sabrinus*; Waters and Zabel, 1995; Meyer et al., 2007),

an important prey species for spotted owls in the Sierra Nevada (Williams et al., 1992).

The disparity between our results and those of Blakesley et al. (2005) could reflect several key differences between our studies. Blakesley et al. (2005) measured their vegetation at a larger spatial scale than our study and consequently used categorical canopy cover data. At our smaller spatial scale, we were able to use continuous canopy closure data. Additionally, their study was conducted in the northern Sierra Nevada which has a more recent history of logging, and thus large trees may be more limited there than in the more pristine forests in Yosemite. Their study site also suffered from decades of fire suppression, which resulted in a dense understory of regenerating white fir. These thickets of young trees could interfere with owl foraging which could explain the negative association of small trees to owl occupancy. Furthermore, Blakesley et al. (2005) quantified habitat only at nest sites, whereas we included roost sites (when nests were unknown). The presence of large trees may be less important in the selection of owl roosts versus nest sites (Verner et al., 1992b). Including roost sites in spotted owl occupancy models provides a more robust model than those excluding such features because the owls may not nest every year (Blakesley et al., 2001, 2005; Steger et al., 2002).

The spatially invariant detection rates reported here compared to the highly variable rates reported for northern spotted owls in Oregon (Olson et al., 2005) could be explained by the disparity in forest management practices. For example, forest managers favored clearcutting in the Pacific northwest over much of the range of the northern spotted owl, while much of the range of the California spotted owl predominantly experienced selective logging. Only a small portion (18%) of our study area was logged during the 1930s (National Park Service, 1930), and none of the study area contained co-habiting, invasive barred owls (*S. varia*), a species that typically has negative effects on detection rates and site occupancy of spotted owls (Kelly et al., 2003; Olson et al., 2005). Consequently, the mean per visit detection rate for spotted owl pairs in our study (0.89 ± 0.1) was higher than in Oregon (0.51) where barred owls and logging were more common (Olson et al., 2005, p. 930). The main factors influencing habitat structure in the montane forests of Yosemite are natural processes, predominately fire. Our results evaluated the role of fire unconfounded by large-scale logging, development, or competition with an aggressive congener.

In a study in the Sierra Nevada, Gutiérrez et al. (1992) found that California spotted owl nest and roost sites had higher snag basal area than random sites. However, study areas of these authors were predominantly in forests with a history of consistent logging, such that large snags likely were limited in availability. In the predominantly unlogged forests of Yosemite, large snags are relatively common and burned and unburned forests had similar basal areas of large snags.

The lower AIC_c value for the BA_T-CWD model indicates that this model has the best fit to the data and, therefore, should reflect the best balance of precision (as measured by standard error) and bias (as measured by log-likelihood). In our candidate model set (Table 2), we hypothesized that CWD would be a positive influence on spotted owl site occupancy due its positive association with food for the northern flying squirrel in forests of the Pacific northwest (Amaranthus et al., 1994; Lehmkuhl et al., 2004). However, studies in the forests of the Sierra Nevada with typically lower fire return intervals have shown no relationship between CWD and northern flying squirrels (Pyare and Longland, 2002; Meyer et al., 2007). Fire transforms CWD into nutrient-loaded ash, resulting in less CWD in burned forests than unburned forests (Shaffer and Laudenslayer, 2006). It is possible that CWD interferes with owl foraging when attempting to extract prey from the ground.

Potentially unpredictable ephemeral effects (e.g., CWD or shrub cover) can be avoided by introducing variable(s) that measure

more temporally stable effects. Our derived variable, BATcan; is based on live trees that typically remain alive and upright for decades after the fire. Summing standardized total tree basal area ($\text{m}^2 \text{ha}^{-1}$) and canopy closure (%) at a site creates a single variable that depicts forest density in the overstory as well as the understory. The model comparisons showed BATcan was an acceptable alternative with greater precision for predicting spotted owl site occupancy in montane forest than the $\text{BA}_t\text{-CWD}$ model. The consistent positive association of BATcan with site occupancy in our study is in agreement with the consensus that dense forest with large trees are important nesting and roosting habitat for spotted owls in the Sierra Nevada bioregion (Bias and Gutiérrez, 1992; Call et al., 1992; Gutiérrez et al., 1992; Verner et al., 1992b; LaHaye et al., 1997; Moen and Gutiérrez, 1997; Zabel et al., 1992). An important benefit to managers in using the BATcan variable is the reduction in field data collection, as canopy closure is quickly and easily measured and requires little field or analysis training and minimal equipment. However, we caution the use of BATcan in models for forests where >70% of the total basal area of a stand is dominated by smaller trees (<50 cm dbh) because in that situation, increases in stand basal area typically indicate increases in tree density rather than tree size. This leads back to the idea that too many small trees negatively affect spotted owl occupancy (Blakesley et al., 2005).

4.2. Population estimate

Similar density estimates of spotted owl pairs in burned and unburned forests (95% confidence intervals, CI: 0.07–0.22 and 0.14–0.28 owl pairs km^{-2} , respectively) of the type that we examined (predominately low to moderate severity burns of a relatively small percent of the landscape) suggest that fire did not affect owl densities in Yosemite. Consequently, detection and occupancy rates were similar in burned and unburned forests. Based on density estimates in Noon et al. (1992, p. 175), we calculated the 95% CI individual owl density for the area surrounding Yosemite including two national forests and a national park. This estimate (0.10–0.21 owls km^{-2}) was markedly lower than our estimate of total individual owl density in Yosemite (95% CI = 0.25–0.46 owls km^{-2}) and suggests that Yosemite has a higher density of spotted owls than the surrounding national forests and nearby parks. However, this comparison is tentative because Noon et al. (1992) presented only 'crude densities' and did not correct for unsuitable areas within their total available habitat. Consequently, if the amount of suitable habitat was substantially lower than the total area they used in their calculations, their spotted owl density estimates could be lower than reported.

For our population size estimate for the park, we caution that these could be biased slightly high because we treated both forest types (lower montane and upper montane) equally in terms of occupancy and detection rates and this may not be true. It is for this reason that we discuss our results in terms of density rather than the overall population estimation for the park.

5. Conclusions

Our data suggest that the landscape-level prescribed burning and wildland fire use programs of Yosemite National Park may benefit California spotted owls by protecting their nesting and roosting habitat from catastrophic fires while simultaneously creating a large, contiguous, and diverse landscape conducive to population persistence for spotted owls. This is especially evident in Sierra Nevada montane forests that historically burned at low to moderate intensity and usually resulted in a mosaic of burn severity, with minimal mortality of medium and large trees (van

Wagtendonk and Fites-Kaufman, 2006). Our results are particularly relevant to forests where large aggregations of residual downed coarse woody debris create spatially continuous fuel loads and extremely flammable environments. Our results suggest that fire, particularly fire resulting in low to moderate tree mortality, can retain residual habitat features that are important for roosting and reproducing California spotted owls.

California spotted owl site occupancy rates and densities were similar in recently burned (<15 years) and unburned montane forests of Yosemite National Park. Our predictive model for site occupancy can assist managers in developing fire management plans with minimal impact and potential benefit to California spotted owls. Currently, the application of our site occupancy model relies heavily on local and site-specific data. A landscape scaled remote sensing and GIS model could assist in the evaluation of fire and land management plans both for Yosemite and more generally for the Sierra Nevada. Integrating remote sensing data with our derived variable, BATcan, would create a reliable and simple model that would allow managers to move beyond the limitations (in both money and time) of having to collect ground based data.

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Differential impacts of wildfire on the population dynamics of an old-forest species

JEREMY T. ROCKWEIT ^{1,3}, ALAN B. FRANKLIN,² AND PETER C. CARLSON¹

¹Cooperative Fish and Wildlife Research Unit, Colorado State University, 1484 Campus Delivery, Fort Collins, Colorado 80523 USA

²National Wildlife Research Center, USDA, 4101 Laporte Ave., Fort Collins, Colorado 80521 USA

Abstract. Ecological disturbances shape and maintain natural communities, but climate change and human land use can alter disturbance regimes and affect population persistence and vital rates in unpredictable ways. Species inhabiting landscapes shaped by wildfire have evolved mechanisms allowing them to persist under this dynamic disturbance type, which creates habitats of varying quality for these species. We utilized data from a 26-yr demographic study of northern spotted owls to analyze the influence of wildfire on apparent survival and recruitment rates. Wildfires occurred across different years and affected different spotted owl territories, which allowed us to implement a retrospective Before-After-Control-Impact (BACI) analysis and model the potential effect of wildfire extent and severity. Our results indicated that mixed-severity fires that burned at predominantly low-severity had little effect on survival and recruitment while fires characterized by more medium to high burn severities negatively affected spotted owl survival, with varying effects on recruitment. Reduced survival and increased recruitment rates on some territories affected by medium to high severity fires suggested that post-fire habitat quality was reduced resulting in territories that were marginally capable of supporting owls. We hypothesize these territories may have represented “sinks” that were supported by nearby “source” territories in a spatially heterogeneous landscape created by the mixed-severity fire regime of the region.

Key words: *apparent survival; mixed-severity; population dynamics; recruitment; spotted owl; Strix occidentalis; wildfire.*

INTRODUCTION

Ecological disturbances play an integral role in shaping and maintaining natural communities. Disturbance regimes occur across multiple spatial and temporal scales and can have both positive and negative effects on the plant and animal species they impact (Rykiel 1985) by, for example, creating habitat conditions that improve vital rates (Fraterrigo and Rusak 2008). As such, species have evolved a set of life history traits adapted to coping with disturbance regimes common to their particular ecosystem. Moreover, the degree to which a species or community is affected by disturbance depends on the intensity of the disturbance, the pre-disturbance conditions, and the quality of the surrounding landscape (Franklin et al. 2002). Thus, a species' ability to respond to a disturbance event may be compromised if the dominant disturbance regime is altered from its historic range of variability (e.g., in scale, intensity, frequency, or type of disturbance) due to past land use practices and climate change.

Wildfire is one such disturbance type that has resulted in fire-adapted ecological communities throughout large

portions of the western U.S. However, the scale (Stephens 2005, Miller et al. 2012) and intensity (Lutz et al. 2009, Miller et al. 2009) of wildfire has been increasing over the past several decades and is causing considerable concern because of the potential for an increased loss of economically and ecologically valuable forests (Thomas et al. 1990, Davis et al. 2011, USFWS 2011). This increase is thought largely to stem from the unintended consequences of effective fire suppression beginning in the early-to-mid 20th century, past and current timber harvest practices such as clear cut logging (Odion et al. 2004), and the growing influence of climate change (Liu et al. 2013, Abatzoglou and Williams 2016, Westerling 2016).

In the southern portion of the Pacific Northwest lies the Klamath Ecological Province of northwestern California and southwestern Oregon, which is considered a global hotspot for biological diversity (Whitaker 1960). Forests in this region are structurally complex and species rich, with a diverse mix of under- and mid-story hardwood species and a canopy of mixed conifer species (Whitaker 1960, Skinner et al. 2006). This high level of biodiversity is partly a function of the dominant disturbance regime of the area, mixed-severity wildfire, which historically had a relatively frequent fire return interval (12–19 yr; Agee 1993, Willis and Stuart 1994). Prior to fire suppression and timber harvesting, this landscape contained a mosaic of seral stages resulting from mixed-severity wildfires (Perry et al. 2011, Hessburg et al.

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³E-mail: rockweit@rams.colostate.edu

2016). Although high severity patches occurred, they generally were smaller in extent and contributed to the seral stage patchwork that made up the landscape (Skinner et al. 2006, Donato et al. 2009, Halofsky et al. 2011, Perry et al. 2011). One species to capitalize on this patchwork landscape created by wildfire was the northern spotted owl (*Strix occidentalis caurina*). Although generally considered an old-growth forest obligate, high quality habitat for northern spotted owls in the Klamath Province encompasses a range of different seral stages that balance early seral stages with older forest in a mosaic that mimics the landscape created by mixed-severity fires (Franklin et al. 2000). This patchwork of seral stages (Fig. 1a) and the relatively short fire return interval combine to create a dynamic landscape for the wildlife species inhabiting the region.

This confluence of ecologically and economically valuable forests with a changing disturbance regime has created intense interest in the effects of wildfire on spotted owls, with some studies reporting negative effects of wildfires on spotted owl survival (Clark et al. 2011), reproduction (Gaines et al. 1997, Jenness et al. 2004), and territory occupancy and colonization rates (Clark et al. 2013, Jones et al. 2016) while others found no discernible effects of wildfires on spotted owl survival and reproduction (Bond et al. 2002), territory occupancy (Bond et al. 2002, Roberts et al. 2011, Lee and Bond 2015), and colonization and extinction rates of territories (Lee et al. 2012). Research has also been ambiguous on the use of burned areas by spotted owls; two studies found spotted owls using forests burned at all severities for foraging but avoiding moderate- and high-severity burned areas for roosting (Bond et al. 2009, 2016), one study found the probability of use decreasing with increasing fire severity (Eyes 2014), while another found spotted owls avoided foraging in large patches of severely-burned forest 1 yr post-fire (Jones et al. 2016). These conflicting results suggest that any categorical conclusion about the influence of wildfire on spotted owls is not warranted, but rather that spotted owls exhibit varied responses to wildfire due in part to the highly variable nature of wildfire itself (e.g., overall burn severity, wildfire size, pre-fire habitat conditions, time since fire, etc.) and the methodologies used to analyze their response (occupancy vs. demography vs. habitat use). Furthermore, many of the studies to date are either confounded by post-fire salvage logging (Bond et al. 2009, Clark et al. 2011, 2013, Lee et al. 2012), lack pre-fire data (Gaines et al. 1997, Bond et al. 2002, 2009, Clark et al. 2011, Roberts et al. 2011, Eyes 2014, Lee and Bond 2015), consist of small sample sizes (Gaines et al. 1997, Jenness et al. 2004, Bond et al. 2009, Clark et al. 2011, Eyes 2014), or examined only short-term effects (Bond et al. 2002, 2009, Clark et al. 2011, 2013, Roberts et al. 2011, Eyes 2014, Lee and Bond 2015, Jones et al. 2016). We attempted to address this ambiguity by analyzing northern spotted owl responses to wildfire using a robust analytical method, the Before-After-Control-Impact (BACI) design, and a wide range of wildfire

severities that burned across a 21-yr period. We hypothesized that the degree to which spotted owls would be influenced by wildfire would be contingent on disturbance intensity (i.e., wildfire severity).

In this study, we capitalized on a natural experiment during a 26-yr study of the population ecology of northern spotted owls in the Klamath Province to examine how wildfire influenced apparent survival and recruitment. Our data was not confounded with salvage logging because post-fire salvage logging did not occur in our study area. Because fires occurred on different northern spotted owl territories between 1987 and 2008, we were able to utilize a BACI design to compare pre- and post-fire survival and recruitment at territories affected by wildfire (treatments) with territories unaffected by fire (control). Based on the natural fire regime in the Klamath province, we predicted lower severity wildfires would have minimal effects on northern spotted owl populations while higher severity wildfires would negatively affect those populations.

METHODS

Field surveys

Our field methods are detailed in Franklin et al. (1996, 2000). Briefly, we surveyed two study areas (Fig. 1b) using vocal surveys to detect northern spotted owls annually between April and August from 1987 to 2012. The first was a contiguous 292 km² area in Humboldt and Trinity counties, California, which we surveyed entirely. The second study area consisted of 34 territories surveyed annually in Humboldt, Trinity, Siskiyou, and Mendocino counties, California. Unlike the first study area, we did not survey the matrix lands between territories in the second; all other survey methods were the same between study areas. Owls located and captured were marked with a uniquely numbered U.S. Geological Survey band and a unique colorband combination that allowed for subsequent identification through resighting the colorband.

We defined spotted owl territories following Franklin et al. (2000) where the territory center was defined as the arithmetic mean of all cumulative roost and nest locations within a given territory. We then created a 1,000 m buffer around each territory center to define the territory boundaries where owls might be affected by fire because, 1) it was approximately halfway between ½ mean nearest neighbor distance (714 m; Franklin et al. 2000) and home range estimates (1,381 m; Bingham and Noon 1997) for spotted owls in this region, and 2) Bond et al. (2009) found that foraging California spotted owls (*Strix occidentalis occidentalis*) selected for all burn severities up to 1,000 m from their roost. Thus, we considered a territory “affected” by fire if the territory center was within 1,000 m of a burn perimeter. Within this 1,000 m buffer, we calculated fire covariates that characterized the extent and severity of wildfire for each affected territory.

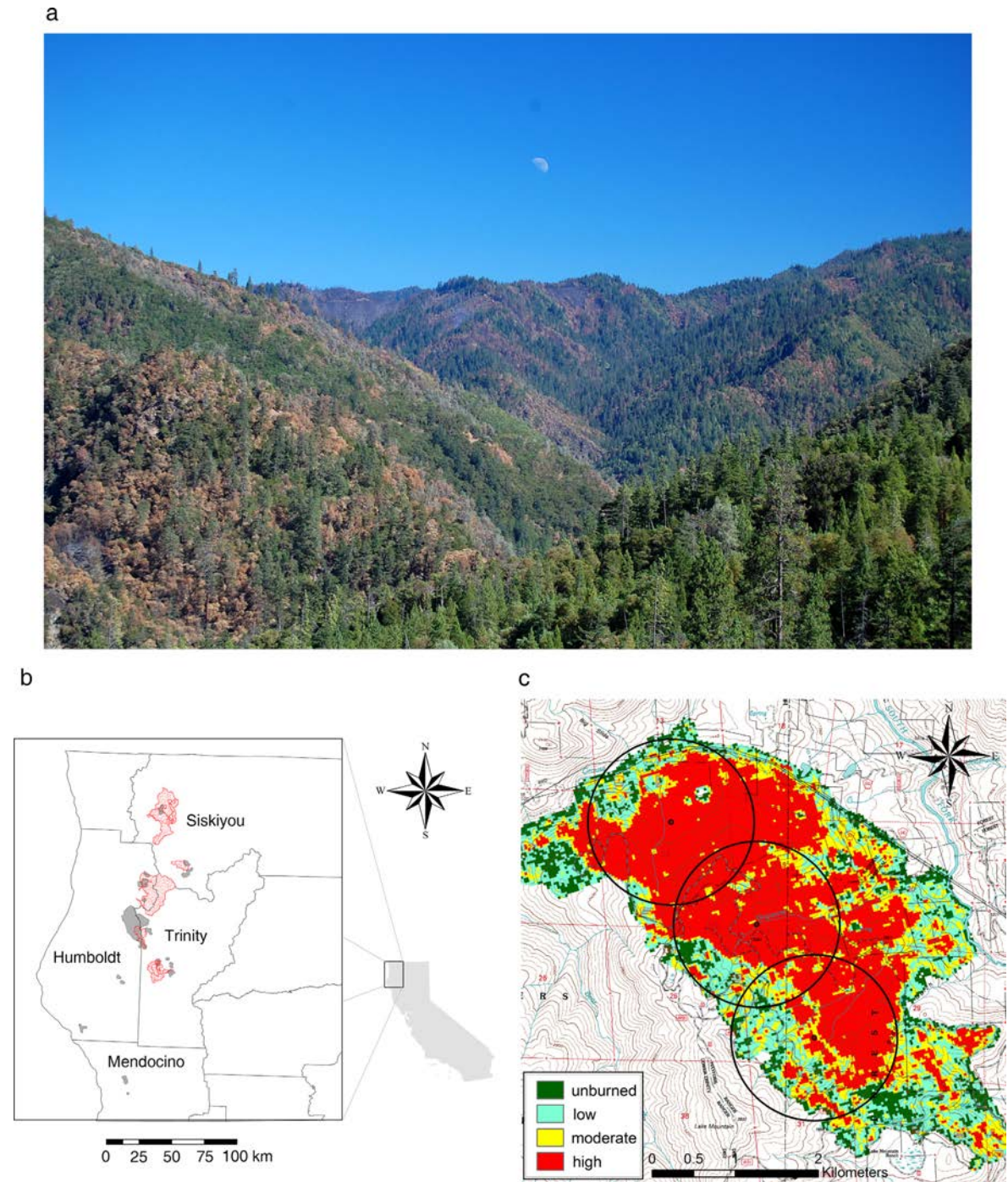


FIG. 1. (a) Landscape typical of the Klamath Province of northwestern California illustrating the patchwork of burn severities created by a mixed-severity fire regime. (b) Location of study area (shaded areas) and burn perimeters of fires (red stippled areas) used to estimate apparent survival and recruitment rates of northern spotted owls. (c) Example of high burn severity from the 2004 Sims Fire that impacted 3 northern spotted owl territories (circles).

Characterization of fire effects

We used data from the Monitoring Trends in Burn Severity (MTBS) project (Eidenshink et al. 2007) to identify fires that occurred on our study areas from 1987

through 2012. The MTBS project was designed to provide consistent, long-term, nation-wide burn severity information by mapping all large fires across the U.S. (>404 ha in the West) and generating spatial information on burn perimeter and fire severity for each fire. Severity thresholds

(unburned, low, medium, high) were derived using the delta Normalized Burn Ratio (dNBR; Cocke et al. 2005, Key and Benson 2006, Eidenshink et al. 2007). Post-fire imagery was taken as close as possible to one year after the pre-fire image to minimize variation in plant phenology (Miller and Thode 2007). This value was then converted into discrete burn severity categories: unburned, low severity, moderate severity, or high severity. Burn severity categories were defined based on ground-based methods of estimating ecological fire effects (Key and Benson 2006) that correlate with the satellite-based methods used by the MTBS project. Low severity wildfire was defined as areas that exhibited >15% of an area burned with an almost complete combustion of litter, but with <25% overstory tree mortality. Conversely, high severity wildfire was defined as areas with a nearly complete combustion of litter and duff, a high degree (35–65%) of medium and heavy woody debris consumed and an overstory tree mortality >75%. Moderate severity fire encompassed everything between low and high severity (Schwind 2007, public communications).

We used the Patch Analyst extension in ArcGIS to calculate annual, individual covariates that characterized the extent and severity of fire within our defined owl territories and were used to represent different hypotheses about the effects of fire on spotted owl survival. We calculated the proportion of each territory that burned at any severity (pBurn) and the distance from each territory center to the nearest burn perimeter (Dist) to characterize the extent of fire within the affected territories. We also calculated the proportion of each territory that burned at low (pLow), moderate (pMod), and high severity (pHigh) fire, and the combined proportions that burned at low and moderate severity (pLowMod), and moderate and high severity (pModHigh) fire. We calculated these latter two covariates because the broad ecological definition of moderate severity fire (25–75% canopy tree mortality) resulted in some uncertainty in how it would affect spotted owls. Four of the territories that burned in 2008 also burned in 1987. When calculating covariates for these territories, we combined the fire effects from 1987 and 2008 because we felt that the effects from the 1987 fires were probably still influencing resident spotted owls 21 yr later. Finally, we calculated a fire severity index (FSI; Shaffer and Laudenslayer 2006) where: $FSI = (pLow \times 1) + (pMod \times 2) + (pHigh \times 3)$, in an attempt to summarize the overall burn characteristics within each territory into a single covariate. Thus, FSI represented the hypothesis that an owl's response to wildfire was a function of the cumulative effects of all burn severities within an owl's territory and not the result of any particular level of burn severity. We tested each covariate separately because many of the covariates were highly correlated with each other ($r = 0.21$ – 0.98). We also examined the linear, quadratic, and pseudo-threshold form of each covariate to determine how spotted owl populations respond to changes in the extent and severity of wildfire within their territory.

Estimating survival and recruitment

We estimated apparent survival (the probability that an individual alive in year t was also alive in year $t + 1$, given the individual remained on the study area) of non-juvenile northern spotted owls (i.e., ≥ 1 yr old) using Cormack-Jolly Seber capture-recapture models (Cormack et al. 1979) and recruitment rates (number of individuals in the population at time $t + 1$ per individual in the population at time t) using Pradel reverse-time Jolly Seber capture-recapture models (Pradel 1996) in program MARK (White and Burnham 1999). These two parameters captured the full dynamic of the treatment (i.e., fire) effect in that apparent survival accounted for both survival and emigration from burned territories (e.g., the reciprocal of survival indicated that the individual either died or left the territory) and recruitment accounted for new immigrants into the affected territories.

We analyzed the capture-recapture data using five groups based on the years when fires occurred (1987, 1999, 2004, 2008, and control group) and the territories affected by the fires in those years. Spotted owls on sites never affected by fire (i.e., territory center >1,000 m from a burn perimeter) during the course of the study were assigned to the control group. We did not have pre-fire data for the 1987 group because that was the first year of surveys at those sites. If a spotted owl moved between treatment and control groups, we truncated its capture history at the last year it was observed in that group, and then began a new capture history the year it showed up in the new group. We used this approach to account for movement between groups because <5% of individuals moved between groups.

We used a multi-step modeling process to estimate apparent survival rates of territorial spotted owls using AIC_c (Burnham and Anderson 2002) to rank models after each step and to determine the best overall model. In the first step, we modeled recapture rates (p) while keeping apparent survival (ϕ) unconstrained by group and year ($g \times t$) to determine the recapture structure with the lowest AIC_c value. We then used the recapture structure from this model to begin modeling apparent survival. In the second step, we modeled the best time structure for ϕ on the control group of owls not affected by fire followed by modeling the best time structure on the pre-fire years of the fire groups. In the third and final step, we modeled the best time structure for the post-fire years of the fire groups. We maintained annual time variation ($g \times t$) in the fire groups while modeling the control group, and in the post-fire years while modeling the pre-fire years. After determining which overall time model best fit the data, we added the annual, individual covariates to determine what fire characteristics helped explain the observed patterns in spotted owl post-fire survival.

We then estimated group-specific recruitment rates (f) to better capture the occupancy dynamics of territories affected by fire. After developing models for apparent survival, we used the Pradel models (Pradel 1996) in

program MARK to estimate recruitment rates using the top time structure from the survival analysis above. We used AIC_c to compare a model with no pre- and post-fire effect on recruitment rates, with a model allowing for different pre- and post-fire effects on recruitment rates.

Lastly, barred owls have been found to negatively affect spotted owl apparent survival, occupancy and colonization rates (Dugger et al. 2016). Barred owl detections on our study areas remained at consistently low levels through the mid-2000s (~8–13% of spotted owl territories surveyed had sporadic barred owl detections annually through 2006) and did not begin to increase until 2007, which is a similar timing as the 2008 fires. However, only one of the territories affected by wildfire in 2008 was occupied by barred owls, so we did not consider barred owl presence in our analysis.

RESULTS

Ten fires ranging in size from 496 ha to 50,386 ha burned through all or portions of 24 of 94 (26%) territories surveyed in our study areas during the course of the study (Table 1). Four of these territories were burned twice in wildfires occurring in 1987 and 2008. Most of the fires were typical of the mixed-severity fire regime of the area (Willis and Stuart 1994, Taylor and Skinner 1998) with average proportions of 0.27, 0.39, 0.19, 0.15 for unburned, low, moderate, and high severity fire, respectively. However, 48% of the 2004 Sims Fire burned at high severity (Table 1, Fig. 1c).

We used 579 unique encounter histories ($n_{1987} = 70$; $n_{1999} = 18$; $n_{2004} = 28$; $n_{2008} = 77$, $n_{\text{control}} = 386$) to estimate pre- and post-fire apparent survival and recruitment rates. The best model structure for recapture rates (p) included a linear time trend ($\hat{\beta} = -0.068$, 95% CI = $-0.094 - [-0.043]$) which indicated that recapture rates slowly declined over the course of the study. The best survival model without covariates (Appendix S1: Table S1) indicated that: 1) each group had constant (no time trend) pre-fire estimates of apparent survival that did not differ from each other or the control group ($\hat{\phi}_{\text{control}} = 0.83$, 95%

CI = 0.81–0.84; $\hat{\phi}_{\text{pre1999}} = 0.93$, 95% CI = 0.83–0.97; $\hat{\phi}_{\text{pre2004}} = 0.88$, 95% CI = 0.81–0.93; $\hat{\phi}_{\text{pre2008}} = 0.82$, 95% CI = 0.77–0.86; Fig. 2a), and 2) fire had a strong, significant negative effect on apparent survival for the 2004 and 2008 fire groups (Fig. 2a). Fire also appeared to have a slight negative effect on the 1999 group. However, there was uncertainty about this effect with overlapping confidence intervals for pre- and post-fire survival estimates (Fig. 2a; $\hat{\phi}_{\text{post1999}} = 0.83$, 95% CI = 0.69–0.91). The 1987 group lacked pre-fire data, but post-fire survival was not different than the control group. There was strong support for this model, which accounted for >62% of the Akaike weight (Appendix S1: Table S1).

The best performing model that included the territory-specific fire covariates (Appendix S1: Table S2) included the combined proportion of moderate and high severity fire within 1,000 m of the owl's activity center ($\hat{\beta}_{\text{pModHigh}} = -1.88$, 95% CI = $-3.36 - [-0.40]$), indicating that as the combined proportion of moderate and high severity fire increased, apparent survival decreased (Fig. 3). Seven other covariate models were within 2 AIC_c units of the top-ranked covariate model suggesting some model selection uncertainty (Appendix S1: Table S2). However, all of the competitive covariates (FSI, pMod, pHigh, pBurn, FSI², pModHigh², and Ln (FSI)) supported the same negative association between fire severity and spotted owl survival. Thus, we found a negative relationship between the probability of spotted owls surviving and remaining on a territory and the extent and severity of wildfire within an owl's territory.

The top recruitment model indicated that post-fire recruitment rates were not statistically different from pre-fire rates or the control group, except for the owls affected by wildfire in 2008, where recruitment rates substantially increased post-fire (Fig. 2b). Point estimates for the other fire groups increased slightly despite the lack of any statistical significance ($\hat{f}_{\text{pre1999}} = 0.10$, 95% CI = 0.04–0.22; $\hat{f}_{\text{post1999}} = 0.12$, 95% CI = 0.05–0.24; $\hat{f}_{\text{pre2004}} = 0.13$, 95% CI = 0.08–0.21; $\hat{f}_{\text{post2004}} = 0.17$, 95% CI = 0.07–0.37), and this slight increase likely contributed to the strong support (Appendix S1: Table S3) for this model.

TABLE 1. Characteristics of wildfires that affected northern spotted owl territories in the Klamath province of northwest California.

Year	Fire name	Territories affected	Size (ha)	Unburned	Low	Moderate	High
1987	Cold	1 ¹	5,988	0.43	0.40	0.13	0.04
	Friendly	1	1,406	0.24	0.39	0.25	0.12
	Glasgow	3	5,462	0.24	0.35	0.23	0.18
	King Titus	3 ²	28,892	0.36	0.42	0.15	0.06
1999	Meagram	2	50,386	0.24	0.41	0.19	0.16
2004	Sims	4	1,541	0.10	0.21	0.20	0.48
2008	Hell's Half	9	6,016	0.39	0.33	0.18	0.10
	Slide	1	496	0.44	0.28	0.18	0.10
	Lime	1 ¹	11,021	0.32	0.48	0.16	0.04
	Panther	3 ²	28,915	0.16	0.36	0.24	0.23

Note: Superscripts correspond to territories that initially burned in 1987 and were reburned in 2008.

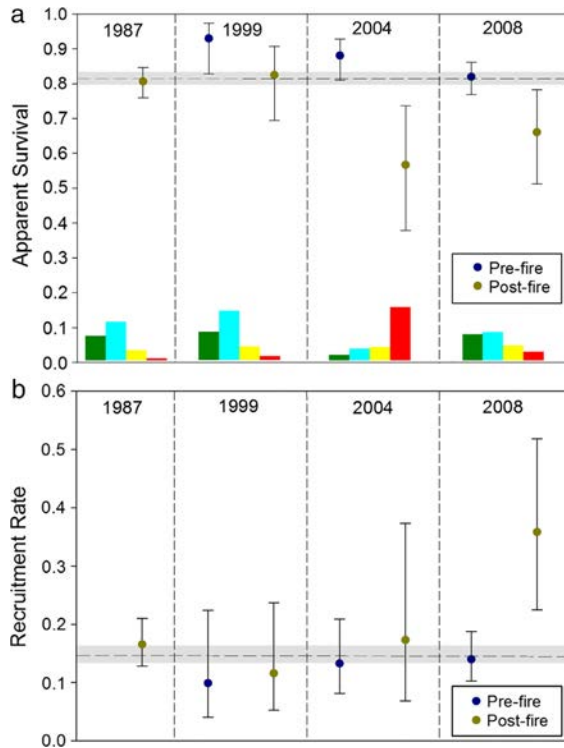


FIG. 2. Point estimates and their 95% confidence intervals of pre- and post-fire apparent survival (a) and recruitment rates (b) for the different fire groups. The point estimate and 95% confidence interval for the control group is shown in each graph as the dashed horizontal line and shaded bar. Bar graphs in Fig. 2a show the comparative amount of unburned (green), low (blue), moderate (yellow), and high (red) severity fire within the spotted owl territories for each group.

The increase in recruitment rates for owls affected by wildfire in 2008 suggested that immigration to these sites increased post-fire, which was partially responsible for maintaining occupancy on some of these territories.

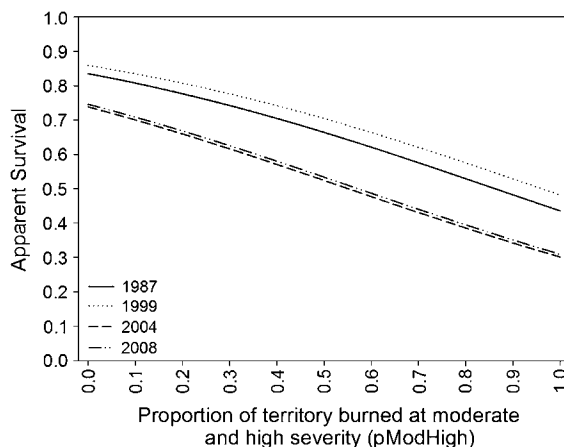


FIG. 3. Results from the top covariate model showing the influence of the combined proportion of moderate and high severity fire (pModHigh) on northern spotted owl apparent survival.

DISCUSSION

Wildfires on our study area occurred across different years, affected different territories and had different burn characteristics, which allowed us to implement a retrospective BACI mark-recapture analysis under a natural experimental design and incorporate covariates that characterized the extent and severity of each wildfire within spotted owl territories. Our results suggest that the degree to which northern spotted owls are influenced by wildfire is partially dependent on the characteristics of that wildfire. Wildfires with different mixtures of burn severity represented a continuum of effects where the predominantly lower severity fires in 1987 and 1999 were associated with minimal impacts on survival and recruitment, moderate to higher severity fires in 2008 were associated with a reduction in survival but allowed for increased recruitment, and the predominantly higher severity fire in 2004 was associated with a large reduction in survival with minimal effect on recruitment (Fig. 2). The 2004 Sims Fire (Table 1, Fig. 1a) was particularly severe, burning for 5 d during above-normal temperatures ($>38^{\circ}\text{C}$); conditions correlated with increased amounts of high severity fire (Agee 1993, Pettit and Naiman 2007, Perry et al. 2011). Nesting and roosting habitat of northern spotted owls is closely associated with mature and old-growth forests that include a multi-layered canopy, high canopy cover ($>70\%$), large amounts of coarse woody debris, and a high basal area of conifers (Forsman et al. 1984, Blakesley et al. 1992, LaHaye and Gutiérrez 1999). Thus, it is likely that post-fire habitat conditions become unsuitable for nesting and roosting by spotted owls following wildfires with large, extensive patches of high severity fire (e.g., 2004 Sims Fire; Jones et al. 2016). Although spotted owls may use high severity patches (Bond et al. 2009, 2016), there is likely a threshold level of high severity fire effects beyond which habitat suitability is appreciably reduced (Lee et al. 2013, Jones et al. 2016).

Following this gradient from lower to higher wildfire severities, the 2008 fires provided us with unique insight into the effects of wildfire on northern spotted owl population dynamics. Post-fire apparent survival of owls affected by wildfire in 2008 decreased (Fig. 2a), while post-fire recruitment rates increased (Fig. 2b) which effectively compensated for the lower survival and created a situation in which territories remained mostly occupied, but with higher turnover. Increased turnover in these territories suggests that habitat quality was reduced post-fire, resulting in marginal habitat that was only capable of supporting owls temporarily before they either emigrated or died (e.g., Redpath 1995, Winker et al. 1995). Thus, the effects of wildfires on wildlife populations goes beyond the individual, territory-scale effects and may also depend on the surrounding landscape (Franklin et al. 2002), particularly in a region such as the Klamath Province where mixed-severity fire creates a patchwork of seral stages and habitat quality. The

resulting landscape may therefore be comprised of some areas with suitable habitat conditions for spotted owls and a sufficient number of individuals to provide new recruits (sources) to areas that burned more severely and are marginally capable of supporting individuals (sinks; Pulliam 1988).

This concept is supported by previous research on our study area (Franklin et al. 2000) on spotted owl habitat quality where it was found that spotted owls occupied a continuum of habitats that range from low to high quality with high quality territories acting as sources and low quality territories acting as sinks. If moderate and high severity fire in 2008 reduced the amount of older forest, a key component of nesting and roosting habitat for spotted owls, source territories could become sink territories that are being supported by immigration of individuals dispersing from nearby areas of higher quality habitat (e.g., areas that experienced less high severity fire; Pulliam 1988, Franklin et al. 2000).

Optimal habitat for northern spotted owls in the Klamath Province appears to be composed of a mosaic of late seral stages for nesting and roosting (conditions that are maintained by low severity fire) with smaller, early seral stages (conditions created by high severity fire) where the owl's primary prey species, the dusky-footed woodrat (*Neotoma fuscipes*), is more abundant (Sakai and Noon 1993, Ward et al. 1998). Thus, it appears that northern spotted owls inhabiting the Klamath Province have capitalized on this seral stage patchwork created by the dominant disturbance regime of the region (mixed-severity wildfire) by nesting and roosting in areas that experienced low severity fire, and foraging across all seral stages including early seral stages created by high severity fire where woodrats become more abundant (Sakai and Noon 1993, 1997, Ward et al. 1998, see Bond et al. 2009).

Patterns of mixed-severity fire in the Klamath Province are influenced by complex interactions between the region's topography, climate, and fuels. The result is a dynamic patchwork of seral stages, but one in which some generalities can be made. Topography and climate were historically the two major determinants of fire severity in the region and have been relatively stable during the recent past, helping to enforce a pattern wherein north and east slopes are usually dominated by lower severity wildfire and south and west slopes generally experience higher severity fire (Taylor and Skinner 1998). Similarly, because of their relatively high fuel moisture content, riparian areas tend to dampen the spread of fires (Pettit and Naiman 2007). However, during periods of extreme fire weather, these regulating mechanisms can break down resulting in large patches of high severity fire which can be detrimental to spotted owls (Jones et al. 2016). Summers in the Pacific Northwest are predicted to become longer, hotter and drier; conditions that are correlated with increased fire activity in the West (Wimberly and Liu 2014, Westerling 2016). Thus, a changing disturbance regime in which

wildfires increase in extent and intensity suggests the long-term persistence of viable northern spotted owl populations may be compromised (Johnstone et al. 2016), especially when combined with multiple recent stressors, such as habitat removal due to logging and increased competition from the recent invasion of non-native barred owls.

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SUPPORTING INFORMATION

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Habitat selection by spotted owls after a megafire in Yosemite National park

Lynn N. Schofield^{a,*}, Stephanie A. Eyes^{b,c}, Rodney B. Siegel^a, Sarah L. Stock^b

^a The Institute for Bird Populations, PO Box 1346, Point Reyes Station, CA 94956, United States

^b Yosemite National Park, 5083 Foresta Road, El Portal, CA 95318, United States

^c U.S. Fish and Wildlife Service, 2800 Cottage Way, Room W-2605, Sacramento, CA 95825, United States¹



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ABSTRACT

As fires in the western United States have become larger and more severe over recent decades, understanding how the changing fire regime affects wildlife has become a key issue for conservation. Spotted owls (*Strix occidentalis*) associate with late-successional forest characteristics and therefore may be particularly sensitive to structural changes in habitat that result from fire. Previous studies have found varying responses of the owls to forest fire. We investigated the effects of the 2013 Rim Fire on territory selection by California spotted owls within Yosemite National Park, which, unlike the surrounding landscape, has been managed with no commercial logging since the early 1900s and minimal fire suppression since the 1970s. We examined specific habitat characteristics associated with spotted owl presence before and after the fire to understand how fire-induced changes in habitat structure may influence spotted owl territory selection. Spotted owls persisted and nested within the fire perimeter throughout the four post-fire years of our study at rates similar to what we observed in areas of Yosemite that were unaffected by the fire. However, within the fire perimeter, spotted owls avoided areas characterized by > 30% percent high severity fire. Prior to the fire, spotted owls selected for areas of high canopy cover relative to the rest of the landscape; after the fire, even though territory centers shifted substantially from pre-fire locations, pre-fire canopy cover remained a stronger predictor of spotted owl presence than post-fire canopy cover, or any other pre- or post-fire habitat variables we assessed. The importance of pre-fire forest structure in predicting owl presence after fire suggests that reported variation in spotted owl population response to different fires across the Sierra Nevada may in part reflect variation in pre-fire forest characteristics, and perhaps different forest management regimes that shaped those characteristics. Pre-fire forest characteristics may impart a legacy of post-fire habitat conditions important to owls that commonly used forest and fire metrics do not effectively describe. Further study of owl response to fire in forests with a broader spectrum of pre-fire forest structure and management regimes is needed to better predict and manage effects of the changing fire regime on spotted owls.

1. Introduction

Spotted owls (*Strix occidentalis*) are often considered vulnerable to habitat disturbances like stand-altering fire (Ganey et al., 2017), although their sensitivity to such disturbance may not be as severe as once assumed (Seamans and Gutiérrez, 2007; Gutiérrez et al., 2017). Spotted owls generally favor late seral forests (Gutiérrez et al., 1995, 2017), but the California subspecies (*S. o. occidentalis*) evolved in a landscape that was frequently disturbed by wildfire (Caprio and Swetnam, 1995; Scholl and Taylor, 2010). The historic fire regime under which California spotted owls evolved was characterized by a short fire return interval and fires that burned large areas at low severities, interspersed with small areas of higher severity in a relatively

heterogeneous mosaic (Jeronimo et al., 2019). Driven in large part by climate change (Miller et al., 2009b; Diffenbaugh et al., 2015; Holden et al., 2018) and a century of fire suppression (Arno et al., 2000; Calkin et al., 2005; Scholl and Taylor, 2010; Stephens et al., 2014), this type of heterogeneous mixed-severity wildfire has become less common across California spotted owls' range while large, more homogenous fires with extensive areas of high severity burn have become more common (Arno et al., 2000; Miller et al., 2009b; Miller and Safford, 2012; Westerling, 2016; Stevens et al., 2017), including so-called 'megafires' that burn > 10,000 ha at high severity (Stephens et al., 2014). Megafires are anticipated to dramatically alter existing habitat during the coming decades (Miller et al., 2009b; Stephens et al., 2016; Wan et al., 2019). Increasing prevalence of large, high severity fire has been identified as

* Corresponding author.

E-mail address: lschofield@birdpop.org (L.N. Schofield).

¹ Present address.

one of the most important conservation threats for spotted owls (USDA Forest Service, 2019), making understanding how and why fire affects the owls critically important for their conservation.

The impact of fire on forested landscapes is often characterized by classifying the burned area into discrete areas of low, moderate, and high severity using the relative differenced normalized burn ratio (RdNBR; a measurement based on satellite imagery taken before and after a fire), calibrated by the composite burn index (CBI; a measurement based on direct observations of changes in vegetation at individual plots) (Miller and Thode, 2007; Miller et al., 2009b; Morgan et al., 2014). These burn severity metrics are useful because they succinctly describe fire severity by integrating multiple kinds of information about fire-induced vegetation changes (Miller et al., 2009a), but this integration introduces challenges in identifying the specific effects of fire on habitat that contribute most to changes in occupancy by wildlife species like spotted owls. Morgan et al., (2014) therefore suggested that, in addition to composite indices, assessments of fire effects on habitat should also individually address relevant habitat attributes changed by the fire that are encompassed by composite metrics.

Spotted owls' response to habitat disturbance may depend on numerous inter-related factors including the cause, severity, frequency, relative size, and spatial configuration of the disturbance (Jones et al., 2016; Collins et al., 2017; Ganey et al., 2017). Low to moderate severity fire may only minimally affect California spotted owl occupancy and productivity (Lee, 2018), because the density of large, tall trees and extent of high canopy cover are often not substantially reduced unless fire burns at high severity (Bias and Gutiérrez, 1992; North et al., 2017). Moderate understory burns may even enhance foraging opportunities for spotted owls (Bond et al., 2010; Ganey et al., 2017). The response of spotted owls to high severity fire appears to vary among fires (Ganey et al., 2017; Lee, 2018; Jones et al., 2019). For example, within the King Fire, which burned nearly 395 km² in the central Sierra Nevada in 2014, nesting spotted owl numbers were significantly reduced during the early post-fire years and owls were not observed at all within the extensive areas of high severity fire (Jones et al., 2016). When tracked via GPS, persisting owls were found to continue to avoid large patches of high severity burn several years after the fire (Jones et al., 2019). In contrast, spotted owls were observed even within high severity burned areas in the year immediately after the 2013 Rim Fire in the Stanislaus National Forest (Lee and Bond, 2015). What proportion of those detections represent true occupancy by territorial individuals is unknown (Berigan et al., 2019).

Differences in spotted owl persistence and territory selection after different fires likely arise from differences in the characteristics of each fire and the pre-fire landscape that it burned (Jones et al., 2020). Jones et al. (2020) found that spotted owls favored areas of high severity when high severity patches represented only a small portion of their total territory (< 5%), but avoided areas of high severity when a larger overall portion of their territory was burned at high severity. Fire size and overall severity may be relatively poor predictors of a fire's effects on spotted owls (Lee, 2018), whose response may also depend on factors such as the heterogeneity of the fire area, size and extent of stand-replacing burn patches, the structure and composition of the forest prior to the fire, or a combination thereof. Perhaps even fairly subtle or fine-scale variation in post-fire vegetation may allow or prevent owl persistence after fire.

The 2013 Rim Fire was the largest forest fire on record in the Sierra Nevada and burned over 1041 km² across the Stanislaus National Forest, private lands within the perimeter of the Stanislaus National Forest, and Yosemite National Park (Lydersen et al., 2017). Yosemite, which includes about 1/3 of the area burned by the Rim Fire (316 km²), provides an opportunity to investigate effects of pre-fire and post-fire forest conditions on post-fire spotted owl occurrence in the context of an extensive area of contiguous suitable spotted owl habitat that approximates the historic Sierra Nevada ecosystem (Jerónimo et al., 2019). The park has been managed distinctly from adjacent National

Forests and private lands, with no commercial logging since the early 1900s and minimal fire suppression since the 1970s (Miller et al., 2012; Kane et al., 2013; Jerónimo et al., 2019). The park's fire management plan emphasizes the "restoration of fire to its natural role in park ecosystems" as being among the higher priorities (Martin, 2009), and this is being achieved through a combination of managed wildfire and prescribed burning. Within the park, naturally occurring fires are allowed to burn to achieve management goals if they do not threaten developed, populated, or culturally important areas (Martin, 2009).

This strategy resulted in the Rim Fire creating a landscape with a more heterogeneous mosaic of mixed severity burn than the adjacent Stanislaus National Forest (Lydersen et al., 2017). In fact, within Yosemite National Park, the Rim Fire yielded a landscape that is considered to represent a restored fire regime that resembles the forest structure and composition found in the Sierra Nevada prior to European settlement (Miller et al., 2012; Jerónimo et al., 2019). This is the only area in the Sierra Nevada that has been identified as being returned to historic conditions (Jerónimo et al., 2019) and it provides a unique opportunity to examine how wildlife species respond to forest fires when they are within the conditions they initially evolved with.

We anticipated that owls would persist within the perimeter of the Rim Fire in Yosemite, as they did in the western portion of the fire footprint on Stanislaus National Forest (Lee and Bond 2015), and perhaps fare even better given the restored fire regime in our study area as suggested by Kramer et al. (in press). We sought to understand how habitat selection changed between the pre-and post-fire eras within this restored system. Spotted owls in low quality habitat or after reproductive failure often disperse to higher-quality habitat (Zimmerman et al., 2003; Blakesley et al., 2006); therefore, we expected that after the fire, spotted owl territories within the Rim Fire perimeter in Yosemite would shift to the best available post-fire habitat, which we predicted would be areas with the least severe fire effects and/or the greatest retention of pre-fire habitat characteristics known to be important to the owls, including canopy height, canopy cover, and overall vegetation greenness as measured by the Normalized Difference Vegetation Index (NDVI; Seamans and Gutiérrez, 2007; Gutiérrez et al., 2017; North et al., 2017; Tempel et al., 2017). We further hypothesized that habitat characteristics in territories found before or after the fire would be distinguishable from the surrounding landscape, but that the differences would be greater after the fire, when more of the habitat would likely have been rendered less suitable.

2. Methods

2.1. Study area

We studied California spotted owls within Yosemite National Park in the central Sierra Nevada of California. The study area comprised all areas within the park that met minimum characteristics of appropriate spotted owl habitat (Gutiérrez et al., 2017; Tempel et al., 2017; USDA Forest Service, 2019; Fig. 1) prior to the 2013 Rim Fire. We considered appropriate spotted owl habitat to be areas of montane forest below 2500 m in elevation with canopy cover $\geq 40\%$ and dominant trees > 28 cm diameter at breast height (USDA Forest Service, 2019). We assessed these characteristics using data from the California Department of Forestry and Fire Protection's CALFIRE Fire and Resource Assessment Program (Vegetation fveg, FRAP 2015; <https://frap.fire.ca.gov/>). Using these criteria for suitable habitat, we found the Rim Fire to have affected 210 km² of the 717 km² (29%) of the total available spotted owl habitat in the park.

2.2. Field methods

We surveyed spotted owl territories in Yosemite National Park between 2015 and 2017 (hereafter referred to as the 'recent era') to determine post-fire occupancy and reproductive status. Surveys were

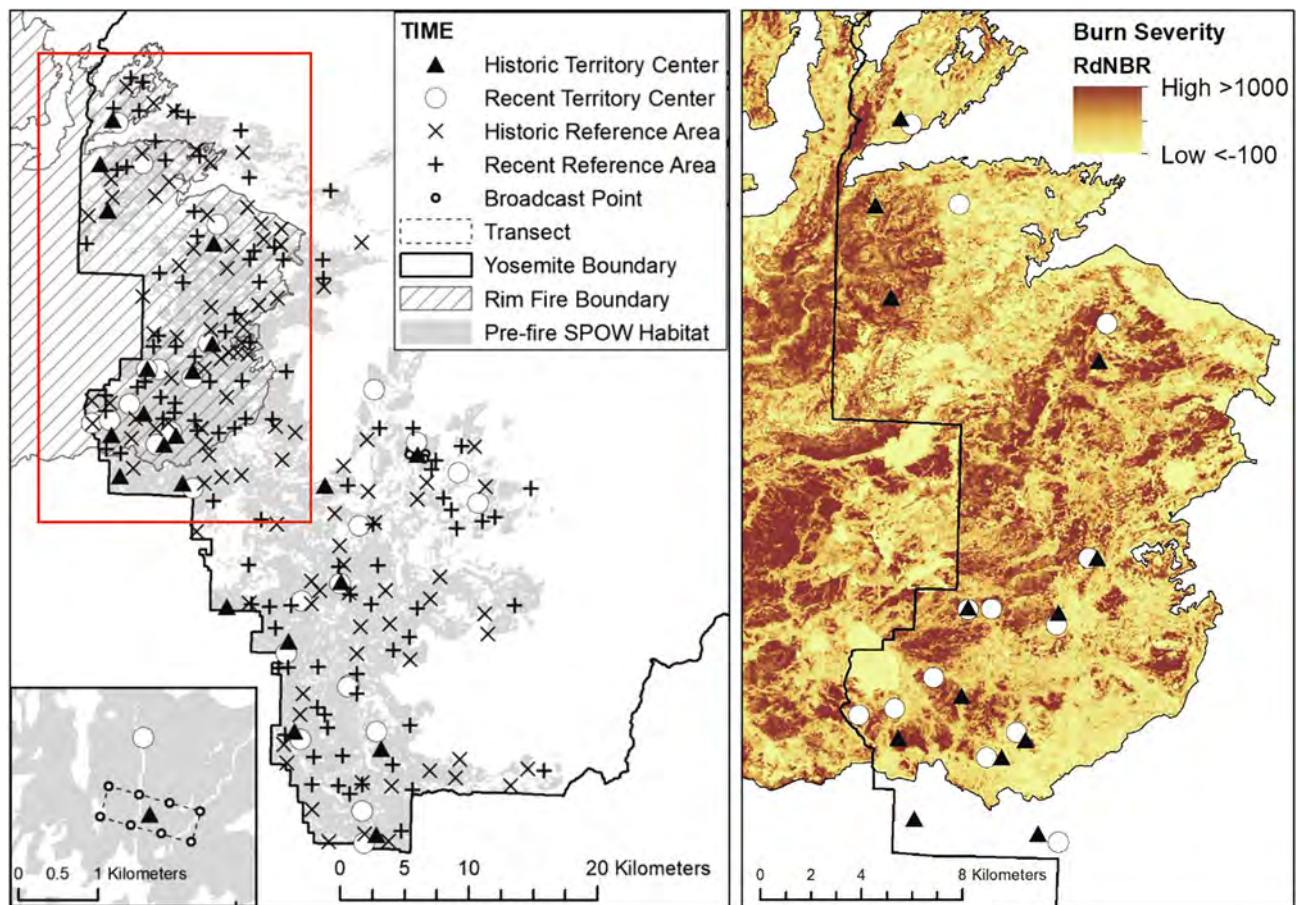


Fig. 1. Left: Locations of historical spotted owl territory centers (triangles; occupied prior to the 2013 Rim Fire), recent spotted owl territories (circles; occupied after the Rim Fire), and randomly generated reference points (crosses and pluses) in Yosemite National Park (Inset: an example of a transect surrounding a historical territory center where broadcast surveys were conducted after the fire). Gray shading indicates appropriate spotted owl habitat prior to the fire, based on the presence of montane forest with > 40% canopy cover and a diameter at breast height > 28 cm. Right: Magnified view of fire severity (RdNBR) across the Rim Fire study area in Yosemite National Park; symbols are as indicated in left panel.

conducted at the location of 36 historical spotted owl territories made between 2004 and 2013 (hereafter referred to as the ‘historical era’) by USGS and NPS personnel either during formal, park-wide surveys or incidentally (Fig. 1; Roberts et al., 2011). Given their density, these historical territories likely represent a sizable proportion of spotted owls within the park. During both historical and recent survey efforts, surveyors used standard methods to find spotted owls, determine reproductive status, and identify nest and roost locations (Forsman, 1983; USFWS, 2012).

We conducted recent era surveys by broadcasting conspecific vocalizations along a 1200 m × 400 m rectangular transect centered on the historical territory center, which we defined as either the nest location or, if no nest had been found during the historical surveys, the most frequently used roost site. Each transect comprised eight call stations distributed at least 400 m apart (Fig. 1, inset). At each call station, we vocally imitated spotted owl vocalizations for 10 min to elicit a response from nearby owls. We visited each transect three times per year and surveyed all stations along each transect during each visit unless we detected an owl, at which point we stopped surveying that transect that year. All visits were conducted between April 1 and August 31 at least 10 days apart and two visits occurred before June 30 each year (USFWS, 2012). Broadcast surveys began no earlier than a half hour before dusk and ended no later than a half hour after dawn. If surveyors detected one or more spotted owls from a transect at any distance, we conducted an active follow-up survey either immediately after the detection or the following day, depending on conditions. We used follow-up surveys to locate owl nests, roosts, or young by walking

through the area of the response, vocally imitating the owl, listening for responses, and looking for owl sign (e.g. pellets, whitewash). If an owl was located, live prey was offered to confirm nesting status using established protocols (USFWS, 2012). If no nest was located during a follow-up survey, we repeated the follow-up protocol at least three more times that year. In subsequent years, transect surveys were re-initiated only if an owl could not be located using active searching methods within a previously identified territory.

2.3. Habitat characteristics

We assessed habitat conditions within a 700-m radius (153 ha) ‘core area’ centered on the nest or most used roost tree associated with each historical and recent territory. The core area is intended to approximate an area which a pair of spotted owls would actively defend from conspecifics (USDA Forest Service, 2019). The 700-m radius defined an average area consistent in size with previously reported areas defended by territorial California spotted owls (Bingham and Noon 1997; Roberts et al., 2017; USDA Forest Service, 2019). This distance is also consistent with the observed distance from California spotted owl nest sites where the canopy structure remains distinct from the surrounding forest (North et al., 2017). The resulting 153 ha circle also aligned closely with the minimum size of a California spotted owl protected activity center (PAC; typically at least 121 ha), established by the USDA Forest Service (Verner et al., 1992; Gutiérrez et al., 2017; USDA Forest Service, 2019), although PACs are not established within the National Park.

The 700-m radius core areas are not intended to represent the true

area of use, because areas of use are often complexly shaped, vary widely in size, and can only be inferred through intensive tracking efforts (Blakey et al., 2019). We did not attempt to exclude less favorable habitat surrounding the nests and roost sites from our core areas, as is done when delineating protected activity centers (PACs) for management purposes, because that would require making a priori assumptions about what is the most appropriate habitat. We assume that even if spotted owls do not spend a significant amount of time within some portion of the core area, forest characteristics in that core area still influence nest and roost site favorability and selection. Our core areas represent the habitat surrounding nest and roost sites, to yield insight into owl habitat preferences relevant to where they center their territories, without presuming to describe the entirety of their territory. When we detected one or more owls at night but never found an associated nest or roost tree during the day, we excluded the observation from analyses because we could not establish a center of a core area, as spotted owls regularly make forays of over 10 km from their territory centers during the breeding season which can create overestimates of occupancy (Berigan et al., 2019; Blakey et al., 2019).

To compare characteristics of historical and recent core areas with unoccupied habitat available across the landscape, we randomly selected reference areas (700-m radius circles) in appropriate but assumed unoccupied spotted owl habitat throughout Yosemite National Park for each era. A distinct set of 100 reference areas was selected for each era, as we wanted to ensure that the center of each reference area was > 700 m from any core area center in the corresponding era. We calculated the mean value for habitat characteristics at core and reference areas both before and after the Rim Fire (hereafter pre-fire and post-fire characteristics) using data derived from LANDSAT imagery. When spotted owls changed their territory center between years within an era but remained within the same core area (i.e. the center shifted < 700 m), we preferentially selected nest sites over roost sites to represent the territory center. In cases where the territory center changed between years and no nest site was identified in either year, we assessed habitat characteristics surrounding each year's territory center each year and averaged them to avoid pseudoreplication.

We assessed habitat within historical and recent core areas, both before and after the fire, by considering four characteristics: mean normalized difference vegetation index (NDVI), percent canopy cover, mean canopy height, and mean relative difference normalized burn ratio (RdNBR; assessed only for core areas within the fire perimeter). We chose these characteristics because they represent habitat features influenced by forest fire that are known to be important to spotted owls and were quantifiable from remotely sensed data available for the entirety of the study area from both before and after the Rim Fire. We chose RdNBR to quantify burn severity because it is designed to reduce bias in fire severity estimations caused by variation in pre-fire conditions and because it is more accurate than change in canopy cover at correctly classifying moderate severity burns (Miller and Thode, 2007; Miller et al., 2009a). We obtained canopy cover and canopy height from the USFS's LANDFIRE database (LANDFIRE 2018; <https://www.landfire.gov/>) and derived NDVI and RdNBR values using surface reflectance imagery data from LANDSAT (<https://www.usgs.gov/land-resources/nli/landsat>). All habitat metrics were calculated at a 30 × 30 m pixel resolution. To capture average breeding season conditions, we calculated NDVI as mean values from June 15 to July 15 from 2004 to 2006 for pre-fire conditions and in 2015–2017 for post-fire conditions. We quantified canopy cover and height, using LANDFIRE data from 2012 for pre-fire conditions and 2014 for post-fire conditions, as these values change negligibly over the timescale of this project except in response to stand-altering events such as the Rim Fire. After initial data collection, we ultimately excluded canopy height from further analysis because it was excessively correlated with canopy cover ($r^2 = 0.93$) and resulted in top-ranked models with excessive collinearity (variance inflation factor [VIF] > 10). AIC_c is able to handle correlated variables to some extent, but it has the potential to suffer from multicollinearity

and inflate the importance of a weakly influential variable when paired with a highly influential and correlated variable (Freckleton, 2011). For this reason, we still chose to include other correlated variables, but did so with caution. This includes three pairs of variables with correlation coefficients > 0.6: pre-fire NDVI and pre-fire canopy cover ($r^2 = 0.79$), post-fire NDVI and post-fire canopy cover ($r^2 = 0.73$), and pre-fire canopy cover and post-fire canopy cover ($r^2 = 0.65$). To assure that top-ranked models found through AIC_c did not inflate the importance of one or more variables, we assessed the variance inflation factor (VIF) to determine whether models created using these data displayed excessive multicollinearity from the inclusion of correlated variables.

2.4. Analytical methods

To verify our assumption that the Rim Fire created quantifiable landscape-level changes in the habitat characteristics of interest that did not occur in suitable spotted owl habitat in portions of Yosemite that were unaffected by the Rim Fire, we used Welch's *t*-tests to compare habitat change between the recent and historical reference areas within the Rim Fire with habitat changes at reference sites outside of the Rim Fire. We also used Welch's *t*-tests to compare changes in habitat before and after the Rim Fire at occupied core areas within and outside of the fire perimeter.

We used a chi-squared test to determine if the fire displaced owls by comparing the number of owl territories within the fire perimeter between recent and historical eras, relative to the number outside of the fire's perimeter during these periods. Because only a single nest/roost site was < 1500 m from the edge of the fire (at 429 m), we assume that all territory centers found within the fire perimeter are substantially influenced by the fire and those outside of the fire are not appreciably influenced by the fire even if owls could hypothetically move across that perimeter. We also used a chi-square test to assess whether the fire reduced the likelihood of breeding, by comparing the proportion of territories with confirmed nests within the fire perimeter between recent and historical eras. To determine if owl density in Yosemite was higher within or outside the Rim Fire perimeter, we compared the proportion of owl territories found in the fire perimeter with the proportion of potentially suitable habitat that was burned using a chi-squared test for both eras.

We used Welch's *t*-tests to ascertain whether the percent of high severity burn within recent occupied core areas in the fire perimeter differed from recent-era reference areas. We also used this test to compare the percent of historical core areas that burned at high severity with the historical-era reference areas.

We assessed the importance of additional separate variables indicative of the fire's effects on the landscape; pre- and post-fire canopy cover and NDVI, and mean burn severity as measured by RdNBR on spotted owl presence within the Rim Fire using logistic regression models in the 'stats' package in R (R Core Team, 2017). One additional variable we intended to include in the models, percent high severity burn, was excluded because, as a composite index, it was excessively multicollinear with the other variables considered and resulted in top models with a VIF of > 10. We retained mean burn severity rather than percent high severity burn within this analyses of individual variables because we address the role of percent high severity in the previous analysis and the inclusion of mean burn severity helps to answer the separate question of whether burn at other severities has an impact of Spotted Owl presence that is not otherwise addressed. We created three model sets, comparing historically occupied core areas with reference areas during the pre-fire era, recent core areas with reference areas during the post-fire era, and historical versus recent core areas during the era in which they were occupied. We determined which models differentiated these areas using Akaike's Information Criterion corrected for small sample size (AIC_c). All results are presented as mean ± standard deviation and considered significant at an α -level of

0.05. We calculated the variance inflation factor (VIF) for the top-ranked models if they included more than one covariate to assure that these models were not affected by excessive collinearity. We also compared single-variable models post-hoc when highly ranked models (with a delta $AIC_c < 2$) included these closely correlated variables to better assess whether the influence of one variable is similar to that of another correlated variable.

3. Results

We found 27 distinct territory centers during recent survey efforts, 12 (44%) of which were within the fire perimeter. This was similar to the share of historical territories (10 of 21 historical territories; 48%) that were found within the same area prior to the fire ($\chi^2 > 0.99$, $df = 1$, $p > 0.99$), indicating that the fire did not change the numbers of spotted owl nest and roost sites within its perimeter relative to the number in surrounding National Park land. The proportion of recent ($\chi^2 = 0.802$, $df = 1$, $p = 0.370$) and historical ($\chi^2 = 1.51$, $df = 1$, $p = 0.219$) spotted owl territories within the Rim Fire in both eras was greater than, but not statistically different from, the proportion of total spotted owl habitat in the park that was within the fire perimeter (20,787 ha of 71,708 ha across the park; 29%).

Across the whole park, nesting was confirmed at 13 historical and 16 recent territories at least once during the relevant survey period. The proportion of total nests within the Rim Fire did not significantly differ between historical (8/13, 62%) and recent (8/16, 50%) eras ($\chi^2 = 0.060$, $df = 1$, $p = 0.806$). Nearly all recent nests were found in 2017, with eight pairs found nesting within the Rim Fire perimeter and eight outside, although two of these nests were also found during the previous years of the study. One pair within the Rim Fire perimeter nested in both 2015 and 2016 and was the only pair confirmed to nest during those years within the park. For analyses, we treated those nests as being from the same territory, as they were located within 700 m of one another.

Pooling data from the entire park, historical and recent core areas were spatially distinct, with mean distance between recent territory centers and the nearest historical territory center > 2 km ($\bar{x} = 2001$ m, ± 1878 m). Recent territory centers within the Rim Fire were on average 1111 m (± 1058 m) from the nearest historical territory center; recent territory centers outside the fire perimeter averaged 2890 m (± 2086 m) from the nearest historical territory center. During the 2015–2017 survey period, territory centers identified as being part of the same core area (i.e. < 700 m apart) moved an average of 285 m (SD 217 m) between years.

Habitat measurements did not significantly differ between historical and recent core areas or historical and recent reference areas outside the fire perimeter, but within the perimeter both canopy cover and NDVI decreased significantly after the fire at core areas as well as reference areas (Table 1). We found no significant difference in RdNBR within the fire between recent core ($\bar{x} = 402.71$, ± 170.12) and reference areas ($\bar{x} = 368.83$, ± 217.03 ; $t = 0.65$, $df = 18$, $p = 0.53$).

Within the fire perimeter, the average percent of high severity fire within recent core areas ($\bar{x} = 10.1$, ± 11.3) was significantly less than in reference areas ($\bar{x} = 26.6$, ± 29.7 ; $t = 3.031$, $df = 54.70$, $p = 0.004$; Fig. 2), but mean values were similar in historical core areas ($\bar{x} = 32.6$, ± 34.5) versus reference areas ($\bar{x} = 26.8$, ± 28.3 ; $t = -0.5217$, $df = 13.41$, $p = 0.610$; Fig. 2). The maximum percent of high severity burn within recent core areas was 27.2 while the maximum within reference areas was 87.6.

Within the perimeter of the Rim Fire, the model that best differentiated historical core areas from reference areas included only pre-fire canopy cover (Table 2), which was significantly greater in historical core areas ($\bar{x} = 53.01$, ± 11.92) than reference areas ($\bar{x} = 39.87$, ± 14.9 ; estimate = -0.089 , SE = 0.037, $Z = -2.408$, $p = 0.016$; Fig. 3). All other variables except change in canopy cover were included in highly ranked models.

Table 1

Comparison of habitat characteristics within 700-m radius circles representing historical (2004–2014) and recent (2015–2017) spotted owl core areas and reference areas within and outside the perimeter of the 2013 Rim Fire in Yosemite National Park.

	Historical	Recent	<i>t</i>	<i>df</i>	<i>p</i>
Reference Areas Outside the Fire Perimeter					
Canopy Cover	43% $\pm$ 11%	44% $\pm$ 11%	−0.34	272	0.73
NDVI	0.55 $\pm$ 0.10	0.55 $\pm$ 0.08	−0.35	260	0.73
Reference Areas Within the Fire Perimeter					
Canopy Cover	44% $\pm$ 14%	33% $\pm$ 11%	6.84	208	< 0.0001
NDVI	0.57 $\pm$ 0.10	0.43 $\pm$ 0.07	12.22	199	< 0.0001
Core Areas Outside the Fire Perimeter					
Canopy Cover	52% $\pm$ 9%	48% $\pm$ 11%	1.04	22.08	0.31
NDVI	0.61 $\pm$ 0.09	0.58 $\pm$ 0.09	0.77	19.88	0.45
Core Areas Within the Fire Perimeter					
Canopy Cover	53% $\pm$ 12%	40% $\pm$ 9%	3.13	17.77	0.006
NDVI	0.62 $\pm$ 0.05	0.44 $\pm$ 0.06	8.11	21.622	< 0.0001

The model that best differentiated recent core areas from reference areas in the Rim Fire also included only pre-fire canopy cover (Table 3), with the pre-fire canopy cover having been significantly greater in recent core areas ($\bar{x} = 55.21$, ± 11.98) than reference areas ($\bar{x} = 43.55$, ± 12.38 ; estimate = -0.094 , SE = 0.037, $Z = -2.543$, $p = 0.001$; Fig. 3). Other top-ranked models included post-fire canopy cover, pre-fire NDVI, post-fire NDVI and change in NDVI. Change in canopy cover and mean RdNBR were not included in the top models for differentiating recent core areas from reference areas.

A null model was best differentiated recent and historical core areas, although post-fire canopy cover, change in canopy cover, and mean RdNBR were also selected in high ranking models (Table 4).

4. Discussion

In Yosemite National Park, the Rim Fire burned nearly 1/3 of potential spotted owl habitat, significantly lowering the affected area's mean NDVI and canopy cover, two variables reported to be strongly associated with spotted owl occupancy and habitat quality in other studies (Carroll, 1998; Seamans and Gutiérrez, 2007; Garcia-Feced et al., 2011; Gutiérrez et al., 2017; North et al., 2017; Tempel et al., 2017). However, spotted owl numbers did not change appreciably after the fire. Although nesting rates appeared quite low in 2015 and 2016, they were relatively high in 2017 and were generally comparable to nesting rates in areas of the park unaffected by the fire across all 3 years.

Multiple studies have reported spotted owls persisting after forest fires, even in areas with substantial high severity fire effects (Lee and Bond, 2015; Stephens et al., 2016; Rockweit et al., 2017; Lee, 2018), although the occupancy estimates of these studies may be inflated (Berigan et al., 2019). In other instances, even where similar methodologies were used, owls appear to have been largely displaced by fire (Jones et al., 2016, 2019; Ganey et al., 2017; Rockweit et al., 2017). Jones et al. (2016) observed the local spotted owl population to decline dramatically immediately after the 2014 King Fire in Eldorado National Forest in California, and to continue avoiding patches burned at high severity in subsequent years (Jones et al., 2019).

Spotted owls in our study area persisted and nested after the Rim Fire in numbers similar to before the fire, even though canopy cover and NDVI were lower in modern core areas within the Rim Fire perimeter than they were in historical core areas in the fire's perimeter. Although the owls were apparently robust to declines in those metrics of habitat suitability, we found that the percent of high severity burn within postfire core areas and reference areas was significantly different. All of the postfire core areas had less than 30% of the area burned at high severity. This is consistent with the findings of a GPS tracking study conducted in Yosemite that found that spotted owls were

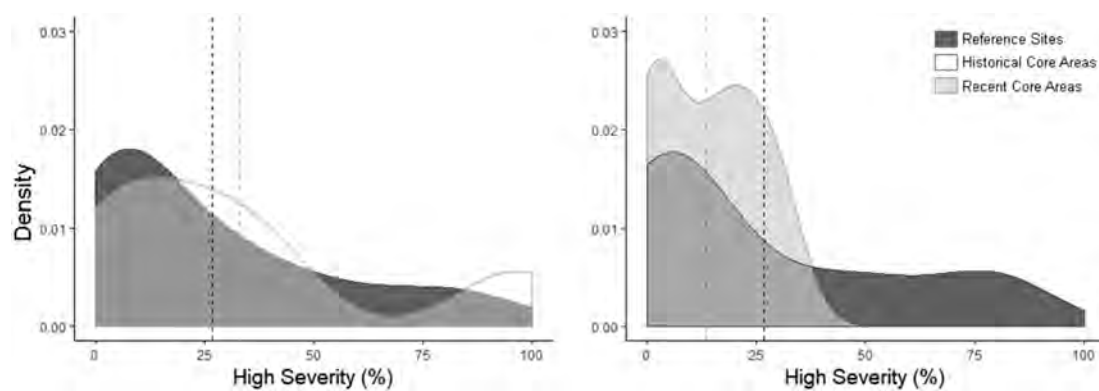


Fig. 2. Comparison of percent area burned at high severity in historical (white) and recent (light gray) spotted owl core areas, and reference sites (dark gray) within the perimeter of the 2013 Rim Fire in Yosemite National Park. Dotted lines represent the mean values of each variable for reference and core areas.

Table 2

Top ranked models (delta AICc < 2) for differentiating historical spotted owl core area from reference areas within the Rim Fire perimeter.

Model	df	logLik	AICc	delta	Wt
Pre-fire Canopy Cover	2	-24.016	52.3	0	0.170
Pre-fire NDVI	2	-24.840	53.9	1.65	0.075
Post-fire Canopy Cover + Mean RdNBR	3	-23.777	54.0	1.75	0.071
Pre-fire Canopy Cover + Post-fire NDVI	3	-23.816	54.1	1.83	0.068
Pre-fire Canopy Cover + Mean RdNBR	3	-23.816	54.2	1.94	0.064
Pre-fire Canopy Cover + Pre-fire NDVI	3	-23.873	54.2	1.98	0.063

neither selecting for nor avoiding areas of high severity burn except in the case where patches of high severity burn was extensive (Kramer et al., in press).

Despite the overall differences in population-level effects on owls between the Rim and King fires, our finding of an apparent threshold of tolerable high severity burn at the scale of the core area within the Rim fire is consistent with findings from the King Fire. Jones et al. (2016) reported that the percent of area burned at high severity by that fire was strongly related to local extinction probability, which was near zero at low percentages of high severity burn, but was extremely high where > 50% of the spotted owl core area burned at high severity. Owls at both fires thus appear to have been displaced from areas where high severity burn was extensive.

Owls in our study, however, appeared to have a lower threshold for high severity burn within their territories than has been found elsewhere. Jones et al. (2016) reported owls occupying territories with up to 50% of the area burned at high severity within the King Fire, and Lee and Bond (2015) observed owls within activity centers with 100% of the area burned at high severity within portions of the Rim Fire on Stanislaus National Forest. However, it is unclear whether observations within these extensive areas of high severity represent occupancy by territorial individuals rather than transient birds (Berigan et al., 2019).

The avoidance of areas with > 30% high severity burn we observed does not necessarily demonstrate that the owls cannot persist in such conditions, but it indicates that Spotted Owls preferentially selected area with less high severity fire when they are available. The King Fire and the portion of the Rim Fire that burned on the Stanislaus National Forest are characterized by notably more extensive, homogeneous areas of high severity burn than what we observed in Yosemite National Park (Kane et al., 2015; Jones et al., 2016; Povak et al., 2019). These homogenous landscapes likely offered fewer options to owls that may have otherwise preferred to shift their territories to encompass less high severity burn.

We further suspect that the spatial distribution of high severity burn, rather than just the total proportion of an area burned at high severity, may affect owls' predilection or ability to persist in burned landscapes. Despite differences in the size of high severity patches

found between the Yosemite and Stanislaus portions of the Rim Fire, the overall percentage of the Rim Fire area burned at high severity was relatively similar between those portions of the Rim Fire (27% and 32% respectively). Within occupied core areas we assessed, the mean burn severity was similar to that within reference areas, even as the proportion of high severity burn differed.

Our results are less consistent with findings from an analysis of post-fire spotted owl persistence across six Sierra Nevada fires (Lee et al., 2012). In that study, an average of 32% of suitable habitat within spotted owl territories burned at high severity, yet rates of colonization and local extinction of established territories and activity centers were not significantly different from those at unburned sites. Spotted owls in that study did not appear to move their territories in response to fire. Heterogeneity in owls' response to the extent of high severity fire between our study area and the six fires studied by Lee et al. suggests that additional habitat variables may be important in mediating the consequences of high severity fire on owl persistence. Although the differences may also be influenced by methodological differences as Lee et al. included spotted owl detections that could have represented transient owls whereas we only included birds found at confirmed nest and roost sites (Berigan et al., 2019).

The variable we examined, especially canopy cover, effectively differentiate historical spotted owl territories from historical reference areas in our study area. However, our prediction that spotted owls remaining in the Rim Fire perimeter would relocate their territory centers to areas with lower mean burn severity and higher available canopy cover and NDVI than the burned landscape at large was partially incorrect.

Spotted owl core areas shifted substantially from historical sites after the Rim Fire, but except for avoidance of areas with > 30% high severity fire effects, we found little distinction between recent territories and the surrounding landscape. Indeed, pre-fire habitat characteristics better predicted spotted owls' post-fire habitat selection patterns, and recent spotted owl core areas were best differentiated from reference areas by their pre-fire canopy cover. Aside from burning with a greater overall percentage of high severity, the habitat characteristics of recent core areas were also not distinct from the characteristics of historical core areas. That is to say, the pre-fire conditions of recent territories matched the pre-fire conditions of historical territories, and post-fire conditions of recent territories matched the post-fire condition of historical territories. The locations of historical and recent territories also experienced a similar mean burn severity. The recent spotted owl core areas in our study were better predicted by pre-fire habitat characteristics than by the habitat characteristics present at the time of occupancy after the fire. Spotted owls actively select productive habitat and, given that spotted owls were nesting up to four years after the fire, it seems reasonable to assume that the habitat they selected was indeed favorable, but it remains unclear why pre-fire

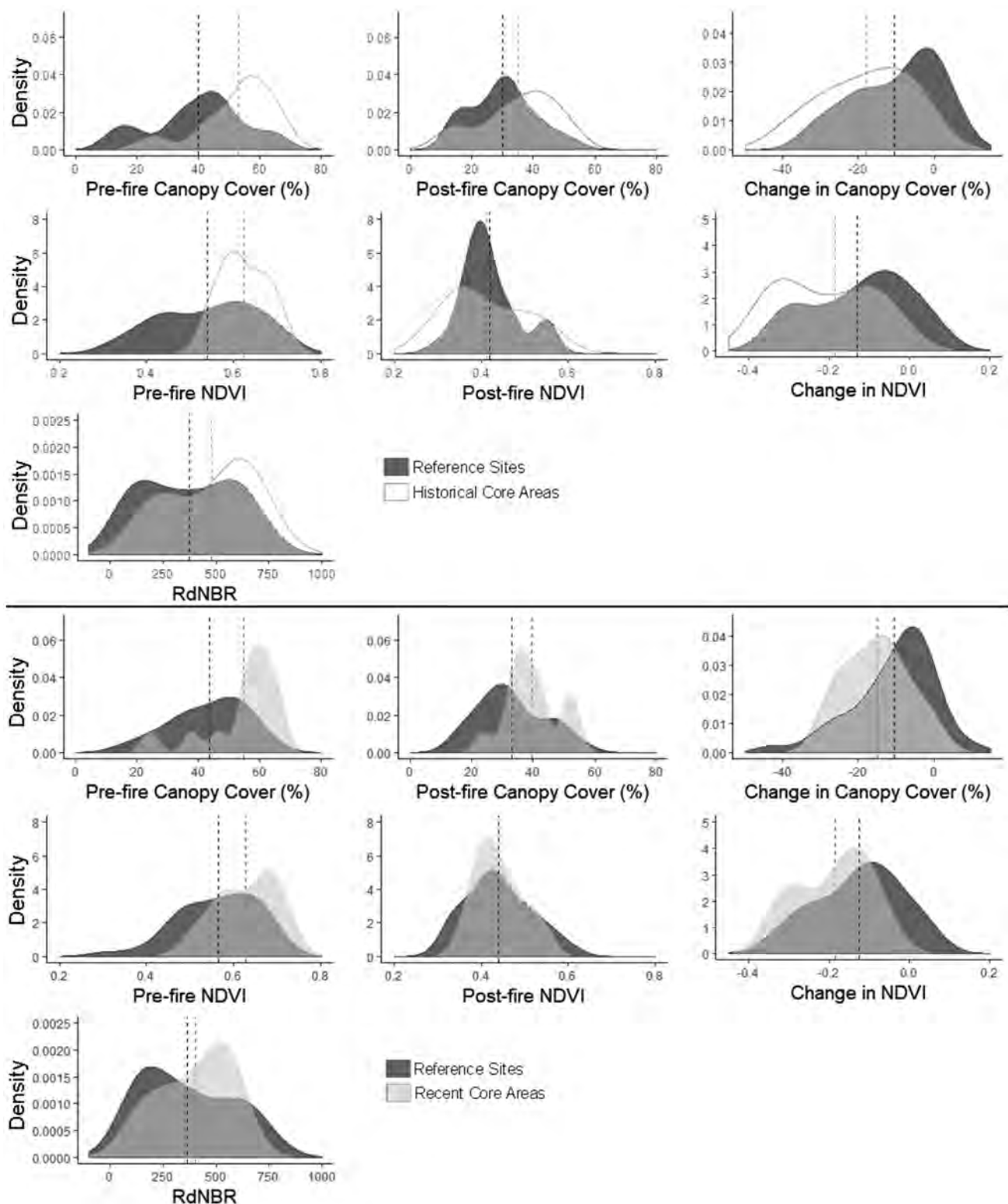


Fig. 3. Comparison of habitat characteristics between historical (white) and recent (light gray) spotted owl core areas and reference sites (dark gray; a distinct set of reference sites was evaluated for each era) within the perimeter of the 2013 Rim Fire in Yosemite National Park. Dotted lines represent the mean values of each variable for reference and core areas.

conditions were more strongly associated with post-fire owl presence than post-fire canopy cover or NDVI.

Forest structure influences how fire affects the landscape (Agee, 1996). Povak et al. (2019) found that the characteristics of the Rim Fire were influenced by the landscape's history and variability in forest

structure prior to the fire. The differences in pre-fire forest structure we observed between occupied core areas and reference areas prior to the fire may have resulted in different post-fire conditions that were not quantified by the available satellite data. A complex suite of factors including, but not limited to, forest management, previous fire history,

Table 3

Top ranked models (delta AICc < 2) for differentiating recent spotted owl core areas from reference areas within the Rim Fire perimeter.

Model	df	logLik	AICc	delta	Wt
Pre-fire Canopy Cover	2	−25.667	55.6	0.00	0.167
Post-fire Canopy Cover Post-fire NDVI	3	−25.111	56.7	1.13	0.095
Pre-fire Canopy Cover + Post-fire NDVI	3	−23.726	57.5	1.98	0.062

Table 4

Top ranked models (delta AICc < 2) for differentiating historical versus recent spotted owl territories within the Rim Fire perimeter.

Model	df	logLik	AICc	delta	wt
Null	1	−16.552	35.3	0.00	0.196
Post-fire Canopy Cover	2	−15.950	36.5	1.18	0.108
Mean RdNBR	2	−16.058	36.7	1.40	0.097
Post-fire NDVI	2	−16.084	36.7	1.45	0.095

topography, tree species composition and geophysical characteristics can all contribute to forest structure, and many of these features may play some role in habitat selection by Spotted Owls after fire. Although spotted owls in the recent era would not have direct knowledge of conditions prior to the fire, the habitat characteristics measured prior to the fire may be related to some hold-over effect caused by pre-fire conditions. For example, high pre-fire canopy cover could be linked to availability of remnant stands of large trees that could continue to provide suitable nest and roost sites after a fire. Pre-fire conditions may also play a role in future prey abundance. Pre-fire conditions influence how a forest regenerates after a fire (Agee, 1996; Broncano and Retana, 2004; Beaty and Taylor, 2007; Crotteau et al., 2013; Young et al., 2019), so perhaps spotted owls prefer certain early-stage characteristics in disturbed habitats. More comprehensive habitat data such as park-wide LiDAR data will be valuable in identifying which habitat features drive post-fire habitat selection.

Regardless of the exact mechanism, if pre-fire conditions are strongly predictive of spotted owl nest and roost site selection after a fire, pre-fire forest management also seems likely to affect spotted owls' response to fire. Indeed, differences in pre-fire management may be related to spotted owls' heterogeneous response to forest fires. Within Yosemite, minimal fire suppression for many decades and prohibitions on logging for over a century have created a landscape characterized by larger areas of forest with old growth characteristics (Collins et al., 2011; Miller et al., 2012; Jeronimo et al., 2019) and more structural diversity than what is currently found across much of the California spotted owl's range (Jeronimo et al., 2019). To the extent that the largely restored fire regime approximates historical conditions (Jeronimo et al., 2019), the Rim Fire in Yosemite may suggest how spotted owls historically responded to forest fires. Yosemite's post-fire landscape likely provides spotted owls different opportunities when selecting territories than are available in burned areas outside of the park. A better understanding of how pre-fire forest management and pre-fire forest conditions influence spotted owl response to fire will require assessing owl response to pre- and post-fire forest conditions across a broader range of forest landscapes with differing pre-fire management regimes. Doing so may help to resolve enduring questions about the implications of changing fire regimes on California spotted owls.

CRedit authorship contribution statement

Lynn N. Schofield: Conceptualization, Formal analysis, Data curation, Writing - original draft, Visualization. **Stephanie A. Eyes:** Conceptualization, Methodology, Investigation, Data curation, Writing - review & editing, Supervision. **Rodney B. Siegel:** Conceptualization,

Writing - original draft, Project administration, Funding acquisition. **Sarah L. Stock:** Conceptualization, Methodology, Resources, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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HABITAT SELECTION IN A CHANGING ENVIRONMENT: THE RELATIONSHIP BETWEEN HABITAT ALTERATION AND SPOTTED OWL TERRITORY OCCUPANCY AND BREEDING DISPERSAL

Author(s): MARK E. SEAMANS and R.J. GUTIÉRREZ

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HABITAT SELECTION IN A CHANGING ENVIRONMENT: THE RELATIONSHIP BETWEEN HABITAT ALTERATION AND SPOTTED OWL TERRITORY OCCUPANCY AND BREEDING DISPERSAL

MARK E. SEAMANS AND R. J. GUTIÉRREZ¹

Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, 1980 Folwell Avenue, St. Paul, MN 55108

Abstract. Understanding the effect of habitat alteration on avian behavior is important for understanding a species' ecology and ensuring its conservation. Therefore, we examined the relationship between Spotted Owl habitat selection and variation in habitat in the Sierra Nevada. We estimated habitat selection by modeling the probability of territory colonization (γ), territory extinction (ϵ), and breeding dispersal in relation to the amount of mature conifer forest within and among territories. Alteration of ≥ 20 ha of mature conifer forest (coniferous forest with $>70\%$ canopy cover dominated by medium [30.4–60.9 cm dbh] and large [>60.9 cm dbh] trees) within individual territories ($n = 66$) was negatively related to territory colonization and positively related to breeding dispersal probability. Although territory extinction was negatively related to the amount of mature conifer forest, it was not clear whether this relationship was due to variation of mature conifer forest within or among territories. Although modeling results for territory colonization and extinction generally supported the hypothesis that individuals are "ideal" when selecting a habitat in the sense that they settle in the highest-quality site available, we did not find a clear benefit in terms of habitat quality for Spotted Owls that exhibited breeding dispersal.

Key words: breeding dispersal, habitat alteration, habitat selection, occupancy, Spotted Owl, *Strix occidentalis*.

Selección de Hábitat en un Ambiente Cambiante: Relación entre la Alteración del Hábitat y la Ocupación de Territorios y la Dispersión Reproductiva en *Strix occidentalis*

Resumen. Entender el efecto de la alteración del hábitat sobre el comportamiento de las aves es importante para comprender la ecología de una especie y asegurar su conservación. Por lo tanto, examinamos la relación entre la selección de hábitat por parte de *Strix occidentalis* y la variación en el hábitat en la Sierra Nevada. Estimamos la selección de hábitat modelando la probabilidad de colonización de un territorio (γ), de extinción de un territorio (ϵ) y de dispersarse para reproducirse en relación con la cantidad de bosque de coníferas maduro dentro de y entre los territorios. La alteración de 20 o más hectáreas de bosque de coníferas maduro (bosque de coníferas con más del 70% de la cobertura del dosel dominada por árboles medianos [30.4–60.9 cm de DAP] y grandes [>60.9 cm de DAP]) dentro de territorios individuales ($n = 66$) se relacionó negativamente con la colonización de los territorios y positivamente con la probabilidad de dispersarse para reproducirse. Aunque la extinción de los territorios se relacionó negativamente con la cantidad de bosque de coníferas maduro, no es claro si esta relación se debió a la variación en el bosque de coníferas maduro dentro de los territorios o entre territorios. Aunque los resultados del modelado de colonización y extinción de los territorios en general apoyaron la hipótesis de que los individuos son "ideales" al seleccionar el hábitat en el sentido en que se establecen en los sitios disponibles de mayor calidad, no encontramos un beneficio claro en términos de la calidad de hábitat para los individuos que se dispersaron para reproducirse.

INTRODUCTION

The effect of habitat alteration on avian habitat choice is a key issue for conservation (Stamps

2001). If birds choose habitats to increase their fitness (Fretwell and Lucas 1969), habitat alteration, both before and after habitat selection has occurred, has the potential to affect population dynamics, particularly if the alteration affects a large area. The consequence of habitat alteration is especially relevant for territorial species that exhibit limited breeding dispersal (individuals switching territories be-

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¹ Corresponding author. E-mail: gutie012@umn.edu

tween breeding attempts). Breeding dispersal is likely an adaptive trait although it is thought to occur infrequently in many species (Greenwood and Harvey 1982). Inbreeding avoidance, mate choice, site choice, or social constraints have all been hypothesized to influence breeding dispersal (Greenwood 1980, Greenwood and Harvey 1982, Dobson and Jones 1985, Payne and Payne 1993). Breeding dispersal that is motivated by habitat alteration could be viewed as adaptive in terms of site choice.

The Spotted Owl (*Strix occidentalis*) is a territorial species that has high site fidelity (Gutiérrez et al. 1995, Blakesley et al. 2006). Most habitat studies have indicated that Spotted Owls preferentially select areas of mature coniferous forest (Forsman et al. 1984, Verner et al. 1992, Chatfield 2005), and that this habitat type influences their population dynamics (Franklin et al. 2000, Olson et al. 2004, Seamans 2005). Because mature coniferous forests in the western United States are prized for lumber production and are also highly susceptible to stand-replacing wildfire, alteration of this habitat type is believed to pose a threat to the owl's long-term viability (U.S. Department of Interior 1990, 1993, Verner et al. 1992). Although the alteration of mature forest is believed to have long-term negative consequences for Spotted Owls, there have been few empirical studies that have attempted to quantify how variation in the amount of mature forest may affect territory occupancy.

In this paper we examine the relationship between the amount of mature conifer forest, alteration of mature conifer forest, and Spotted Owl territory occupancy and breeding dispersal over a 15-year period. We use the term "habitat alteration" because we are not sure that all habitat changes in forest structure can be considered "habitat loss." Thus, habitat alteration represents a change from mature conifer forest to some other forest cover type by logging or wildfire. Ideally, a true experiment (i.e., random allocation of replicated experimental units to treatments) should be used to estimate cause and effect relationships between habitat alteration and Spotted Owl population processes. However, designing and executing true experiments has proven difficult because of constraints involved with endangered species management and because the scale of potential

treatments poses significant logistical challenges. Therefore, we used a combination of quasi-experimental (Cook and Campbell 1979) and observational approaches. We accepted treatment units (Spotted Owl territories) as they occurred and recorded observations of forest alteration, territory occupancy, and individual movement among territories over time. Valid inference from this approach required controlling for the confounding effect of variation in the amount of mature conifer forest among Spotted Owl territories. Because of the difficulty in controlling for this confounding effect, and because of the overall study design, we did not infer cause and effect relationships from our results. Rather, our goal was to evaluate whether: (1) alteration of mature conifer forest was correlated with immediate, short-term territory colonization probability (probability of an unoccupied territory becoming occupied), extinction probability (probability of an occupied territory becoming unoccupied), or breeding dispersal probability; (2) alteration of mature conifer forest was correlated with long-term territory colonization or extinction probability; and (3) territory colonization or extinction probability, or breeding dispersal, was related to variation in the amount of mature conifer forest among territories. We sought to increase our knowledge of the relationships between habitat alteration and Spotted Owl habitat choice. Further, our results can be used to identify specific habitat types that should be targeted by experimental studies whose goal is to test the effect of habitat alteration on Spotted Owls.

METHODS

STUDY AREA

Our 925 km² study area was located in the central Sierra Nevada, California, between the North and South Forks of the American River (Seamans et al. 2001). Within this area, we surveyed owls in a 355 km² "density study area" from 1990 to 2004. We surveyed the density study area completely for Spotted Owls each year regardless of land ownership or past occupancy by owls. In 1997 we established a "regional study area," which surrounded the density study area. The regional study area consisted of previously known owl territories and territories that were located from 1997 to

1999. Areas between owl territories in the regional study area were not completely surveyed.

The Sierra Nevada was the dominant physical feature of the area. The study area was typical of the midelevation Sierra Nevada, with mountainous terrain bisected by steep river canyons. Elevations ranged from 366 to 2401 m. Climate was Mediterranean, with cool wet winters and hot dry summers (Olson and Helms 1996). Sierran mixed conifer forest was the principal vegetation type (Sierra Nevada Ecosystem Project 1996) and was dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), and Douglas-fir (*Pseudotsuga menziesii*) in the canopy and black oak (*Quercus kelloggii*), tanoak (*Lithocarpus densiflora*), and big leaf maple (*Acer macrophyllum*) in the understory. Red fir forest was less abundant but common at higher elevations, and montane manzanita chaparral, black oak woodland, and barren rock were less abundant but locally important vegetation or landscape features (Sierra Nevada Ecosystem Project 1996).

DATA COLLECTION

Spotted Owl surveys. We surveyed Spotted Owls from 1 April to 28 August of each year from 1990 to 2004, following methods described by Franklin et al. (1996). We used two types of surveys: (1) nighttime surveys to initially locate owls in an area; and (2) daytime surveys to locate roosts and nests, and to capture, band, and assess the reproductive status of owls. Nighttime surveys consisted of imitating Spotted Owl vocalizations between dusk and dawn at established survey locations and listening for a response. Survey locations were consistent from year to year and were placed to obtain complete survey coverage of the density study area and each Spotted Owl territory in the regional study area. There were 5–12 survey points for each Spotted Owl territory, depending on the topography of the territory. A complete survey for a territory was achieved when we imitated owl territorial calls at all survey points within a territory over a four-day period without receiving a response. We conducted up to six surveys at each Spotted Owl territory to determine owl presence.

If an owl responded during a nighttime survey we conducted a daytime survey within

four days of receiving the response. We counted a nighttime survey with a response and the subsequent daytime survey as only one survey for the purpose of modeling occupancy (see below). We attempted to capture and band all Spotted Owls detected using the methods of Franklin et al. (1996). Once captured, we fitted owls with a U.S. Fish and Wildlife Service locking aluminum band on the tarsometatarsus of one leg. On the other leg we marked individuals ≥ 1 year old with a unique color-band and tab combination. We determined the sex of owls based on the pitch of their calls and their behavior (Forsman et al. 1984). We identified four age-classes based on plumage characteristics (Forsman 1981, Moen et al. 1991): juvenile; one-year-old (first-year subadult); two-year-old (second-year subadult); and ≥ 3 years old (adult).

Habitat metrics. Using a combination of aerial photographs, digital-orthophoto-quarter quadrangles, and extensive ground sampling we created a forest cover map with eight vegetation cover types for the entire density study area and a vegetation cover type map for each regional study area owl territory (Chatfield 2005, Seamans 2005). We defined vegetation cover types based on the dominant vegetation structure (tree diameter at breast height [dbh; measured 1.4 m above the forest floor on the uphill side of the tree] and canopy cover). Because Seamans (2005) estimated that the area of coniferous forest with $>70\%$ canopy cover dominated by medium (30.4–60.9 cm dbh) or large (>60.9 cm dbh) trees was the best predictor of demographic parameters for owls in our study population, we chose to examine only the effect of alteration of this vegetation type. Hereafter, we refer to this vegetation type as “mature conifer forest.” Minimum polygon size for mapping was 0.1 ha. Map accuracy for mature conifer forest was 91% (Chatfield 2005).

We estimated the total amount of each of the eight cover types within a 400 ha circle in each owl territory using the spatial analyst extension in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California). This area was based on a circle with a radius of 1128 m, which was half the mean nearest neighbor distance of occupied territories in the density study area averaged over the years 1990 to 2002. We determined the center of the circle for each territory by estimating the geometric

center of all owl locations from each year the territory was occupied. The area encompassed by this circle was approximately one-quarter to one-half of the estimated home range size for Spotted Owls in the central Sierra Nevada (Laymon 1988, Call et al. 1992). Although we did not know if the entire 400 ha area was used by owls, the circles did encompass all nests and >90% of all roosts in each territory. We used the term "territory" to depict the spatial location and area for which we estimated habitat metrics because: (1) owls responded to conspecific calls from these areas during surveys; (2) the 400 ha we used for analyses contained all known nest locations of owls responding in that area; and (3) all areas surrounding the nest were vocally defended by owls during daytime surveys.

We used aerial photographs (a complete set was created approximately every four years of study) to determine the location and extent of habitat alteration. We estimated the year of timber harvest based on: (1) our own field notes; (2) USDA Forest Service harvest records; (3) University of California Berkeley Blodgett Experimental Forest harvest records; and (4) core samples of trees. We used an increment borer to extract complete cores of ≥ 4 trees immediately adjacent to a clear-cut or within a forest stand that had been thinned. We then estimated the year of harvest by locating a sustained increase in widths of tree rings, indicating reduced competition from other trees.

STATISTICAL ANALYSES

Territory occupancy. For female Spotted Owls, we estimated territory colonization (γ) and extinction (ϵ) probabilities (vital rates of territory occupancy) following MacKenzie et al. (2003). Territory colonization probability is the probability that a territory unoccupied in year $t - 1$ becomes occupied in year t , and territory extinction probability is the probability that a territory occupied in year $t - 1$ is unoccupied in year t . The probability of occupancy (ψ) in year t can be calculated from γ , ϵ , and ψ_{t-1} (MacKenzie et al. 2003) by:

$$\psi_t = \psi_{t-1}(1 - \epsilon_{t-1}) + (1 - \psi_{t-1})\gamma_{t-1}.$$

We modeled occupancy vital rates for females only because the most appropriate method for coding data of single male versus

single female responses from surveys was not clear. Modeling females only was a good indication of pair occupancy of a territory because unpaired females were rare during our study (we located only two females in 15 years that may have been unpaired during a year). Each territory was surveyed up to six times each year for 15 years.

We estimated γ and ϵ using program MARK (White and Burnham 1999). In addition to γ and ϵ , the analytical approach we used directly estimated the proportion of territories occupied in the first year of study. We accounted for imperfect detectability of owls while modeling γ and ϵ . We examined the following temporal structures for detection probability within and among years: constant (means model); linear trend; log-linear trend; and quadratic trend. We fitted a model for each combination of these temporal structures within and among years and ranked models using Akaike's information criterion (AIC; Burnham and Anderson 1998). We used the top-ranked detection probability structure for inference regarding the effect of habitat alteration on γ and ϵ .

We created three statistical models to examine the relationship between mature conifer forest and γ and ϵ . For all models we predicted that: (1) increasing amounts of mature conifer forest would be positively related to γ and negatively related to ϵ ; and (2) alteration of mature conifer forest would be negatively related to γ and positively related to ϵ . The first model included a time-varying individual covariate that depicted the amount of mature conifer forest in each territory each year. For the second model we used a categorical treatment effect with two levels, no alteration of mature conifer forest versus >0 ha mature conifer forest altered, to estimate if alteration of mature conifer forest affected territory extinction or colonization probability the subsequent year. The treatment effect for this model occurred regardless of the amount of mature conifer forest altered. Lastly, we created a third model that hypothesized that the amount of mature conifer forest altered in an individual territory had a long-term effect on colonization and extinction probability. This latter model was essentially an interrupted time series model and included a continuous variable that depicted the total area of mature conifer forest in each territory at the beginning of the

study, and a nominal variable with three levels that depicted the size of treatment: no mature forest altered, between 0 and 20 ha altered, or ≥ 20 ha altered. Unlike the second model above, we coded the categorical treatment variable to carry the effect forward in time. For example, if a territory had 30 ha of mature forest altered in 1992, the model was coded to examine a ≥ 20 ha treatment effect on γ and ε for this territory from 1993 to 2004. Our use of a 20 ha cutoff for the treatment level was arbitrary. We also examined variations of this latter model that included the starting amount of mature forest and a nominal variable with two treatment levels (< 20 ha versus ≥ 20 ha), and an interaction between the starting area of mature forest and the categorical treatment effect. We ranked the plausibility of these competing models using AIC_c (AIC corrected for small sample size) and examined the 95% confidence intervals around the model coefficients to determine whether γ or ε was related to the area of mature conifer forest or categorical treatment effect. For analysis of γ and ε we divided the covariate depicting the total area of mature conifer forest in a territory by 260 to aid numerical optimization. Model coefficients presented in results are based on this transformation.

Breeding dispersal. Before examining the effect of habitat alteration on breeding dispersal, we first examined the probability of breeding dispersal as a function of owl sex, age, social status, and breeding status with the same approach used by Blakesley et al. (2006) in a study of Spotted Owls in the northern Sierra Nevada. We defined breeding dispersal probability as the probability that an individual moved to a different territory between year t and year $t + 1$. We created a dataset comprised of uniquely marked individuals and their dispersal histories. Each observation in the dataset consisted of a two-year period for one individual, whether the individual dispersed (switched territories) between years, and the U.S. Fish and Wildlife Service band number for the individual. We coded the binomial response as "0" for no dispersal and "1" for dispersal. We considered owl sex, age (first-year subadult, second-year subadult, or adult) during year 1, reproductive status during year 1 (successfully produced young or not), and social status (unpaired, paired, or paired but apparent death

of mate during the interval) as factors that might explain variability in dispersal probability. We also considered an interaction term between individual sex and breeding status. We analyzed data using a logistic regression (PROC GENMOD in program SAS release 8.02; SAS Institute Inc., Cary, North Carolina) and considered all possible subsets of factors. We ranked models based on their ability to explain variation in dispersal probability using QAIC (AIC corrected for overdispersion; Burnham and Anderson 1998). We calculated overdispersion of the data as χ^2 divided by the degrees of freedom. We calculated the Pearson χ^2 value using the "AGGREGATE" option of the GENMOD procedure and specified age, sex, social status, and breeding status as subpopulations.

Unlike Blakesley et al. (2006), we did not include a factor depicting territory quality in the all possible subsets modeling of dispersal probability. Instead, we included the variables in the top-ranked model from the all possible subsets regression and constructed two statistical models that were similar to the two treatment models we constructed for γ and ε : (1) a model with a categorical treatment effect with two levels, no alteration of mature conifer forest versus alteration of mature conifer forest; and (2) a model that included a continuous variable that depicted the total area of mature conifer forest in each territory during year 1, and a nominal variable with three levels that depicted the size of treatment (no mature conifer forest altered, between 0 and 20 ha altered, or ≥ 20 ha altered). We also considered variations of this latter model that included only two categorical levels of treatment (< 20 ha versus ≥ 20 ha) and an interaction term between the amount of mature conifer forest in year 1 and treatment level. For the two treatment effect models we used a repeated measures approach with generalized estimating equations (Liang and Zeger 1986) to determine if habitat modification was related to dispersal probability. Observations were repeated on individuals (i.e., the blocking factor was the individual owl) and we determined statistical significance using the 95% CI for the regression parameters.

We compared the quality of the original territory with that of the new territory for owls that dispersed. We estimated the quality of

individual territories based on their expected survival. We calculated expected survival ($E(\phi)$) following Seamans (2005) using the equation:

$$E(\hat{\phi}) = \{ \exp[1.5886 + 0.0420(\text{SEX}) + 1.5938(\text{COR57}) - 1.5602(\text{LAMT1}) - 1.2481(\text{LAMT23})] \} \div \{ 1 + \exp[1.5886 + 0.0420(\text{SEX}) + 1.5938(\text{COR57}) - 1.5602(\text{LAMT1}) - 1.2481(\text{LAMT23})] \}^{-1},$$

where SEX was a dummy variable coded 0 for females and 1 for males, COR57 was the amount (ha) of interior mature forest, LAMT1 was the natural log of the amount of hardwood forest, and LAMT23 was the natural log of the amount of pole, sapling, and brush cover types. Habitat covariates were transformed before estimation of the above equation to improve numerical optimization by dividing COR57 and AMT1 by 160, and AMT23 by 350. This model explained 93% of the variability in survival among territories (Seamans 2005). We did not consider reproduction when estimating habitat quality because the relationship between reproductive success and habitat was unclear for this population (Seamans 2005).

RESULTS

TERRITORY OCCUPANCY

We located and monitored Spotted Owls in 66 territories in our study areas from 1990 to 2004. Detection probability was constant among years, followed a log-linear trend within years, and varied between the density and regional study areas (Fig. 1). The area of mature conifer forest in individual territories ranged from 0 to 257 ha among years. Thirty-eight territories (58%) experienced some habitat alteration during our study. Habitat alteration in two territories was the result of stand-replacing wildfire while habitat alteration in all others was the result of timber harvest.

The probability of territory colonization (γ) and extinction (ϵ) was related to the area of mature conifer forest in a territory and alteration of this habitat (Table 1). The top three colonization models had essentially the same AIC_c weight (w_i), suggesting a high degree of model selection uncertainty. However, the only

model coefficient (β) with a confidence interval that did not include zero was the categorical effect of alteration of ≥ 20 ha mature conifer forest (gt20). The top model included the amount of mature conifer forest in a territory at the beginning of the study (1990) and the alteration of ≥ 20 ha of mature conifer forest. Alteration of ≥ 20 ha of mature conifer forest was negatively related to γ ; $\hat{\beta}_{\text{gt20}} = -1.16$ (95% CI = -2.02 to -0.29). The beginning amount of mature conifer forest (BMF) in a territory was positively related to γ , but had a confidence interval that included zero; $\hat{\beta}_{\text{BMF}} = 1.34$ (95% CI = -0.70 to 3.39). The top model, $\gamma(\text{BMF} + \text{gt20})$, indicated that territories in which ≥ 20 ha of mature conifer forest was altered experienced a 2.5% decline in occupancy probability.

The top territory extinction model ($\epsilon[\text{CMF}]$; Table 1) suggested that ϵ was negatively related to the amount of mature conifer forest in a territory ($\hat{\beta}_{\text{CMF}} = -2.58$, 95% CI = -4.48 to -0.68). "CMF" was a time-varying individual covariate depicting the amount of mature conifer forest in a territory. Model $\epsilon(\text{CMF})$ was four times as plausible as the second-ranked model; therefore, we chose to use model $\epsilon(\text{CMF})$ for inference. The structure of this model precluded us from separating the confounding effect of habitat alteration within territories versus variation in the amount of mature conifer forest among territories. However, if we assume that differences in mature

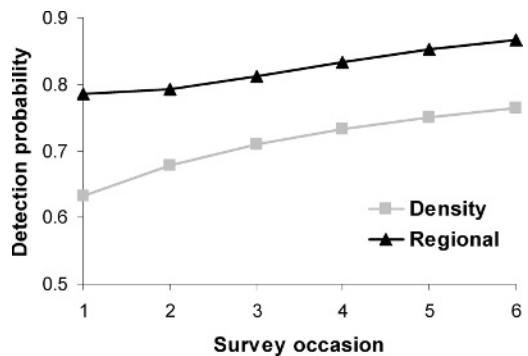


FIGURE 1. Female Spotted Owl within-year detection probability used to model territory colonization and extinction probability in the "density" and "regional" study areas in the central Sierra Nevada, 1990–2004. Each year we surveyed the complete density study area for Spotted Owls, whereas we did not survey areas between owl territories in the regional study area.

TABLE 1. Ranking of models (95% confidence set) depicting the relationship between the amount of mature conifer forest present and altered at individual territories and Spotted Owl territory colonization and extinction probability ($n = 66$ territories), and Spotted Owl breeding dispersal probability ($n = 565$), in the central Sierra Nevada, 1990–2004. Ranking of colonization and extinction models based on Akaike’s information criterion corrected for small sample size (AIC_c), while ranking of breeding dispersal models based on AIC corrected for overdispersion (QAIC). $\text{Log}(\mathcal{L})$ is the log-likelihood, K is the number of parameters, ΔAIC_c is the difference in Akaike’s information criterion from the top model, and w_i is the model weight.

Model ^a	$-2\text{log}(\mathcal{L})$	K	ΔAIC_c^b	w_i
Territory colonization probability (γ)				
$\gamma(\text{BMF} + \text{gt}20)$	3364.84	9	0.00	0.26
$\gamma(\text{BMF} + \text{gt}20 + \text{BMF}*\text{gt}20)$	3362.79	10	0.01	0.26
$\gamma(\text{BMF} + \text{ltgt}20)$	3362.87	10	0.09	0.25
$\gamma(\text{BMF} + \text{ltgt}20 + \text{BMF}*\text{ltgt}20)$	3360.53	12	1.87	0.10
$\gamma(\text{CMF})$	3369.65	8	2.77	0.07
Territory extinction probability (ϵ)				
$\epsilon(\text{CMF})$	3363.84	8	0.00	0.68
$\epsilon(\text{BMF} + \text{ltgt}20)$	3362.55	10	2.81	0.17
$\epsilon(\text{BMF} + \text{gt}20)$	3366.69	9	4.90	0.06
$\epsilon(\text{BMF} + \text{ltgt}20 + \text{BMF}*\text{ltgt}20)$	3361.39	12	5.77	0.04
Breeding dispersal probability (d) ^c				
$d(\text{BMF} + \text{gt}20 + \text{BMF}*\text{gt}20)$	274.83	9	0.00	0.56
$d(\text{BMF} + \text{ltgt}20 + \text{BMF}*\text{ltgt}20)$	273.69	11	2.86	0.14
$d(\text{BMF} + \text{gt}20)$	279.95	8	3.12	0.12
$d(\text{gt}0)$	283.13	7	4.30	0.07
$d(.)$	285.31	6	4.48	0.06

^a Abbreviations for model parameters: BMF = individual covariate representing amount of mature conifer forest at beginning of study; CMF = time-varying individual covariate representing amount of mature conifer forest; gt20 = categorical treatment effect for mature conifer forest of <20 ha or ≥ 20 ha; ltgt20 = categorical treatment effect for mature conifer forest of 0 ha, >0 and <20 ha, or ≥ 20 ha; gt0 = categorical treatment effect of mature conifer forest of 0 ha or >0 ha.

^b AIC_c of top colonization model = 3383.07 and of top extinction model = 3385.84; QAIC of top breeding dispersal model = 292.83.

^c All breeding dispersal models included the variables Age (age of owl: 1, 2, or ≥ 3 years old); Reproduction (did owl fledge young the previous year); and Social (a combination of pair status and mate loss).

conifer forest among territories caused the variation in territory extinction probability, model $\epsilon(\text{CMF})$ suggested that occupancy probability increased approximately 1.1% for every 20 ha difference in the amount of mature conifer forest among territories.

BREEDING DISPERSAL

We observed 51 incidences of breeding dispersal among 565 owl-years (i.e., total dispersal opportunities of 159 owls in 15 years of study). Overall, 33 females switched territories (of which 12 were single or had lost their mate), while 18 males switched territories (of which 10 were single or had lost their mate). Overdispersion in the dataset was slight ($\hat{c} = 1.15$). Results from the all possible subsets modeling suggested that owl age, sex, and social status best described variation in the probability of

breeding dispersal. The only two competing models (≤ 4 $QAIC_c$ units from top model) included these same three variables plus: (1) reproductive status (repro) in the previous year; and (2) the interaction of reproductive status in the previous year and owl sex. However, model coefficients for these additional variables had confidence intervals that significantly overlapped zero ($\hat{\beta}_{\text{repro}} = -0.19$, 95% CI = -0.57 to 0.17 ; $\hat{\beta}_{\text{sex} \times \text{repro}} = 0.10$, 95% CI = -0.28 to 0.53). Therefore, we chose to use a model with owl age, sex, and social status for further inference.

The probability of breeding dispersal (d) was related to the area of mature conifer forest in a territory and alteration of this habitat (Table 1). The top-ranked model, $d(\text{BMF} + \text{gt}20 + \text{BMF}*\text{gt}20)$, suggested that d was negatively related to the area of mature conifer

TABLE 2. Parameter estimates from the top-ranked logistic regression model examining breeding dispersal probability of California Spotted Owls in the central Sierra Nevada, 1990–2004.

Parameter	Estimate	CI
Intercept	6.42	2.55 to 10.30
Age class (S1)	1.08	0.09 to 2.08
Age class (S2)	1.68	0.79 to 2.57
Sex (F)	1.00	0.24 to 1.75
Social status (Pair)	−1.30	−2.04 to −0.57
Social status (Single)	1.85	0.54 to 3.16
BMF ^a	−0.55	−0.90 to −0.20
gt20 ^b (0)	−8.61	−12.29 to −4.94
BMF*gt20 (0)	0.53	0.19 to 0.88

^a BMF = individual covariate representing amount of mature conifer forest in territory in year prior to potential or actual dispersal; transformed for analysis by dividing raw numbers by 10.

^b Categorical treatment effect for mature conifer forest coded “0” for <20 ha or “1” for ≥20 ha.

forest in a territory just prior to actual or potential dispersal, and positively related to alteration of ≥20 ha of mature conifer forest. Confidence intervals for model coefficients representing mature conifer forest and alteration of ≥20 ha of mature conifer forest did not overlap zero (Table 2). The interaction term suggested a steep increase in d in territories with <150 ha of mature conifer forest that experienced alteration of ≥20 ha of this forest type (Fig. 2). This steep increase in d was disproportional in comparison to territories with lesser amounts of this forest type that did not experience habitat alteration. For example, an individual in a territory with 100 ha of mature conifer forest (median = 99 ha for our study population) in which ≥20 ha were altered was estimated to have a much higher d than an individual in a territory that started with 80 ha yet had no mature conifer forest altered. For owl-specific variables in the top model, d was: (1) 0.09 times higher for first-year subadults than adults and 0.14 times higher for second-year subadults than adults; (2) 0.08 times higher for females; and (3) 0.11 times less for owls that were paired and did not lose their mates than for owls that were paired but lost their mates, and 0.15 times higher for unpaired owls than for paired owls who lost their mates.

Owls that switched territories apparently did not select new territories based on higher quality; only 53% of owls that switched territories moved to a territory with higher

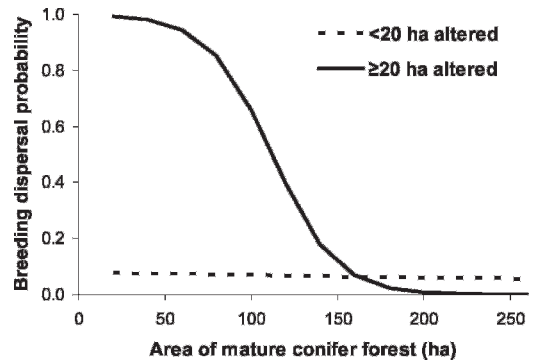


FIGURE 2. The relationship between paired female Spotted Owl breeding dispersal probability and the amount of mature conifer forest in a territory in the central Sierra Nevada, from 1990 to 2004. Dispersal probability increased rapidly at territories with <150 ha of mature conifer forest when ≥20 ha of this habitat type was altered. The x-axis represents the amount of mature conifer forest prior to actual or potential dispersal. The dashed and solid lines represent predicted dispersal probability when <20 ha or ≥20 ha of mature conifer forest were altered, respectively.

expected survival. We estimated that approximately 6% (three of 51) of owls that dispersed were unpaired after they switched territories, compared to 5% (51 of 1092) of all owls during the study. However, in the year prior to dispersal, 45% (23 of 51) of owls that switched territories were either unpaired or had lost their mate. We observed 14 breeding dispersal events in which one or both pair members switched territories and both formed a pair with a new mate.

DISCUSSION

We found that the amount of mature conifer forest was correlated with Spotted Owl habitat choice. Territories with more mature conifer forest had a higher probability of being colonized and a lower probability of becoming unoccupied. Further, alteration of mature conifer forest appeared to decrease the probability of colonization. Although we estimated that breeding dispersal was more likely when habitat alteration occurred, it was not clear if this increase or changes in other demographic processes were responsible for variability in territory extinction probability. For example, because Spotted Owl survival is correlated with the area of mature conifer forest in individual

territories (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005, Seamans 2005), it is possible that habitat alteration affected survival, which in turn increased the probability of a territory becoming unoccupied. Conversely, it is possible that habitat alteration did not result in decreased survival but in increased emigration from the study population. In a related study, Olson et al. (2005) estimated that Spotted Owl occupancy declined 5%–15% in three study areas ($n = 125$ to 146 sites) when Barred Owl (*Strix varia*) presence increased, and noted that these declines could have been the result of either death or emigration.

Our use of a categorical variable to depict the amount of habitat altered allowed us to examine the relationship between alteration of mature conifer forest and Spotted Owl habitat selection. However, our use of broad categories may not have adequately represented the effect of very large or very small changes in mature conifer forest. For example, alteration of 20 ha of mature conifer forest was considered the same as alteration of 80 ha. Although this range within the categorical habitat variables likely made detecting statistical relationships more difficult, creating more detailed categories would have resulted in small sample sizes within categories. Thus, the inference that territory extinction was not related to alteration of mature conifer forest because a categorical treatment variable was not in the top model should be made with caution. In addition, the broad range of values in the categorical variable may be partially responsible for the steep increase in dispersal probability in territories with <150 ha of mature conifer forest.

Our estimate of Spotted Owl breeding dispersal probability (9%) is similar to estimates by Forsman et al. (2002; 7%) and Blakesley et al. (2006; 7%) for other Spotted Owl populations. The relationship between breeding dispersal probability and age, sex, and social status appears to be consistent for Spotted Owls. Similar to our study, Forsman et al. (2002) and Blakesley et al. (2006) estimated that younger owls were more likely to disperse than older owls, females were more likely to disperse than males, and unpaired owls were more likely to disperse than paired owls. However, Forsman et al. (2002) and Blakesley et al. (2006) also estimated that owls that nested during the previous year were less likely to disperse than

owls that did not nest, whereas the effect of reproductive status in the previous year was poorly supported in our analysis. Prior to our study, the effect of habitat alteration on dispersal probability had not been examined in depth for the Spotted Owl, although Bond et al. (2002) examined Spotted Owl territory fidelity after wildfire and found that 11% (two of 18) of Spotted Owls switched territories the year after wildfire.

Breeding dispersal is an important life history trait that has likely evolved to increase individual fitness (Greenwood and Harvey 1982). Although the mechanisms behind the evolution of breeding dispersal are unclear, it is generally agreed that breeding dispersal can have significant effects on individual fitness and population dynamics (Greenwood and Harvey 1982, Clobert et al. 2001). Most theoretical models either predict or assume that dispersing individuals should be “ideal” when selecting a habitat, in the sense that they should settle in the highest-quality site available (Fretwell and Lucas 1969, Pulliam and Danielson 1991). Our results regarding the effect of habitat alteration on breeding dispersal, territory colonization, and territory extinction support this hypothesis. However, we did not find that Spotted Owls chose sites with more mature conifer forest, i.e., sites of higher quality, following breeding dispersal. This may indicate that the disturbance associated with habitat alteration, regardless of the extent of area altered, was an important factor motivating breeding dispersal, yet owls were either imperfect in their ability to assess habitat quality of new territories or chose a territory in which to settle based on other factors. It did appear that mate acquisition was a primary factor in selecting a territory; 43% of dispersing individuals were unpaired prior to dispersal compared to 6% after dispersal. Thus, it is surprising that we did not find that previous reproductive success was a good predictor of breeding dispersal probability. Prior reproductive success has been suggested as a primary factor determining breeding dispersal of many bird species (Wiklund 1996, Haas 1998, Catlin et al. 2005), including Spotted Owls (Forsman et al. 2002, Blakesley et al. 2006). Further, Ens et al. (1995) viewed site choice for the Oystercatcher (*Haematopus ostralegus*) as a “career decision” because of the long-term consequences for

individual fitness. We suspect a similar scenario is possible for the Spotted Owls we studied because they exhibited a relatively low probability of breeding dispersal, and because there appeared to be substantial differences among territories in terms of their quality (Seamans 2005).

Individual Spotted Owls may choose territories for something other than their intrinsic quality. We found evidence that selection of new territories by breeding individuals was not correlated with the amount of mature forest, but may have been associated with the presence of a mate. In addition, Seamans and Gutiérrez (2006) estimated that immigrants (it was unknown if they reflected breeding or natal dispersal events) appeared to use conspecifics as cues for settlement, although conspecifics may not always indicate the highest quality territory available. A further confounding factor for estimating the mechanisms responsible for selection of territories is the unknown effect anthropogenic actions have on the selective pressures responsible for breeding dispersal and habitat selection (Stamps 2001). For example, cues (e.g., the amount of mature conifer forest, the presence of a mate, or the occupancy of neighboring territories) that Spotted Owls once used to evaluate habitat quality may no longer reliably indicate quality (Hildén 1965). Our results for breeding dispersal partially support this hypothesis, while our results for territory colonization and extinction probability suggest that Spotted Owls are occupying higher quality territories.

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California Spotted Owl, Songbird, and Small Mammal Responses to Landscape Fuel Treatments

SCOTT L. STEPHENS, SETH W. BIGELOW, RYAN D. BURNETT, BRANDON M. COLLINS, CLAIRE V. GALLAGHER, JOHN KEANE, DOUGLAS A. KELT, MALCOLM P. NORTH, LANCE JAY ROBERTS, PETER A. STINE, AND DIRK H. VAN VUREN

A principal challenge of federal forest management has been maintaining and improving habitat for sensitive species in forests adapted to frequent, low- to moderate-intensity fire regimes that have become increasingly vulnerable to uncharacteristically severe wildfires. To enhance forest resilience, a coordinated landscape fuel network was installed in the northern Sierra Nevada, which reduced the potential for hazardous fire, despite constraints for wildlife protection that limited the extent and intensity of treatments. Small mammal and songbird communities were largely unaffected by this landscape strategy, but the number of California spotted owl territories declined. The effects on owls could have been mitigated by increasing the spatial heterogeneity of fuel treatments and by using more prescribed fire or managed wildfire to better mimic historic vegetation patterns and processes. More landscape-scale experimentation with strategies that conserve key wildlife species while also improving forest resiliency is needed, especially in response to continued warming climates.

Keywords: adaptive management, mixed conifer, restoration, Sierra Nevada, wildlife conservation

The role of wildfire in many of the world's forests that are adapted to frequent, low- to moderate-intensity fire regimes has been altered through fire exclusion, timber harvesting, livestock grazing, and urbanization (Agee and Skinner 2005, Collins et al. 2010). In the western United States, these land-use practices have affected forest structure and species composition, increasing surface fuel loads, tree density, the dominance of shade-tolerant tree species, and forest homogeneity (Hessberg et al. 2005, North et al. 2009, Chiono et al. 2012). As a consequence, many forests in the western United States are experiencing higher-severity burns—in some cases, producing large patches of tree mortality that can severely hinder the reestablishment of conifer forests (Roccaforte et al. 2012, Collins and Roller 2013). Consequently, one of the primary focuses of contemporary forest management is the treatment of fuels and vegetation to reduce fire hazards, especially as climate continues to warm (Stephens et al. 2013).

There is increased recognition that forests adapted to low- to moderate-intensity fire regimes experienced some high-severity fire (Perry et al. 2011, Marlon et al. 2012). Patchy, high-severity fire provides opportunities for early-seral habitat development and the production of large pieces of deadwood resources that are important to many wildlife species (Fontaine and Kennedy 2012). As such, forest fuel treatments should not be used to eliminate all

high-severity fire. Rather, treatments should allow for patterns of fire effects that approximate those occurring under more natural forest conditions. What little information we have on fire patterns under these conditions suggests that high-severity fire constitutes fairly low proportions of the overall burned area (5%–15%) in these forest types, which is generally aggregated in relatively small patches (smaller than 4 hectares [ha]), as is the case in the upper mixed-conifer forests in Yosemite National Park (Collins and Stephens 2010, Mallek et al. 2013).

Forest management involving habitat used by wildlife species at risk has been one of the principal challenges to US federal land managers for the last 25 years. In the Sierra Nevada, an ongoing debate is focused on several species that use old-growth forest, including the California spotted owl (CSO; *Strix occidentalis occidentalis*) and the Pacific fisher (*Martes pennanti pacifica*). Forest managers need information on appropriate levels of forest manipulations to create the desired balance between habitat conservation for wildlife populations and modifications of forests to improve their resilience to large high-severity fires that could prove more expensive and detrimental than the short-term effects of restoration treatments.

Fuel-reduction treatments reduce the potential impacts of wildfire by reducing the only aspect of the fire behavior



Figure 1. Fuel treatments implemented in the Meadow Valley project area. (a) Pretreatment mixed-conifer forest. (b) Whole-tree harvester cutting small trees (thinning from below). (c) Small trees, tree tops, and limbs being chipped and shipped by truck to a bioenergy plant to produce electricity. (d) Posttreatment defensible fuel profile zone, taken from the same perspective as in panel (a). Photographs: Keith Perchemlides.

triangle (i.e., topography, weather, fuel) that can be modified by managers: the quantity and continuity of fuel. A number of techniques are employed to reduce fire hazards, and each technique has associated effects on forest structure (Agee and Skinner 2005). Mechanical treatments can reduce stand density, basal area, and ladder and canopy fuel. To reduce accumulated surface fuel and to offset the detritus added from harvest operations, prescribed fire is sometimes used following forest thinning to reduce fire hazards, but whole-tree harvesting (i.e., complete tree removal, with the materials chipped and trucked to a processing facility; figure 1) can also effectively keep much of the harvest detritus from being added to the forest floor. Broadcast burning alone is very effective in elevating canopy base height and in reducing surface fuel (Agee and Skinner 2005).

Recent research confirms the ability of fuel treatments to alter potential fire behavior (Fulé et al. 2012) and actual wildfire effects (Safford et al. 2012). Research has also

determined that fuel-reduction treatments achieve their objectives with generally positive or neutral ecological effects (Stephens et al. 2012); however, almost all research on the effects of fuel treatments has been performed at the stand scale (10–25 ha). Given the large home ranges of many key wildlife species commonly at the crux of forest management issues in the western United States (e.g., the CSO, the northern spotted owl [*Strix occidentalis caurina*], the Pacific fisher), it is important to understand fuel-treatment impacts at larger spatial scales. This is particularly relevant because many fuel-treatment projects are being proposed—and, in a few instances, implemented—at landscape scales (15,000–40,000 ha; Ager et al. 2007, Collins et al. 2010).

Fuel treatments directly alter wildlife habitat by removing both aerial (trees) and ground (coarse wood, shrubs) cover. These altered conditions can affect both habitat suitability, which influences the number of individuals that an area can support, and habitat quality, which directly affects the fitness

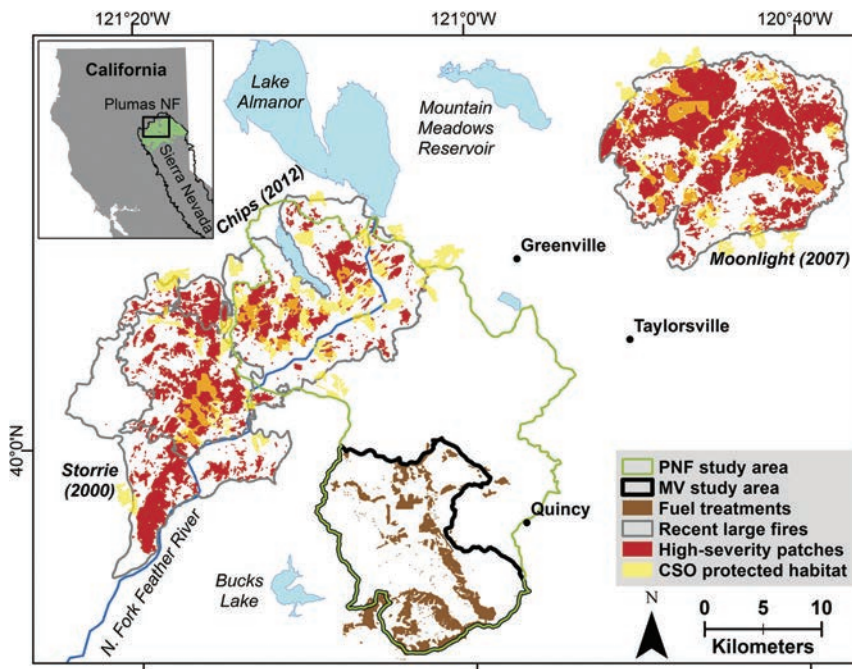


Figure 2. Meadow Valley study area with completed landscape fuel-treatment network. Recent large wildfires and the resulting patches of high-severity fire effects are also indicated. Three wildfires are shown: Storrie (2000), Moonlight (2007), and Chips (2012). These were selected on the basis of the following criteria: proximity to the study area (closer than 25 kilometers), vegetation type (conifer dominated), size (larger than 10,000 hectares), and age (since 2000). Abbreviations: CSO, California spotted owl; MV, Meadow Valley; N, north; NF, national forest; PNF, Plumas National Forest; W, west.

and productivity of individuals. Because more-suitable habitat for certain at-risk wildlife species is associated with greater aerial and ground cover, the effects of fuel treatments are generally perceived as negative. However, large patches of wildfire-caused tree mortality can also negatively affect both habitat suitability and quality (Tempel et al. in press). To the extent that fuel treatments reduce the potential for large patches of tree mortality in wildfire, there may also be an indirect benefit of fuel treatments to certain species' habitat. Finding a balance between these influences is a crucial management need.

Over the past decade, we have studied the ecological effects of one of the few completed landscape-level fuel-treatment networks in western US forests. Here, we distill the results of these efforts. We quantify change in vegetation structure and modeled fire behavior as a result of fuels treatments and assess treatment effects on the CSO, songbirds, and small mammals. Modeling studies have been published in which the trade-offs in these systems have been conceptually examined (Lee DC and Irwin 2005), but this is one of the first studies in which these questions have been empirically examined at landscape scales.

Study area and design

Our study area is located in the Meadow Valley area of the Plumas National Forest, situated in the northern Sierra

Nevada, at 39 degrees (°) 56 minutes (') north, 121°3' west (figure 2). The climate is Mediterranean, with warm, dry summers and cool, wet winters, which is when most precipitation (1050 millimeters per year; Ansley and Battles 1998) occurs. The core study area is 19,236 ha, with elevations ranging from 850–2100 meters (m). The vegetation is primarily mixed-conifer forest, consisting of white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*Pinus jeffreyi*), incense-cedar (*Calocedrus decurrens*), California black oak (*Quercus kelloggii*), and other less common hardwood species. White fir is the most abundant tree, although large (e.g., larger than 1 m in diameter) stumps of pines encountered frequently in the forest attest to a change in composition and structure in recent history. Red fir (*Abies magnifica*) is common at higher elevations, where it mixes with white fir. In addition, a number of species are found occasionally in or on the edge of the mixed-conifer forest, including western white pine (*Pinus monticola*) at higher elevations, lodgepole pine (*Pinus contorta* var. *murrayana*) in cold

air pockets, and western juniper (*Juniperus occidentalis*) on xeric sites. California hazelnut (*Corylus cornuta*), dogwood (*Cornus* spp.), and willow (*Salix* spp.) are found in moister riparian areas. Montane chaparral and some meadows are interspersed in the landscape. Tree density varies as a result of recent fire- and timber-management history, elevation, slope, aspect, and edaphic conditions. Historical fire occurrence, which can be inferred from fire scars recorded in tree rings, suggests that the fire regime was predominantly frequent, low- to moderate-severity fires, at intervals ranging from 7–19 years, with the last widespread fires occurring 85–125 years ago (Moody et al. 2006).

Fire activity in the last 15–20 years has been notably higher in the northern Sierra Nevada than in the rest of the range (Collins 2014). Since 2000, there have been three megafires (covering more than 10,000 ha; Stephens et al. 2014) within 25 kilometers (km) of our study area, burning a total of 73,000 ha (figure 2). These fires burned predominantly in mixed-conifer forests, encompassing approximately 60 CSO protected activity centers (figure 2). Cumulatively, 34% of the area burned in these three fires suffered high-severity fire (more than 95% dominant tree mortality; figure 3a; Miller et al. 2009). More important than the total proportion of area severely burned is the distribution of high-severity patches over the burned area, because this can limit tree seed

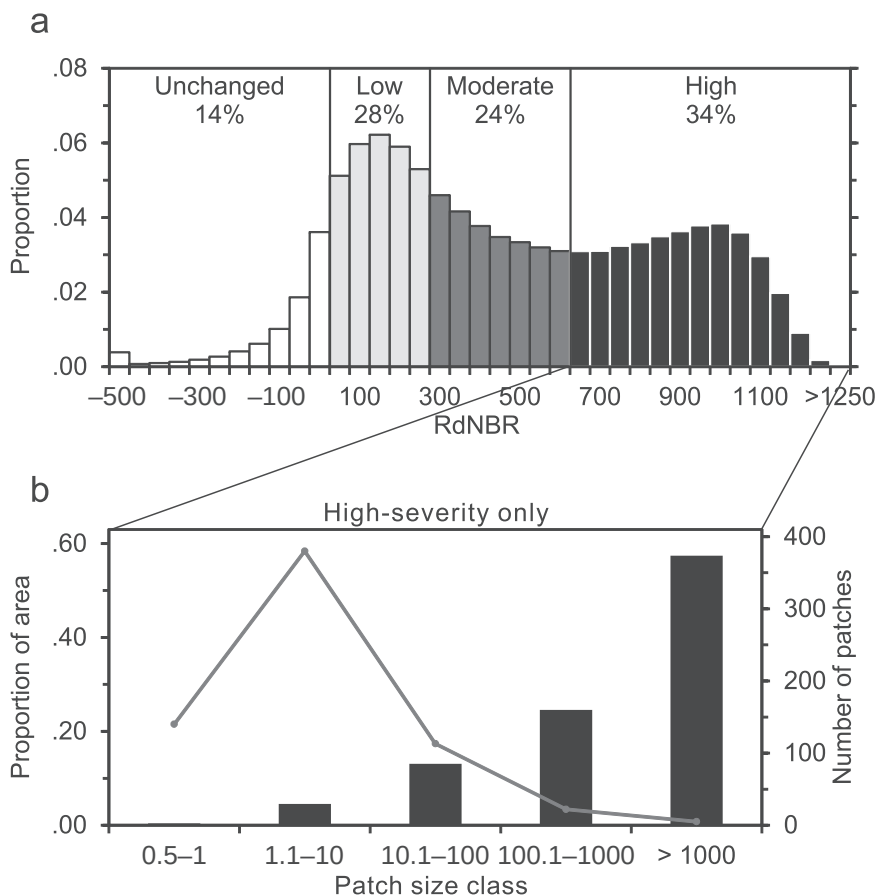


Figure 3. (a) Fire severity distribution for the three recent large fires in the Meadow Valley study area (see figure 2). The fire-severity estimates are based on the relative differenced normalized burn ratio (RdNBR; Miller and Thode 2007). (b) The proportion of total high-severity area (bars) and the number of patches (line) as a function of patch size class.

dispersal from wind and animals (Perry et al. 2011, Collins and Roller 2013). Large patches (defined here as larger than 1000 ha) accounted for a disproportionate amount of the total high-severity-fire area in the recent wildfires near the study area (figure 3b).

The projects that contributed to the fuel-treatment network are part of the larger Herger-Feinstein Quincy Library Group Pilot Project (USHR 1998). This project was directed by the US Congress to involve local communities in forest management. The project objectives included improving forest health, reducing uncharacteristic high-severity fire, conserving wildlife habitats, and stabilizing economic conditions in local communities. The projects in Meadow Valley encompassed a range of treatment types and intensities reflecting changes in regional management directions and differing land-management constraints across a complex landscape (Collins et al. 2010, Moghaddas et al. 2010). The primary fuel treatment used in Meadow Valley was defensible fuel profile zones (DFPZs), which are areas approximately 0.4–0.8 km wide in which surface, ladder, and crown fuel loads are reduced with a combination of moderate

thinning from below (Moghaddas et al. 2010) and prescribed fire treatments (figure 1).

The DFPZs were excluded from portions of the landscape set aside as reserves and from designated CSO protected activity centers, which are 121-ha areas of high-suitability nesting habitat designated by forest biologists. In addition, the project predominantly excluded all riparian habitat conservation areas or stream buffers intended to protect riparian and aquatic resources (figure 4). The activities conducted in the DFPZs were chainsaw thinning and pile burning of trees up to 30 centimeters (cm) in diameter at breast height (dbh); mastication: primarily shrubs and small trees were shredded and chipped in place, with the material left on site; prescription burning: stands were burned under conditions of moderate relative humidity and fuel moisture; and a combination of mechanical thinning and prescription burning of trees up to 51 or 76 cm dbh, depending on whether the stands were in the wildland–urban interface, using a whole-tree harvest system (figure 1) to achieve a residual canopy cover of approximately 40%, and some were underburned (Moghaddas et al. 2010). In addition to the DFPZs, group-selection treatments were implemented as part of the project. The group-selection treatments included the removal of all

conifers up to 76 cm dbh within an area of 0.8 ha, followed by residue piling and burning, then either natural regeneration or replanting to a density of 270 trees per ha with a mix of sugar pine, ponderosa pine, and Douglas-fir. These treatments collectively covered 3688 ha (3448 ha in the DFPZs, 240 ha in the group-selection treatment), or 19% of our study area, and were implemented between 2003 and 2008.

Forest structure and microclimate

Although they are designed to reduce fire hazards, forest treatments alter stand conditions directly by reducing tree density and canopy cover, and indirectly by altering microclimate conditions affecting the understory community. To assess these changes we measured stand structure, light, understory plant cover, micro-meteorological variables, soil moisture, and fuel moisture in replicated control, thinning, and group-selection treatments plots embedded within the landscape-level treatments (see Bigelow et al. 2009, 2011, Bigelow and North 2012 for detailed methods).

The mean forest canopy cover was 69% (standard deviation [SD] = 7%) before treatment; after treatment it was 53%

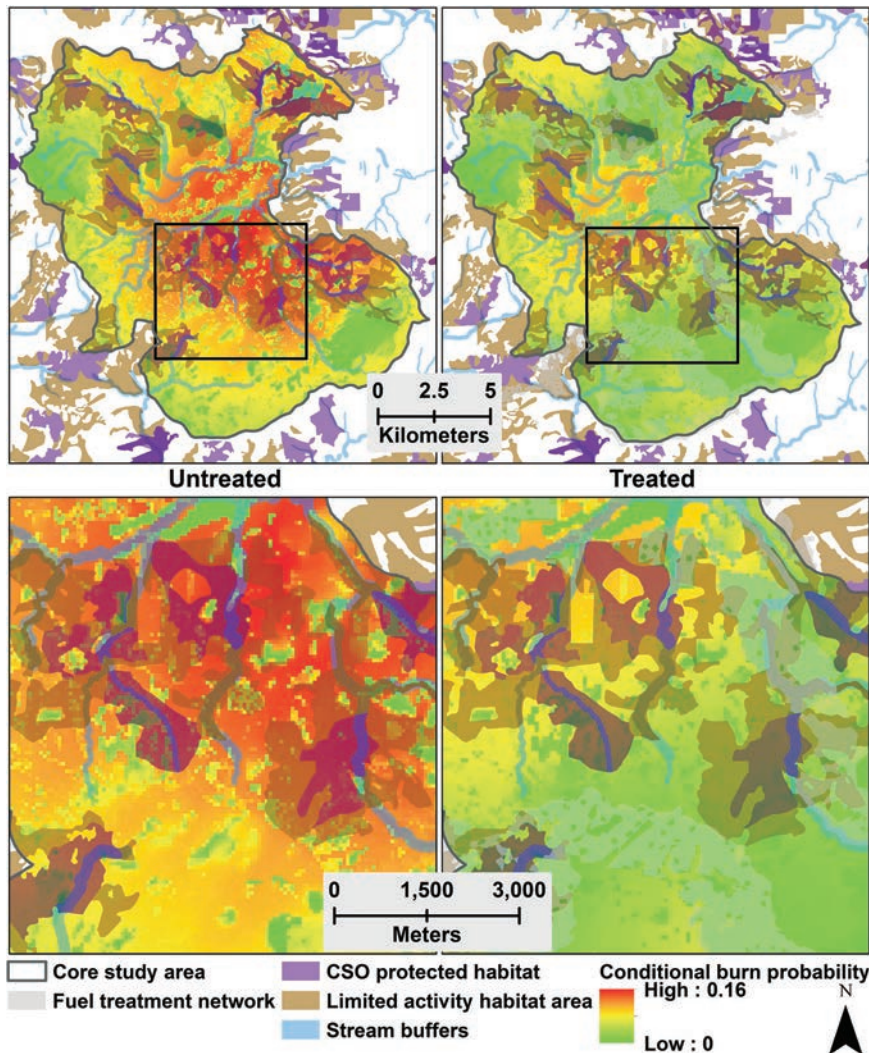


Figure 4. Hazardous fire potential across the Meadow Valley study area for the untreated and treated landscape conditions. This fire potential is based on the conditional burn probability of fire occurring with flame lengths greater than 2 meters, which is consistent with tree torching (see Collins et al. 2013 for specific details). Land designations that often limit or exclude active forest management (e.g., California spotted owl [CSO] protected habitat, stream buffers) are also shown to illustrate off-site effects of the landscape fuel-treatment network. The black square in the upper panels indicates the focal area shown in the bottom panels.

(SD = 7%) in thinned stands and 12% (SD = 6%) in the group-selection openings (Bigelow et al. 2011). These differences were reflected in growing-season understory light, which averaged 17% of full sun before treatment and increased to 26% in thinned stands and 67% in group-selection openings. Models of regenerating tree growth and light availability demonstrated that the height growth rates of shade-intolerant yellow pines (ponderosa and Jeffrey pines) and shade-tolerant white fir were equal at 41% of full sun. Light levels greater than this correlated exponentially with the height growth of the pines. The group-selection treatments provided ample light to recruit shade-intolerant species to the canopy, but only

8% of the sample locations in the thinning treatments had light levels exceeding the 41% crossover point, which suggests that these treatments would not substantially contribute to pine restoration across the landscape. An analysis of hemispherical photographs showed that the treatments decreased canopy closure following thinning. At the plot (1-ha) scale 3 years after treatment, cover of understory plant life-forms only changed under group selection ($p < .05$). Shade-tolerant conifers decreased, and graminoids, forbs, and broad-leaved trees (mainly California black oak and dogwood) increased (figure 5). There was no increase in exotic plant species cover with any of the treatments (Chiono 2012).

Changes in abiotic conditions followed differences in canopy cover for only some of the variables measured (Bigelow and North 2012). Soil moisture increased and duff moisture decreased in the group-selection treatments relative to the thinned and pretreatment conditions. Wind gust speeds (measured 2.5 m above ground) averaged 31% higher in the thinned stands than in the controls, but this was far less than the 128% increase in the group-selection openings. However, there was no difference in air temperature or relative humidity among the treatments, possibly because the increase in understory wind increased air mixing and eliminated any gradients in air temperature and humidity that might have resulted from increased irradiance.

Treatment increased within-stand variability for some vegetation and microclimate conditions but, in general, did not create the landscape-level heterogeneity characteristic of historic forest conditions in the Sierra Nevada (North et al. 2009). Mixed-conifer forests support the highest

vertebrate diversity of California forests (Verner and Boss 1980), and studies suggest that this may result from habitat variability associated with the observed range of tree species diversity, canopy cover, microclimate, and deadwood conditions (Rambo and North 2009, Ma et al. 2010, White et al. 2013). This historic forest heterogeneity appears to reflect differences in fire intensity and site productivity associated with local and large-scale changes in slope, aspect, soil, and slope position (North et al. 2009, Lydersen and North 2012). On average, more mesic sites (e.g., drainage bottoms and north-facing slopes) historically supported greater stem density, canopy cover, and tree basal area, whereas drier and

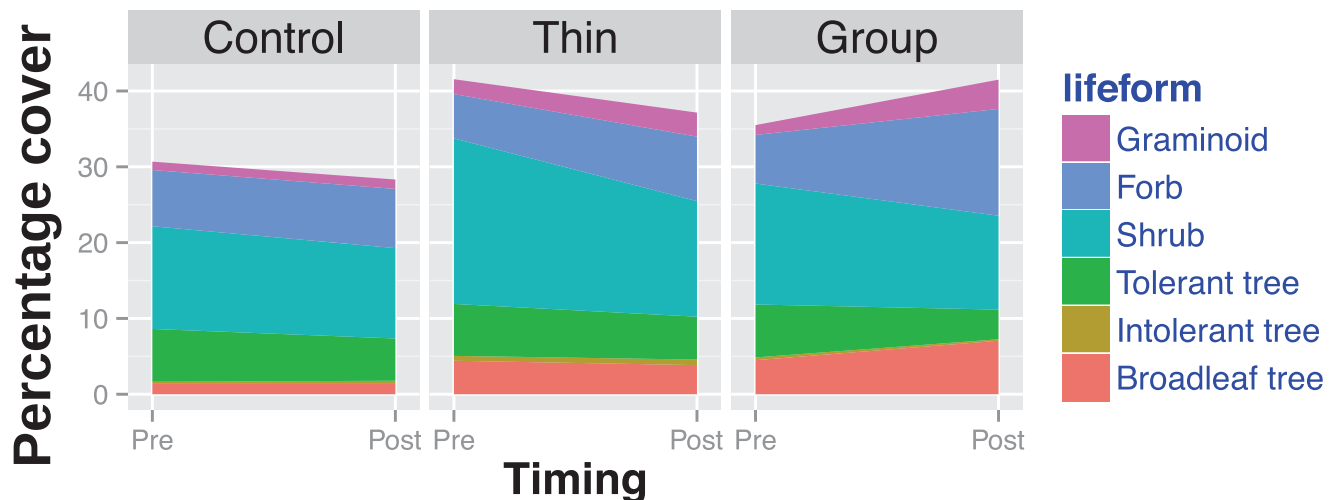


Figure 5. The percentage cover of plant life forms before (pre) and 3 years after (post) fuel-reduction thinning and group-selection treatments ($n = 300$ subplots per treatment) that were implemented in 2007 in Meadow Valley. Changes in understory cover in thinned stands were not significant ($p > .16$). Graminoids, forbs, and broadleaf trees increased and shade-tolerant conifers decreased ($p < .05$) in group selection openings.

steeper areas burned more frequently and intensely, creating more-open, pine-dominated forests (North et al. 2009). Although the Meadow Valley treatments did increase within-stand heterogeneity, they were not explicitly designed to vary with site topography or local productivity to produce this historic landscape variability.

Potential fire behavior

We employed a spatially explicit fire behavior model (Finney et al. 2007) to simulate fire spread across the Meadow Valley area. We simulated 10,000 individual fire events, with random ignition locations, and compared patterns of burn probability based on the number of times a particular area burned with the given ignition locations and simulated flame lengths for the study area prior to and following the implementation of landscape fuel treatments. Each fire event simulated burning for 240 minutes (one 4-hour burn period) under 97th percentile fuel moisture and wind conditions. These are the conditions associated with large-fire growth in this region (Collins et al. 2013). The burn period duration was selected such that the simulated fire sizes (for one burn period) approximated large-spread events observed (daily) in nearby recent wildfires (Collins et al. 2013). One of the primary assumptions with this approach is that, during these large-spread events (burn periods), fire suppression operations have limited impact, which is consistent with observed large-fire occurrence throughout the western United States (Finney et al. 2007). We summarized the burn probabilities across the Meadow Valley area into land allocations determined by the US Forest Service (USFS; Moghaddas et al. 2010).

The simulated fire behavior indicated that the landscape-scale network of DFPZs and prior fuel treatments were effective at reducing conditional burn probabilities across all

land-allocation types, except the small area of off-base lands (figure 4; Moghaddas et al. 2010). Because burn probabilities are correlated directly and positively to fire size (Finney et al. 2007), it is clear that the pretreatment landscape was more conducive to large-fire growth than the posttreatment landscape was (Moghaddas et al. 2010, Collins et al. 2013). Although the influence of the treatments on the modeled burn probabilities of each land allocation varied, the untreated stands (e.g., those designated for protected CSO habitat, riparian and aquatic resources, and reserve lands) and the remaining private and unclassified lands all experienced reduced burn probabilities from the application of fuel treatments at the landscape scale (figure 4; Moghaddas et al. 2010). A similar reduced burn severity immediately adjacent to treated areas has been reported for actual fires across the western United States (Finney et al. 2005).

The substantial reduction in both the total area and the area burned at higher flame lengths under a posttreatment wildfire scenario was notable, given that only 19% of the study area had been treated (Moghaddas et al. 2010, Collins et al. 2013). Both the orientation of the treatments (approximately orthogonal to the predominant wind direction throughout the duration of the simulated fire), and the long, continuous shape of the DFPZs resulted in potential wildfires' intersecting fuel treatments in multiple places. In addition, the treatments were somewhat concentrated in the southwestern portion of the study area (figure 2), which is the dominant direction of strong winds during the fire season (Collins et al. 2013). In combination, these factors limited the ability of the simulated fire to both circumvent the treated areas and to regain spread and intensity after encountering the treatments. These results are important to managers, because similar installations of fuel and restoration treatments are needed in many Sierra Nevada

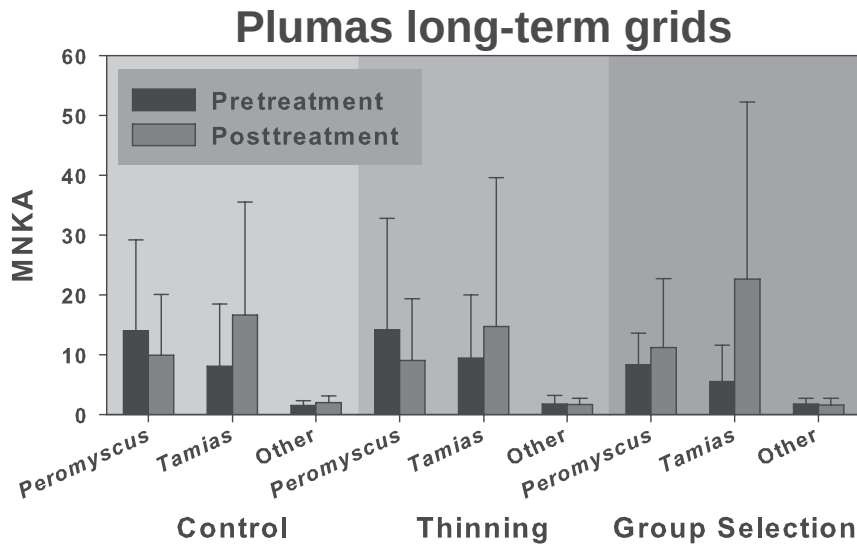


Figure 6. The mean minimum number of small animals known alive (MNKA), recorded before and after fuel treatments in the Plumas National Forest study area. For ease of presentation, we present three species groups (*Peromyscus boylii* and *Peromyscus maniculatus*; *Tamias quadrimaculatus* and *Tamias senex*; all other species; see Kelt et al. 2013 for details). The bars represent the means of the replicate sampling grids. The error bars represent the positive standard deviation.

mixed-conifer forests, where the present treatment rates are very low (North et al. 2012).

Small mammals

The northern Sierra Nevada supports a diverse fauna of small mammals that play key ecological roles as consumers, seed and fungal dispersers, and prey for both terrestrial and aerial predators (Hallett et al. 2003, Kelt et al. 2013). We studied small mammals in the Meadow Valley study area and the greater Plumas National Forest study area (PNFSA; figure 2), with a particular focus on two species that are key prey of the CSO (Gutiérrez et al. 1995): the dusky-footed woodrat (*Neotoma fuscipes*) and the northern flying squirrel (*Glaucomys sabrinus*). Results on focal species efforts have been reported elsewhere (Innes et al. 2007, Smith et al. 2011), but one finding merits emphasis here. California black oak, the primary hardwood in mixed-conifer forests, is an important habitat element for both the woodrat and the flying squirrel. Woodrat density was positively correlated with black oak density (Innes et al. 2007), and both species strongly preferred black oaks for nest sites (Innes et al. 2008, Smith et al. 2011). California black oak may be important for other wildlife species as well (Zielinski et al. 2004), but its persistence in our study landscape is in doubt. California black oak is shade intolerant, and across our study area, there were few thriving seedlings and many mature trees in decline as adjacent conifers overtopped them. California black oak trees were present in only 133 of 602 plots placed randomly in the PNFSA and were in a codominant canopy position in less than 10% of the plots in which it was present (see supplement S1).

Our broader studies on the management needs of entire small mammal assemblages included two complementary efforts. We sampled small mammals annually for 8 years on replicate trapping grids in treated and untreated mixed-conifer forests dominated by white fir in order to evaluate the responses of the small mammal community to canopy thinning (Kelt et al. 2013). To determine whether the habitat associations of the mammals in these forests were similar to those of mammals in other forest types, we expanded our efforts to include stratified random sampling of the PNFSA that encompassed the Meadow Valley study area (figure 2).

Whereas canopy thinning in white-fir-dominated mixed-conifer forests caused some significant changes in forest structure, small mammal assemblages were similar before and after canopy thinning and group selection (Kelt et al. 2013), which suggests a minimal response in the short-term to these treatments

(*contra* Suzuki and Hayes 2003, Gitzen et al. 2007, but see Carey and Wilson 2001). Although each treatment may have elicited somewhat different responses (figure 6), the variance across replicate plots eroded any such differences even in the face of the substantial variation in canopy cover. The lack of a short-term response may not be surprising in a system characterized by high interannual variation in weather and in a system dominated by generalist species; we look forward to resampling these sites after 10–15 years to assess potential longer-term responses. Because our manipulative experiment was focused on white-fir-dominated mixed-conifer forests, we pursued a more general assessment of mammalian responses to habitat and environmental variation across the entire PNFSA, capitalizing on a series of point-count transects established throughout the forest in a stratified (by forest type) random manner (see the “Songbirds” section below). We sampled eight randomly selected points on each of 74 transects to characterize how small mammals respond to broader variation in forest structure.

We assessed assemblage-wide responses to this variation with ordination (canonical correspondence and canonical correlation) and species-specific responses with multiple stepwise regression. All data were standardized (both rows and columns) by centering and normalizing, and the mammal data were log-transformed to prevent domination of the axes by common species. The results from all of the analyses were qualitatively identical to those of the Meadow Valley experimental grids, which indicates minimal responses of small mammal assemblages to variation in forest structure or composition. Although the spatial arrangement of the

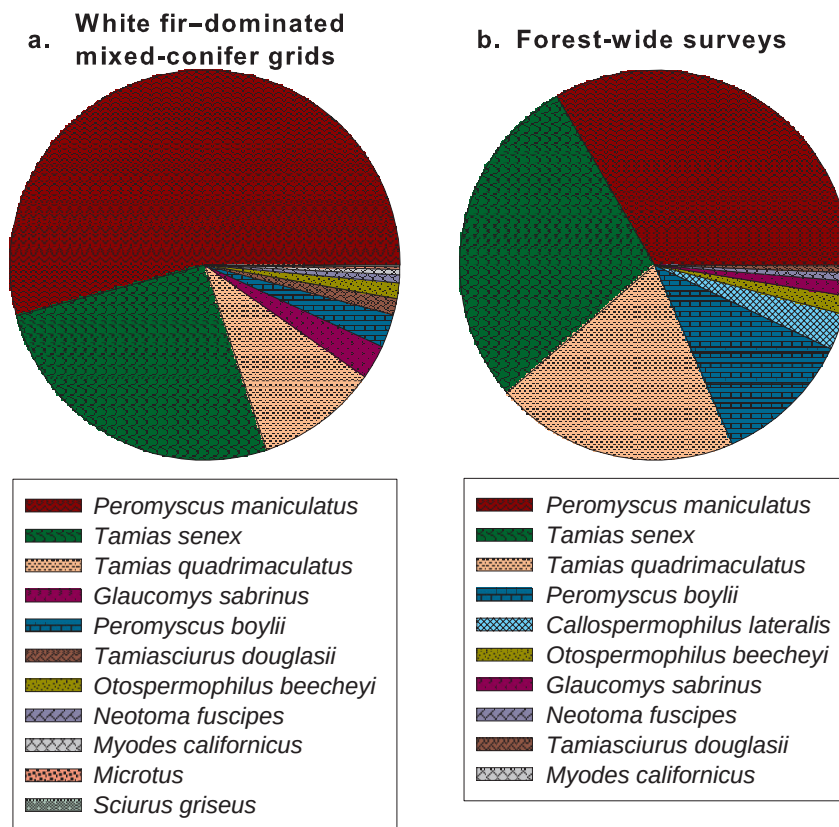


Figure 7. Small mammal composition at two spatial scales in the Plumas National Forest study area. At both scales, captures were dominated by three species. At the forest scale, only one other species was highly represented. All other species at both scales were only minor elements.

small mammal species in the ordination space was ecologically reasonable (e.g., woodrats and brush mice [*Peromyscus boylii*] associated with oaks, and chipmunks [*Tamias*] and Douglas squirrels [*Tamiasciurus douglasii*] associated with conifers and with a high basal area of trees and snags), ordination explained only a small proportion of variance in the distribution of small mammals. Similarly, regression failed to produce compelling associations for any species (or for community metrics such as species richness or diversity). The coefficients for both sets of analyses were universally low (Kelt et al. 2013).

In trapping efforts on the Meadow Valley experimental grids and in the larger PNFSA (figure 2), our captures were overwhelmingly dominated by 3–5 species (figure 7). Deer mice (*Peromyscus maniculatus*) dominated the captures at both spatial scales, comprising a full 55% of the captures on the Meadow Valley experimental grids and just over one-third of the captures in the PNFSA. Two species of chipmunk (*Tamias quadrimaculatus*, *Tamias senex*) represented an additional 40%–44%, and brush mice were an additional 8% in the PNFSA. Therefore, our samples were dominated by ecological generalists known to be tolerant of diverse habitats. What appears to be missing is a reasonable representation of species with more restricted

niche requirements. Our sampling was not designed to sample shrews (*Sorex*), but California red-backed voles (*Myodes* [formerly *Clethrionomys*] *californicus*) may have been more common in this region in the 1940s and 1950s (Kelt et al. 2013) and should have been present in our study. This species forages on fungi, however, and requires large downed woody debris and a closed-canopy forest to allow sufficient moisture retention to promote fungal growth (Alexander and Verts 1992). In 177,216 trap nights of effort, we captured only 11 *Myodes* (all but one on Meadow Valley experimental grids). Other species that are mesic habitat specialists were not sampled (e.g., *Zapus trinotatus*, *Sorex palustris*).

It is not clear whether the taxonomically depauperate assemblage structure documented in our study represents a relatively recent reduction or is more historic for this region. No data on mammal assemblages exist prior to European settlement and the beginning of widespread changes to the Sierra Nevada forest ecosystems (Merchant 2012). However, one implication of this research is that, in spite of nearly a kilometer of vertical elevation relief and diverse forest types from ponderosa pine to red fir, the current forest conditions support a relatively

homogeneous small mammal community dominated by ruderal species. It is unclear whether this reflects a legacy of fire exclusion and the resulting accumulation of fine woody debris or, perhaps, a response to a history of logging and fire suppression in this region. In contrast, other recent work in Yosemite (Roberts et al. 2008) confirms that small mammals respond strongly to variation in burn history. Taken together, these results support the fundamental ecological role of fire and broadscale forest heterogeneity in managing mixed-conifer forests in the Sierra Nevada (North et al. 2009).

Songbirds

To evaluate the effects of the Meadow Valley fuel-treatment network on songbirds, we compared avian community diversity before and after treatment. From 2004 to 2011, we surveyed the breeding community in and adjacent to Meadow Valley, using standardized point-count surveys with a 50-m radius (Ralph et al. 1995). Surveys were conducted at 51 stations where DFPZs were implemented (treated) and 201 stations where no treatments were implemented (untreated), proportional to the 19% of the study area treated. An additional 180 stations were surveyed in adjacent untreated PNFSA (figure 2) watersheds (the reference group). We used geographic information systems to establish locations

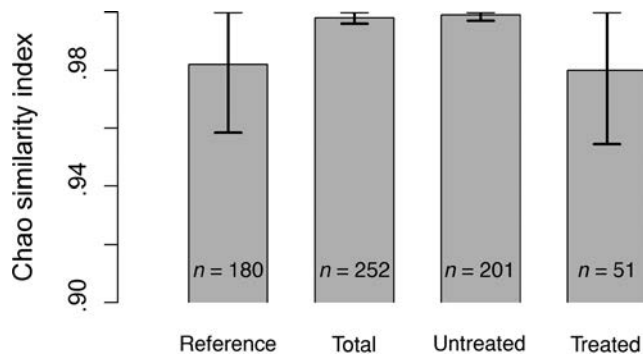


Figure 8. Chao similarity index for the avian community (60 species) before and after treatment at treated and untreated locations in the Meadow Valley study area and reference locations in the adjacent Plumas National Forest study area that also received no treatment. This metric ranges from 0–1, with 1 representing perfect similarity (all species and relative abundances shared among both samples). The error bars are 95% confidence intervals.

for the untreated and reference stations from a randomly selected origin (constrained by slopes lower than 35% and on USFS land) along a random compass bearing in a linear array of 4–12 points. The treated stations were placed within proposed DFPZ treatments across the breadth of treatment types and geography described above. All of the stations were a minimum of 250 m apart.

We surveyed all of the stations in both 2004 and 2005, prior to treatment, and for 2 years after all treatments were implemented (2010–2011). In each year, we surveyed every station twice during the peak of the breeding season (15 May–10 July), with a minimum of 10 days between visits. We limited our analyses to the 60 species breeding in upland habitats that were reliably recorded with point counts (Hutto et al. 1986). The results were summarized at the level of the three treatment groups described above (treated, untreated, reference) and for treated and untreated locations in Meadow Valley combined. For all of the analyses, we summed detections across four surveys (two visits per year over 2 years) for the pre- and posttreatment periods. We compared avian assemblages before and after the treatment with Chao–Jaccard’s similarity index (Chao et al. 2005), calculated using EstimateS (version 9.1, University of Connecticut, Storrs). Chao–Jaccard similarity is sensitive to changes in species composition and abundance. Differences in avian diversity were evaluated using the exponent of the Shannon index (Nur et al. 1999). For both analyses, 95% confidence intervals were derived from estimated standard errors from 1000 bootstrap samples.

Our results indicate little change in the Meadow Valley avian communities in response to treatment. The communities were similar across the treated, untreated, and

reference samples (figure 8). There was some evidence that the treated areas were less similar to each other than were the untreated areas, but this was not statistically significant ($p > .05$). Avian diversity (the Shannon index) was lowest for the treated sample prior to treatment but increased more in the posttreatment period, such that the Shannon index after treatment was equivalent in the treated and untreated samples (figure 9).

Evaluating the effects of fuel treatments with coarse metrics such as similarity and diversity can cause one to overlook large effects on select species (Hurteau et al. 2008). Numerous studies in seasonally dry fire-prone US forests have shown that fuel treatments can result in at least modest changes in the abundance of a broad range of avian species (Fontaine and Kennedy 2012). We recently reported that mechanical fuel-reduction treatments in the northern Sierra Nevada (including Meadow Valley) resulted in modest decreases in the abundance of a few closed-canopy associates and increases in some edge and open forest associates (Burnett et al. 2013). None of the 15 species evaluated in that study showed a significant decline following the construction of shaded fuel break DFPZ treatments—the primary treatment used in the Meadow Valley study area. With the moderate portion of the landscape treated, small differences in avian community similarity and diversity resulting from treatment, and the results from our previous evaluation of individual species response, we conclude that the effects of the Meadow Valley fuel-treatment network on the songbird community were minimal.

The fuel treatments implemented in Meadow Valley were typically less intense than those shown to result in large changes in avian communities (for a review, see Vanderwel et al. 2007). The treatments were applied to 19% of the landscape, and the prescriptions left relatively high canopy cover. Fire suppression and silvicultural practices over the last century have reduced forest heterogeneity and increased stand density (Scholl and Taylor 2010, Collins et al. 2011). In the Sierra Nevada, most fuel treatments changed the forest structure moderately from historic forest conditions (North et al. 2007). The Meadow Valley mechanical treatments primarily removed ladder fuels, which reduced crown fire potential but did not substantially alter the existing habitat features associated with songbirds, such as shrub cover or large overstory trees.

Our results should be considered in the context of the conditions that existed in the study area prior to the implementation of the landscape treatments. If an objective of these treatments was to maintain the existing avian assemblage and diversity, they appear to have been successful. However, a frequently stated objective for fuel reduction is to act as a surrogate for the natural fire regime (Stephens et al. 2012). Therefore, the maintenance of the pretreatment wildlife community may not always be the most desirable outcome in landscapes such as Meadow Valley and the larger PNFSA, where fire has been excluded for 85–125 years (Moody et al. 2006). Creating or enhancing

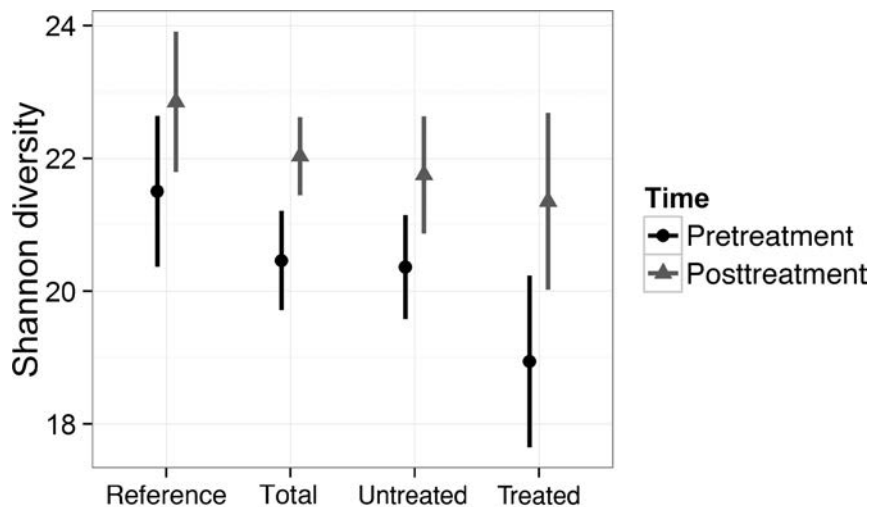


Figure 9. Shannon diversity index of avian diversity before (pretreatment) and after (posttreatment) fuel treatments were implemented at treated ($n = 51$) and untreated ($n = 201$) locations and the first two combined (Total; $n = 252$) in the Meadow Valley study area and in reference locations in the adjacent Plumas National Forest study area, which received no treatment ($n = 181$). The error bars are 95% confidence intervals.

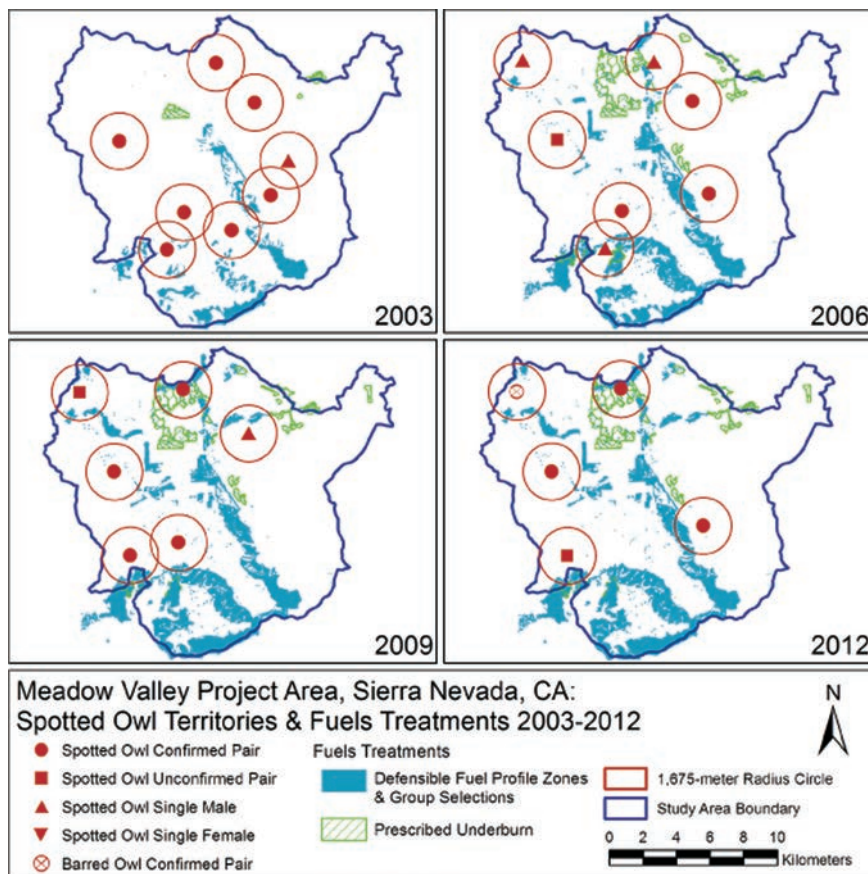


Figure 10. Distribution of territorial California spotted owl sites and landscape forest fuel treatments within the Meadow Valley study area from 2003 to 2012.

conditions for species associated with postdisturbance habitat, some of which have experienced recent declines, may be a prudent approach for achieving some biological diversity objectives (Fontaine and Kennedy 2012). If fuel-reduction treatments are to be a complementary tool to fire in achieving biological objectives, we suggest that they be designed to further increase landscape heterogeneity in fire-excluded forests.

California spotted owls

Modeling studies have projected that fuel treatments on a portion of the landscape (20%–35%) may have minimal effects on owl habitat and that the longer-term benefits of reduced wildfire risk may outweigh the short-term treatment effects on owl habitat (Ager et al. 2007, Roloff et al. 2012). However, no empirical data are available to assess the effects of landscape fuel treatments on the CSO and its habitat.

We used standardized surveys and color banding of individual owls to monitor the distribution, occupancy, survival, and reproduction of CSO sites annually across 1889 square kilometers between 2003 and 2012 in the Plumas and Lassen National Forests. Within this area, four areas were identified for implementation of landscape-scale fuel and restoration treatments. Our initial objectives were to establish baseline values for CSO distribution and abundance and to monitor the owl's response in the treated and untreated landscapes in posttreatment years. However, complete implementation of the fuel-treatment network only occurred on one (Meadow Valley; figure 10) of the four landscapes because of legal challenges to the proposed US Forest Service management strategy.

In the Meadow Valley study area, the number of territorial owl sites declined after treatment. Prior to and throughout the implementation of the treatment, the number of owl sites ranged from seven to nine. Between the final year of the DFPZ and group-selection installations (2008) and 2 years after treatment (2009–2010), the number of owl sites declined by one (six territorial sites), and by 3–4 years after treatment (2011–2012), the number of sites had declined to four—a decline of 43% from the pretreatment numbers

(figure 11). These results mirror similar declines of the CSO in the larger Plumas-Lassen CSO study area over the past 20 years (Conner et al. 2013) but suggest a greater magnitude of decline within Meadow Valley (figure 11).

The CSO nests and roosts in dense, multilayered, mature forest patches, and the adult survival and territory occupancy of these owls is positively correlated to the amounts of mature forest in core areas around CSO sites (Dugger et al. 2011). For foraging, however, the CSO uses a broader range of vegetative conditions. Radio-telemetry conducted in Meadow Valley indicates that the CSO avoids foraging in DFPZs in the first 1–2 years after fuel treatments and that the owl's home range size was positively correlated with the amount of treatment within the home range (Gallagher 2010). Barred owls (*Strix varia*) began to colonize the Meadow Valley study area in 2012 and are likely to become a threat to the CSO and a confounding factor to be accounted for in assessments of forest management effects (Keane 2014).

Although inference must be tempered from a single study, the Meadow Valley area is the first large area to receive full the implementation of landscape-scale DFPZ and group-selection treatments in which CSOs were monitored annually both before and after treatment. CSOs are long-lived (up to 20 years) and exhibit high site fidelity as adults, although there is high annual variation in reproduction associated with weather and food (Gutierrez et al. 1995). Given these traits, individual CSOs may exhibit both short- and long-term responses to fuel treatments or wildfire, and understanding both is important to land-use managers. Our results documented a decline in CSO territories as a result of landscape fuel treatments, but the factors driving the decline remain unknown.

Conclusions

This study has shown that coordinated landscape-scale fuel treatments can substantially reduce the potential for hazardous fire across a large montane region, even when a moderate proportion of the area that could not be treated because of management constraints. In many cases, lands with designated management emphasis, such as wildlife habitat reserves and stream buffers, are distributed throughout the landscape. Creating fuel treatments that exclude these lands can result in a patchwork of treated areas heavily dissected by, for example, untreated stream buffers. Hazardous fire potential decreased in untreated areas, but that effect is not stable over time. Even if the existing network was maintained in a “treated” condition (i.e., periodic prescribed fire to keep surface and ladder fuels low) hazards will continue to increase in untreated areas because of stand development (Collins et al. 2013).

Our results indicate negative CSO responses to treatments, supported by the avoidance of DFPZs by foraging owls, larger owl home ranges associated with increasing amounts of treatment within the home ranges, and a 43% decline in the number of territorial CSO sites across the Meadow Valley study

area within 3–4 years of the implementation of landscape treatments. In addition to changes in the number of owls, we also observed spatial redistribution of owl sites over time across the landscape (figure 10). The specific mechanisms driving these observations are unclear, but given the region-wide decline in the CSO population (Conner et al. 2013) and the increasing barred owl populations, it is difficult to disentangle fuel treatment effects from background or external pressures. Despite the challenges of working at landscape scales, studies such as this provide opportunities for addressing scale-dependent ecological phenomena, such as population-level species responses and responses to management strategies that cannot be addressed at smaller spatial scales.

To date, little discussion has been focused on what may constitute sustainable, viable CSO populations under various landscape conditions designed to address projected fire and climate scenarios. Furthermore, there is not a clear understanding of the balance between the potential short-term impacts from treatments and the longer-term benefits provided by introducing landscape heterogeneity (North et al. 2009), reducing potential for severe fire (Ager et al. 2007, Collins et al. 2013), increasing the potential for more desirable fire effects (North et al. 2012), and increasing resilience to climate change (Stephens et al. 2010). The Meadow Valley study is an important step in learning about the responses of wildlife species to fuel-reduction treatments.

Recent research in Yosemite National Park suggests that CSOs are not adversely affected by low- to moderate-severity fire (Roberts et al. 2011, Lee et al. 2013). Studies of the CSO both in Yosemite and in Sequoia and Kings Canyon National Parks have not shown population declines that have been found in several national forests in California. There are many differences between the two ownerships: National forest lands generally contain younger forests and lack the large tree structures associated with preferred owl habitat. With continued fire suppression, national forest lands continue to develop dense, small-tree stand conditions, reducing the habitat heterogeneity associated with a variety of small mammals that constitute the CSO's prey base. Because of these differences, it is difficult to determine whether more recent mechanical treatments or existing fire-suppressed conditions might be associated with declining CSO populations. Uncertainty also persists regarding the potential thresholds at which the amounts and patch sizes of high-severity fire reduce the postfire probabilities of CSO occupancy, survival, and reproduction. This is a significant information gap, given the trend for increasing amounts and patch sizes of high-severity fire in many Sierra Nevada forests (Miller et al. 2009). Unfortunately, only one CSO pair in Meadow Valley used an area that received prescribed burn treatments, but unlike those in some of the mechanically treated areas, these owls continued to occupy the burned area through the duration of the study and foraged within the burn-treatment areas (Gallagher 2010). The introduction of barred owls to Meadow Valley adds another important factor that may

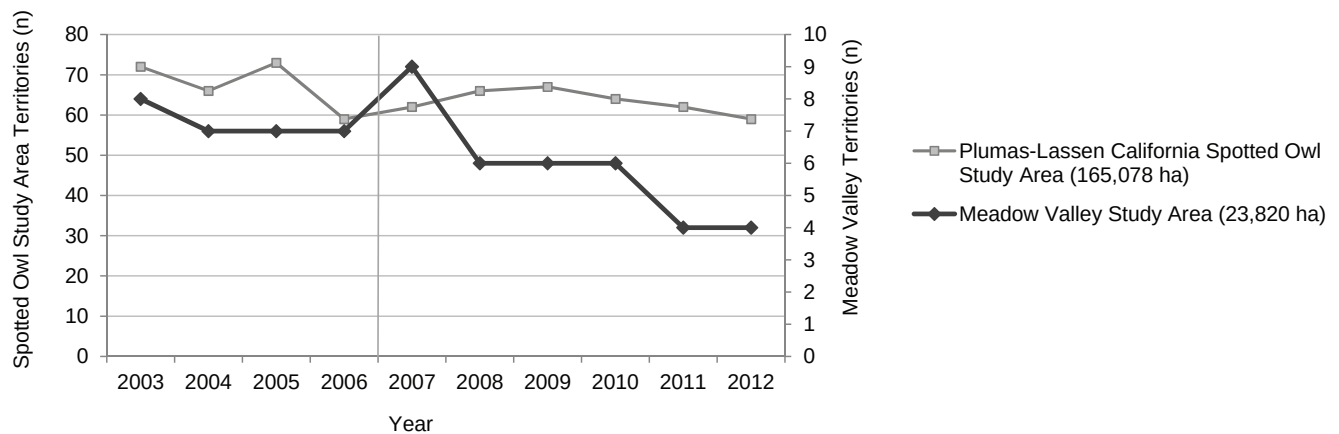


Figure 11. The annual number of territorial California spotted owl sites from 2003 to 2012 within the Meadow Valley study compared with the rest of the Plumas-Lassen study area (in the Plumas and Lassen National Forests). Vertical line represents completion of >80% of treatments.

reduce the population and viability of the CSO, possibly independent of forest structure.

Mechanical treatments can reduce fuels, but, in this study, they also left the largest trees and retained more than 40% canopy cover, two structural characteristics associated with CSO habitat use (Verner et al. 1992). However, although mechanical treatments retain these live features, they often remove snags for operator safety and fuel objectives; reduce tree density and canopy layering; reduce canopy cover to the minimum level (around 40%) considered to function as owl foraging habitat; and simplify the ground structure through a reduction of logs and small trees. Furthermore, DFPZ treatments are often uniformly implemented over large areas along roads, which results in extensive patches of simplified stand structure with regularly spaced trees. Another concern is that treatment size and placement are determined by land-use constraints (gentle slopes, access to roads) and opportunities to affect fire behavior. We have little information about how the location of treatments may affect CSOs' use of areas outside their core nesting locations. Several small mammals appeared to favor sites with steeper slopes (Kelt et al. 2013), possibly reflecting the spatial allocation of treatments in this landscape.

The importance of increasing heterogeneity within stands and across the landscape in mixed-conifer forests is well documented to meet restoration objectives (North et al. 2009, Stephens et al. 2010). Our ability to optimize heterogeneity at large scales may be more effectively achieved with prescribed and managed fires that are allowed to burn under moderate weather conditions. This type of burn often produces variable forest conditions that mimic historic patterns (Collins et al. 2011) to which this fauna, including the CSO, has adapted. Alternatively, mechanical treatments that produce the complex forest structure and composition that more closely mimic the patterns generated under a more active fire regime (North et al. 2009) may provide habitat conditions to support CSOs and a diverse fauna superior to those of the DFPZ and group-selection treatments implemented in Meadow Valley.

Although mean stand conditions (e.g., canopy cover) have often been used to infer management impacts on preferred habitat (Tempel et al. in press), the historic heterogeneity of frequent-fire forests suggests we have yet to identify the optimal scales at which to create variable forest conditions.

We encourage further work to examine landscape-level treatments that are intended to emulate the influence of fire in creating spatial heterogeneity in vegetation and fuel conditions. A working hypothesis is that increased habitat heterogeneity, including the retention and development of currently limited but ecologically important forest conditions (areas of large, old trees) and more-open, patchy, early-seral stage conditions, would promote a diverse wildlife community while providing a more fire-resilient landscape. The results from the Meadow Valley study area illustrate the benefits and challenges of working at the landscape scale. Rigorous and controlled experiments are difficult because of the inherent variability across landscapes, sociopolitical constraints, and competing management objectives that can influence planned treatments. However, inferences from these studies can be strengthened by careful replication of management strategies across multiple landscapes.

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Supplemental material

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Scott L. Stephens (sstephens@berkeley.edu) is affiliated with the Division of Ecosystem Science at the University of California, Berkeley. Seth W. Bigelow, Brandon M. Collins, Claire V. Gallagher, John Keane, Malcolm P. North, and Peter A. Stine are affiliated with the US Department of Agriculture, Forest Service, Pacific Southwest Research Station, in Davis, California. BMC is also affiliated with the University of California Center for Fire Research and Outreach, in the College of Natural Resources at the University of California, Berkeley. Ryan D. Burnett and Lance Jay Roberts are affiliated with Point Blue Conservation Science, in Petaluma, California. Douglas A. Kelt and Dirk H. Van Vuren are affiliated with the Department of Wildlife, Fish, and Conservation Biology at the University of California, Davis.

Effects of forest management on California Spotted Owls: implications for reducing wildfire risk in fire-prone forests

DOUGLAS J. TEMPEL,^{1,4} R. J. GUTIÉRREZ,² SHEILA A. WHITMORE,¹ MATTHEW J. REETZ,¹ RICKA E. STOELTING,¹
WILLIAM J. BERIGAN,¹ MARK E. SEAMANS,³ AND M. ZACHARIAH PEERY¹

¹Department of Forest and Wildlife Ecology, 1630 Linden Drive, University of Wisconsin, Madison, Wisconsin 53706 USA

²Department of Fisheries, Wildlife and Conservation Biology, 1980 Folwell Avenue, University of Minnesota, St. Paul, Minnesota 55108 USA

³Division of Migratory Bird Management, 755 Parfet Street, Suite 235, U.S. Fish and Wildlife Service, Lakewood, Colorado 80215 USA

Abstract. Management of many North American forests is challenged by the need to balance the potentially competing objectives of reducing risks posed by high-severity wildfires and protecting threatened species. In the Sierra Nevada, California, concern about high-severity fires has increased in recent decades but uncertainty exists over the effects of fuel-reduction treatments on species associated with older forests, such as the California Spotted Owl (*Strix occidentalis occidentalis*). Here, we assessed the effects of forest conditions, fuel reductions, and wildfire on a declining population of Spotted Owls in the central Sierra Nevada using 20 years of demographic data collected at 74 Spotted Owl territories. Adult survival and territory colonization probabilities were relatively high, while territory extinction probability was relatively low, especially in territories that had relatively large amounts of high canopy cover ($\geq 70\%$) forest. Reproduction was negatively associated with the area of medium-intensity timber harvests characteristic of proposed fuel treatments. Our results also suggested that the amount of edge between older forests and shrub/sapling vegetation and increased habitat heterogeneity may positively influence demographic rates of Spotted Owls. Finally, high-severity fire negatively influenced the probability of territory colonization. Despite correlations between owl demographic rates and several habitat variables, life stage simulation (sensitivity) analyses indicated that the amount of forest with high canopy cover was the primary driver of population growth and equilibrium occupancy at the scale of individual territories. Greater than 90% of medium-intensity harvests converted high-canopy-cover forests into lower-canopy-cover vegetation classes, suggesting that landscape-scale fuel treatments in such stands could have short-term negative impacts on populations of California Spotted Owls. Moreover, high-canopy-cover forests declined by an average of 7.4% across territories during our study, suggesting that habitat loss could have contributed to declines in abundance and territory occupancy. We recommend that managers consider the existing amount and spatial distribution of high-canopy forest before implementing fuel treatments within an owl territory, and that treatments be accompanied by a rigorous monitoring program.

Key words: California Spotted Owl; fire severity; forest management; fuels reduction; high-canopy-cover forest; Sierra Nevada, California, USA; *Strix occidentalis occidentalis*; timber harvest; wildfire.

INTRODUCTION

Forest managers in North America are challenged by the need to balance the potentially competing objectives of reducing wildfire risk and protecting threatened species. For millennia, low- to moderate-severity wildfires occurred at frequent (often less than 20-year) intervals in many western forests. These fires naturally removed fuels such as woody debris, shrubs, and small trees, and shaped the ecology of these forests (Agee 1993, Noss et al. 2006). However, decades of wildfire suppression have disrupted historic fire regimes, in-

creased the amount of surface and ladder fuels, and have led to more frequent high-severity wildfires that now threaten ecological and human communities (Westerling et al. 2006). In addition, warmer and drier conditions associated with climate change may lead to further increases in fire activity over the next century (Westerling and Bryant 2008, Liu et al. 2013). As a result, policy makers and forest managers have proposed landscape-scale forest treatments to remove surface and ladder fuels and reduce the risk of high-severity fires in many western forests (e.g., USFS 2004).

Proposed fuel-reduction measures pose a potential risk to wildlife species associated with older forests because they change forest structure in ways that may negatively affect the species' ability to survive and

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⁴ E-mail: dtempel@wisc.edu

reproduce. Species such as the Spotted Owl (*Strix occidentalis*), fisher (*Pekania pennanti*), and American marten (*Martes americana*) have already declined because of habitat loss and fragmentation resulting from more than a century of timber harvest (Gutiérrez 1994, Zielinski et al. 2005). Although fuels management may provide long-term benefits to such species by reducing future habitat loss from high-severity fires (Finney 2001, Ager et al. 2007, Finney et al. 2007, Collins et al. 2011), regulations protecting sensitive species often constrain the placement and number of potential fuel treatments (Collins et al. 2010). Thus, there is an urgent need to understand the effects of fuel-reduction treatments on old-forest-associated species so that fire risk can be managed while maintaining viable populations of these species (Zielinski et al. 2013). Doing so, however, is challenging because many of these species are rare and long-lived such that impacts may not be immediately apparent. Thus, long-term studies are needed to provide sufficient statistical power to discriminate between the effects of forest management and other sources of variation in demographic rates.

A high-profile example of the attempt to balance wildfire risk and species conservation is the management of public forests and Spotted Owls in the Sierra Nevada, California, USA. As with other western forests, the area burned by high-severity fires in the Sierra Nevada has increased over the past several decades (Miller et al. 2009). However, the implementation of landscape-scale fuel treatments in the Sierra Nevada (USFS 2004) has been contentious because of the potential for these fuel treatments to negatively affect the Spotted Owl and other sensitive species. For example, site occupancy of California Spotted Owls declined following the alteration of >20 ha of habitat within territories (Seamans and Gutiérrez 2007a). However, Seamans and Gutiérrez (2007a) did not attribute habitat changes to specific causes (e.g., fire, different types of logging) or assess the relationship between these events and reproduction, survival, or fitness. Thus, considerable uncertainty remains about the impact of forest management on California Spotted Owls.

We assessed the effects of timber harvest, wildfire, and vegetation conditions on a declining population of California Spotted Owls in the central Sierra Nevada, California, from 1993 to 2012. Specifically, we assessed the effects of forest treatments and vegetation conditions on reproduction, survival, and territory occupancy of California Spotted Owls and used these vital rates to determine the sensitivity of population growth and occupancy to changes in vegetation conditions due to wildfire or timber harvest. Our objectives were to understand the potential direct, short-term impacts of management actions intended to reduce wildfire risk on Spotted Owls, and to gain insight into the causes of an approximate 30% decline in abundance on our study area over the past two decades (Tempel and Gutiérrez 2013). Moreover, our study is particularly timely

because of heightened public concern following the 2013 fire season in the Sierra Nevada, which included one of the largest wildfires in California history (Rim Fire) and a wildfire that burned part of our study area (American Fire).

MATERIAL AND METHODS

Study area

Our study area was located in the central Sierra Nevada, California, between the North and South Forks of the American River. Within this area, we had a 345-km² Density Study Area (DSA) that we completely surveyed for Spotted Owls each year from 1993 to 2012, regardless of land ownership or past occupancy by owls. About 60% of the DSA was National Forest, and the remainder was privately owned land. In 1997 we established a Regional Study Area (RSA) surrounding the DSA. The RSA consisted of historical (previously known) owl territories and territories that we began surveying during 1997–1999. We then conducted annual surveys within owl territories on the RSA from 1997 to 2012, but we did not completely survey the landscape between these territories. In 2007, we established the 248-km² Last Chance Study Area (LCSA) as part of the Sierra Nevada Adaptive Management Project, 2013 (SNAMP).⁵ The LCSA was adjacent to the northern boundary of the DSA and was also completely surveyed for Spotted Owls each year from 2007 to 2012, regardless of land ownership or past occupancy by owls. We detected no Barred Owls (*Strix varia*) during our study, although we did detect two Barred × Spotted Owl hybrids that were not included in our assessment.

The study area consisted of mountainous terrain bisected by steep river canyons with elevations ranging from 300 to 2500 m. The study area had a mediterranean climate with cool, wet winters and hot, dry summers. Sierran mixed-conifer forest was the principal vegetation type and had a canopy dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), sugar pine (*P. lambertiana*), and Douglas-fir (*Pseudotsuga menziesii*). California black oak (*Quercus kelloggii*), tanoak (*Lithocarpus densiflora*), and big-leaf maple (*Acer macrophyllum*) were common understory species. Forests dominated by red fir (*A. magnifica*) and lodgepole pine (*P. contorta*) occurred at the highest elevations. Montane chaparral and black oak woodlands were vegetation types that were locally distributed at lower and middle elevations. The area has experienced a complex history of timber harvests over the past century, which added to the spatial complexity of vegetation conditions.

Spotted Owl surveys

Each year we conducted nighttime surveys from April through August to locate individuals by imitating vocalizations of Spotted Owls for a minimum of 10

⁵ <http://snamp.cnr.berkeley.edu>

TABLE 1. Description of vegetation classes used to characterize forest conditions used by Spotted Owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, California, USA.

Class	Description	dbh (cm)	Canopy cover (%)
1	Hardwood forest		>10 hardwood; <10 conifer
2	Shrubs and/or saplings	<15.2	
3	Pole conifer forest	15.2–30.4	
4	Medium-sized conifer forest with low canopy cover	30.5–60.9	30–69
5	Medium-sized conifer forest with high canopy cover	30.5–60.9	≥70
6	Large-sized conifer forest with low canopy cover	≥61.0	30–69
7	Large-sized conifer forest with high canopy cover	≥61.0	≥70
8	Water or barren rock		
9	Medium/large-sized, conifer forest with very low canopy cover	≥30.5	<30

minutes at call stations spaced ~0.8 km apart, or while walking routes that connected multiple call stations. If owls were detected, we conducted walk-in surveys at dawn or dusk in an attempt to identify owls and locate nests and roosts. We attempted to capture and band all Spotted Owls following the methods of Franklin et al. (1996). We fitted captured owls with a U.S. Geologic Survey (USGS) locking aluminum band on one leg and a unique color band and tab combination on the other leg. We determined sex of individuals by the pitch of calls and behavior (Forsman et al. 1984). We identified four age classes based on plumage characteristics: juvenile, first-year subadult, second-year subadult, and adult (≥3 years old) (Moen et al. 1991).

We estimated reproduction of Spotted Owls (i.e., the number of young produced per pair per year) by feeding live mice to owls (Franklin et al. 1996). Reproducing owls usually take offered prey to their nest or young, whereas nonreproducing owls usually eat or cache the mice. We inferred that owl pairs were nonreproductive if: (1) an owl took two or more mice and cached the last mouse without bringing a mouse to a nest or young; (2) an owl ate or cached four or more mice without bringing a mouse to a nest or young; (3) an owl ate two mice and ignored a third mouse for >1 hour; (4) a female owl was captured prior to 1 June and did not have a brood patch; or (5) a female owl was observed roosting for ≥60 minutes before 1 June, which suggested that the female was not incubating eggs or brooding. The number of young fledged from successful nests was determined by observing the delivery of offered mice from parents to young and by counting young during visual searches of the nest stand.

We determined site occupancy following the protocol of Tempel and Gutiérrez (2013). We divided the survey season each year into 10 bimonthly sampling periods (i.e., 1–15 April, 16–30 April, 1–15 May, 16–31 May, and so forth). We identified 74 owl territories using the criterion that reproduction must have been observed at least once at that location during our study. We considered the detection of at least one owl at a territory to indicate site occupancy. We eliminated nocturnal detections >400 m from the territory core area (i.e., areas frequently used by nesting and roosting owls at a territory; Berigan et al. 2012) to minimize the inclusion

of false positive detections of non-territorial floaters or residents straying from nearby territories.

Vegetation and forest treatment mapping

We interpreted aerial photographs to map vegetation cover types and changes in cover type that resulted from forest management, succession, and wildfire within all 74 owl territories during 1993–2012. Our vegetation map represented a spatial and temporal expansion of a similar map developed for our study area that also relied upon aerial photo interpretation, but was limited to a subset of territories and years (Chatfield 2005, Seamans and Gutiérrez 2007a). We mapped cover types within a 1128 m radius (400-ha) circle around each owl territory center; this radius was equal to half of the mean nearest neighbor distance during our study. We did not know if territorial owls used the entire 400 ha, but owls responded to our vocal surveys within these areas, and these areas encompassed all known nest locations on our study area (Seamans and Gutiérrez 2007a). We estimated a single center for each owl territory as the geometric mean of the most informative owl location(s) from each year that the territory was occupied. We used a nest location if one was located that year, but if we did not find a nest, we used the mean location of all roost trees located that year.

Vegetation cover was assigned to one of nine possible classes based on species composition, canopy cover, and the size class of dominant trees (Table 1; Appendix A). We used vegetation classes based upon the California Wildlife Habitat Relationships system (CWHR; Mayer and Laudenslayer 1988). As noted, we used a cover map developed by Chatfield (2005) as our base map, which had an overall accuracy (i.e., correct classification of cover types) of 83% based on randomly sampled vegetation plots. We updated this map for each year of our study using National Agriculture Imagery Program images, USGS 1-m digital orthophoto quarter quads (DOQQs), and geo-rectified aerial photographs (1:15 840 scale) obtained for the following years: 1993, 1996–1998, 2000, 2005, 2009, and 2010–2012. We drew polygons around relatively homogenous vegetation classes visible on the images using a minimum polygon size of ~1 ha. When we could not reliably assign a year to a visible change in cover type between available

images, we assumed that the change occurred at the midpoint between image years (see Fig. 1 as an example of the vegetation cover map for a single owl territory).

We identified the timing, location, and type of timber harvests from the U.S. Forest Service (USFS) Activity and Tracking System (FACTS; database *available online*),⁶ the California Department of Forestry and Fire Protection (CDFFP) Timber Harvest Plans (database *available online*),⁷ and information provided by private landowners. These databases contained 16 different timber harvest practices that we pooled into three broad categories for analytical purposes: low-intensity, medium-intensity, and high-intensity timber harvest (Appendix B). The classification scheme was based on the expected change in forest structure and was developed after consultation with three local forest managers who were naïve to the objectives of our study. We confirmed or modified the year and boundary of all treatments in the databases by visually examining the imagery and obtaining supplementary information from field visits, the USFS, and private landowners. We acquired fire perimeter data from the CDFFP Fire and Resource Assessment Program (*available online*).⁸

We did not specifically test for effects on Spotted Owls of Forest Service-implemented fuel-reduction treatments as proposed in USFS (2004) because implementation of these treatments was relatively recent (only 11 owl territories were affected by these treatments after 2007). However, these recent fuel-reduction treatments had effects on forest structure similar to those of other treatments in the medium-intensity category, most of which also occurred on USFS land. Prior to 2004, USFS timber harvests were governed by an “interim” management plan designed to maintain viable Spotted Owl populations (USFS 1993). Similar to the 2004 plan, the 1993 interim plan was designed to protect known owl nest stands from any significant modification, to protect large trees (≥ 76.2 cm dbh), to retain at least 40% canopy cover, and to reduce the threat of stand-destroying fires. The primary change implemented by the 2004 plan was a greater emphasis placed on the removal of understory fuels. Thus, we identified the occurrence of understory treatments through conversations with USFS and private timber company personnel and visual interpretation of aerial photos, and further categorized these treatments as “medium-intensity with understory removal.”

We extracted spatial data relevant to Spotted Owl ecology (see *Methods: A priori model development and selection*) from the cover maps with ArcGIS 10.0 (ESRI, Redlands, California, USA) using Patch Analyst 5.1.0.0 (Rempel et al. 2012) for subsequent use in demographic analysis. To calculate the amount of edge between vegetation classes, we used Patch Grid after first

converting vector data to raster data at a 30-m scale (Rempel et al. 2012). All other spatial variables were calculated directly from the vector maps. All habitat and timber harvest variables that we extracted from our vegetation maps were time-varying and could change annually because of natural disturbance, timber harvest, or regrowth. We expected that reproduction, survival, and occupancy at a territory would be impacted by timber harvest and wildfire in previous years, as well as the current year. Thus, we calculated harvest and wildfire covariates over three temporal scales: 3 years, 6 years, and 9 years. For example, at the 6-year time scale, the area of a specific disturbance type was the sum of those disturbances that occurred in the previous five years and the current year.

A priori model development and selection

We modeled putative relationships between vegetation classes and four vital rates (reproduction, survival, territory colonization, and territory extinction) by evaluating the level of support for competing, a priori models. We used Akaike's information criterion (AIC) values to rank competing models (Burnham and Anderson 2002). When evaluating support for covariate effects within a given model, we assessed whether the 95% confidence interval of the associated parameter estimate overlapped zero. We conducted the modeling in three steps to reduce the number of candidate models and thus reduce the likelihood of finding spurious relationships (Table 2). In the first step, we evaluated covariates that represented the amount of potential owl nesting and roosting habitat within territories. In the second step, we used the covariates from the top-ranked model from the first step and included additional covariates for potential owl foraging habitat, amount of private land, and the spatial distribution of forest cover types. In the third step, we used the covariates from the top-ranked model in the second step and included additional covariates that represented different types of forest disturbance. By using this hierarchical approach, we were able to control for existing habitat conditions within each territory when assessing the impacts of forest disturbance. For steps 1 and 2 of our modeling, we used the entire 20-year data set. For step 3, we used the covariates from the most parsimonious models from step 2, but then used reduced data sets for the three temporal scales because we lacked timber harvest data for years prior to 1993. None of the covariates that we used were highly correlated with each other ($r > 0.60$).

Previous studies of our study population revealed that high canopy cover and large trees were important components of nesting and roosting conditions used by Spotted Owls (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997). Therefore, in step 1 of our analysis we evaluated support for the combined areas of vegetation classes 5 and 7 (57; model 1.1) and the combined areas of vegetation classes 6 and 7 (67; model 1.4). Vegetation

⁶ www.fs.usda.gov/main/r5/landmanagement/gis

⁷ ftp.fire.ca.gov/forest/

⁸ <http://frap.fire.ca.gov/data/frapgisdata-subset.php>

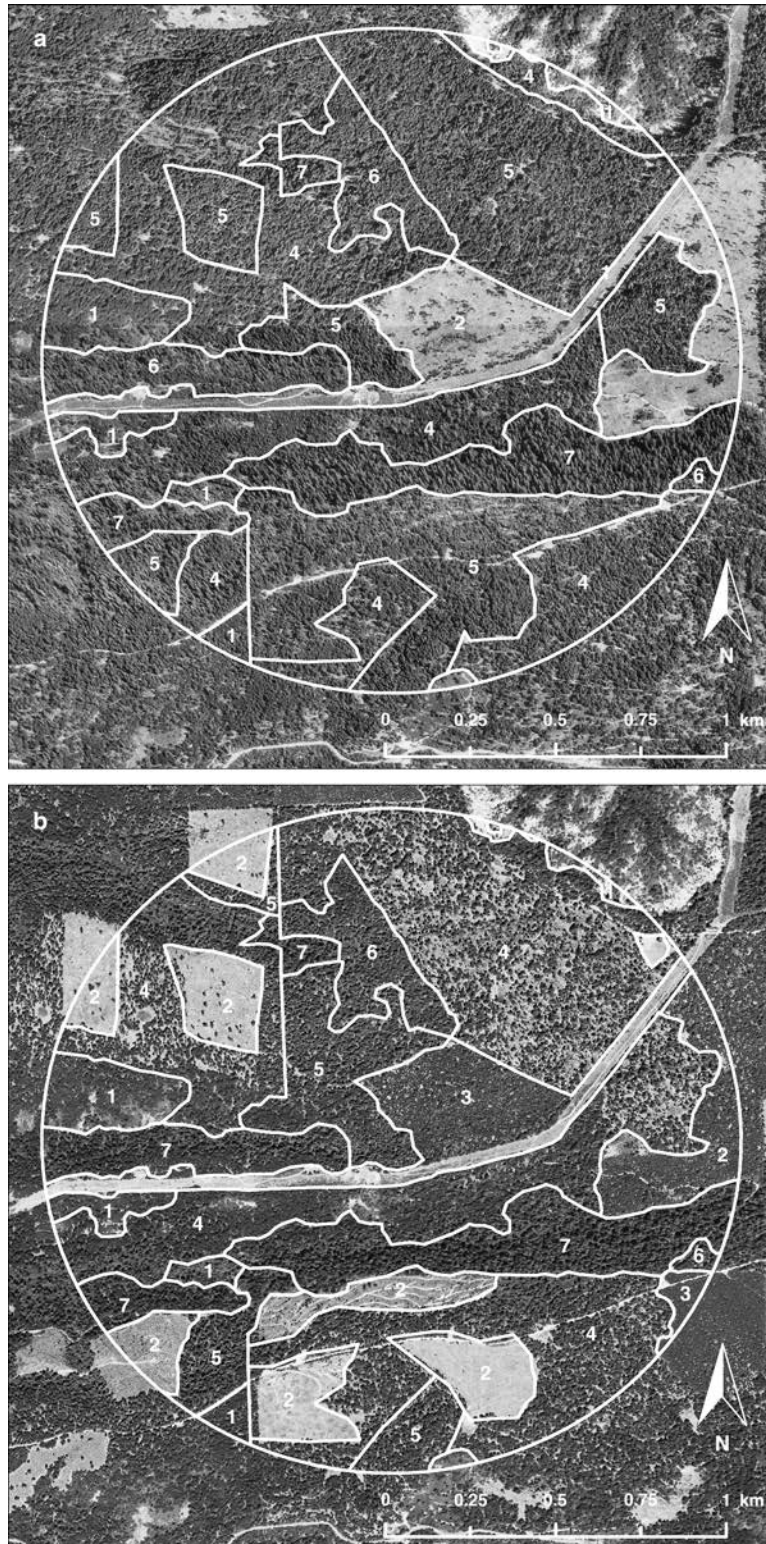


FIG. 1. Example of a vegetation cover map based on aerial photographs taken in 1993 (a) and 2012 (b) for a California Spotted Owl (*Strix occidentalis occidentalis*) territory on our study area in the central Sierra Nevada, California, USA. The territory is delineated by a circular boundary that encompasses 400 ha. See Table 1 for definitions of the numbered vegetation classes.

TABLE 2. List of a priori models for three-step modeling of reproduction, survival, and territory occupancy of Spotted Owls in the central Sierra Nevada, California, USA.

Model	Covariates	Description
Step 1		
1.1	57	linear relationship with area (ha) of classes 5 + 7
1.2	log(57)	log-linear relationship with area (ha) of classes 5 + 7
1.3	57 + (57) ²	quadratic relationship with area (ha) of classes 5 + 7
1.4	67	linear relationship with area (ha) of classes 6 + 7
1.5	log(67)	log-linear relationship with area (ha) of classes 6 + 7
1.6	67 + (67) ²	quadratic relationship with area (ha) of classes 6 + 7
Step 2		
2.1	[step 1]† + hardwoods	[step 1] + area (ha) of hardwoods
2.2	[step 1] + edge	[step 1] + edge (km) between vegetation class 2 and classes 4, 5, 6, and 7
2.3	[step 1] + private	[step 1] + area (ha) of private land
2.4	[step 1] + habitat diversity	[step 1] + habitat diversity (Shannon-Wiener)‡
2.5	[step 1] + mean patch size	[step 1] + mean habitat patch size (ha)‡
Step 3		
3.1	[step 2]§ + high	[step 2] + area (ha) of high-intensity harvests
3.2	[step 2] + fire	[step 2] + area (ha) of wildfire
3.3	[step 2] + understory	[step 2] + area (ha) of medium-intensity harvests with understory removal
3.4	[step 2] + medium	[step 2] + area (ha) of all medium-intensity harvests
3.5	[step 2] + low	[step 2] + area (ha) of low-intensity harvests
3.6	[step 2] + [treatment] + interaction between habitat and treatment	[step 2] + variables from best model among 3.1–3.6 + interaction with step 1 habitat

Note: We used the same models for all three time scales that we considered (3, 6, and 9 years); vegetation classes are defined in Table 1.

† The variables from the top model in step 1.

‡ Habitat diversity and mean patch size were calculated using either 57 or 67, depending on which habitat variable (if any) was in the best step 1 model. Combined area of vegetation classes 5 and 7 includes the amount of forest with high ($\geq 70\%$) canopy cover and a dominant tree size of ≥ 30.5 cm dbh; combined area of vegetation classes 6 and 7 includes the amount of forest dominated by large trees ≥ 61.0 cm dbh with a lower threshold ($\geq 30\%$) for canopy cover.

§ Variables from the top model in step 2.

classes 5 and 7 represented the amount of forest with high ($\geq 70\%$) canopy cover and a dominant tree size of ≥ 30.5 cm diameter at breast height (dbh). In addition to providing nesting and roosting conditions, this forest type provides habitat for northern flying squirrels (*Glaucomys sabrinus*; Waters and Zabel 1995), which were the primary prey item of Spotted Owls on our study area (R. J. Gutiérrez, unpublished data). Vegetation classes 6 and 7 represented the amount of forest dominated by large trees (≥ 61.0 cm dbh) with a lower threshold ($\geq 30\%$) for canopy cover. The current management plan for national forests in the Sierra Nevada (USFS 2004) contains harvest limits on both canopy cover (minimum 40–50% postharvest) and tree size (< 76.2 cm dbh). Although these two covariates (57, 67) were correlated ($r = 0.60$), we chose to retain both covariates in our analyses to test whether high canopy cover or large trees were more important components of owl habitat. We also considered log-linear (models 1.2, 1.5) and quadratic (models 1.3, 1.6) relationships because such relationships between habitat and Spotted Owl vital rates have been detected in other regions (Franklin et al. 2000, Dugger et al. 2005, Forsman et al. 2011). We included a covariate for age (a subadult is 1 or 2 years old, an adult is at least 3 years old) when modeling survival and reproduction, and a covariate for sex when modeling survival, because age and sex have been shown to be important predictors of these vital

rates for Spotted Owls (Blakesley et al. 2010). Finally, we included a null model without explanatory covariates in which each vital rate had a constant value over time.

In step 2 of our analysis, we hypothesized that hardwood forests (vegetation class 1; model 2.1) may support greater densities of dusky-footed woodrats (*Neotoma fuscipes*) than other forest types (Sakai and Noon 1993, Innes et al. 2007); woodrats are an important prey item for Spotted Owls on our study area, especially at lower elevations (unpublished data). We posited that the amount of edge between shrubs or saplings (vegetation class 2) and forests dominated by trees ≥ 30.5 cm (vegetation classes 4, 5, 6, and 7; model 2.2) may have positively affected Spotted Owl vital rates because the presence of brush fields adjacent to older forest may increase the availability of woodrats to owls (Sakai and Noon 1997). We hypothesized that the area of private land (model 2.3) may negatively affect Spotted Owl vital rates because data from a radiotelemetry study conducted in our study area during 2006–2007 suggested that owls use private lands less than expected, possibly owing to a history of more intensive timber harvests on private land (Williams et al. 2014). Finally, we hypothesized that the spatial arrangement of owl habitat may affect owl vital rates (Franklin et al. 2000). For example, high interspersed of different forest cover types within a territory may allow owls to more easily meet all of their life history requirements (nesting,

roosting, foraging). We first examined the correlation between several potential territory spatial metrics (mean distance between patches, mean patch size, number of patches, diversity) and found that most were correlated with each other or with habitat covariates from step 1 ($r > 0.60$). Thus, we chose to use two metrics that were not highly correlated with each other or with the step 1 covariates: the Shannon-Wiener diversity index (model 2.4) and the mean size of owl habitat patches (model 2.5). We calculated these metrics for the owl habitat type (57 or 67) found in the best model from step 1. We log-transformed all step 2 covariates (except for the Shannon-Wiener diversity index) for our analyses because their distributions were right-skewed.

In step 3 of our analysis, we introduced covariates that represented the potential effects of forest disturbances. Disturbances generally consisted of timber harvest, but also included wildfires that occurred within 12 owl territories during our study. We expected all types of disturbance to negatively impact vital rates of Spotted Owls, and ranked them in order of the expected magnitude of their effects as follows: high-intensity harvests, wildfire, medium-intensity harvests with understory removal, all medium-intensity harvests, and low-intensity harvests (models 3.1–3.5). We ranked wildfire second because most of the acreage burned on our study area was the result of a single fire in 2001 that was predominantly a stand-replacing fire and impacted eight territories to varying degrees. We then sequentially added the disturbance covariates to the best model from step 2 in order of their expected impact and retained the covariate in the model if it reduced the model's AIC value. Finally, we considered a model (model 3.6) in which the amount of habitat (57 or 67) interacted with the disturbance covariate(s) from the best model among models 3.1–3.5. We considered this a test of the hypothesis that territories containing relatively large amounts of Spotted Owl habitat would be more resilient to disturbance (Seamans and Gutiérrez 2007a). All step 3 covariates were right-skewed, so we added 1 to their values and log-transformed them for our analyses.

Statistical modeling

Reproduction.—We used mixed-model analysis of variance (PROC MIXED in SAS 9.3; Littell et al. 2006) to test the a priori hypotheses described previously with respect to reproduction. In these analyses, we treated reproduction (i.e., the number of young fledged per territory per year) as the dependent variable, habitat covariates and female age (subadult or adult) as fixed effects, and territory identity and year (1993–2012) as random effects. We considered territory to be a random blocking factor because reproduction within a territory may not be independent among years. We treated reproduction as a normally distributed variable because McDonald and White (2010) found that analysis of variance procedures based on a normal distribution performed well for small count data similar to ours.

Moreover, before examining a priori habitat models, we used restricted maximum likelihood estimation to model the following potential variance–covariance structures within territories across years: compound symmetric, first-order autoregressive, heterogeneous first-order autoregressive, and log-linear (Littell et al. 2006). Once we identified the best variance–covariance structure (i.e., lowest AIC value), we used full maximum likelihood estimation to model the influence of the fixed effects on reproduction according to the framework just described. We considered female age a factor in all models, based on differences in reproduction between subadults and adults in previous studies (Blakesley et al. 2010).

Survival.—We used the Cormack-Jolly-Seber open-population model (CJS; Cormack 1964, Jolly 1965, Seber 1965) implemented in the R package *marked* (Laake et al. 2013) to test the a priori hypotheses previously described with respect to apparent survival of Spotted Owls. Apparent survival refers to the inability to differentiate between true mortality and permanent emigration from the study area. Although capture histories were developed based on the capture and resighting of individual Spotted Owls, our goal was to make inferences based on the habitat occupied by an owl, which varied by territory. Thus, we modified the capture histories used for the temporal analyses to reflect movement among territories (sensu Franklin et al. 2000). If an individual was not resighted for one or more years and was then resighted on a new territory, we removed the portion of its capture history pertaining to the original territory. We did this to avoid making assumptions about the owl's location during the intervening period. As a result, we used partial capture histories for 14 of the 350 individuals in our data set.

No methods exist for estimating overdispersion ($\hat{c}$) in CJS models containing individual covariates (Jeff Laake, *personal communication*), so instead we used Program MARK to estimate $\hat{c}$ for our most highly parameterized model without covariates, $\phi(\text{age} \times \text{sex} \times \text{year})$ and $p(\text{age} \times \text{sex} \times \text{year})$. We found no evidence for a lack of model fit ($\hat{c} = 0.998$). Prior to modeling survival rates, we first examined a priori model structures for the probability of recapture (p). We examined three covariates that may influence recapture probabilities: age (subadult or adult), sex, and survey effort (the amount of time spent conducting walk-in surveys each year) (Blakesley et al. 2010). Using the best model structure for p , we then followed the framework described previously to model the influence of habitat and forest disturbance on apparent survival.

Occupancy.—We used a multi-season occupancy model with parameters for local extinction (ϵ_t) and local colonization (γ_t) of Spotted Owl territories (MacKenzie et al. 2003). We separately modeled the extinction and colonization processes using Program PRESENCE v. 5.9 (Hines 2006). When modeling extinction, we specified a full time structure for colonization (i.e.,

different parameter estimates for each year), and vice versa when modeling colonization. The primary sampling periods were each year of the study, and the secondary sampling periods were the 10 bimonthly intervals within each year. Two critical assumptions of this model were: (1) occupancy status at each territory did not change during the survey season (i.e., no permanent emigration); and (2) detections at each territory were independent (MacKenzie et al. 2006). Because nearly all of the owls on our study area were marked, we could determine when individuals moved among territories during the survey season. Such movements only occurred on 10 occasions during our study, and we only considered one of the territories to be occupied in these situations (i.e., where the individual was most frequently detected). In addition, we excluded nocturnal detections >400 m from a territorial core area to help ensure independence of detections at territories. Finally, we interpreted occupancy as the proportion of territories used by owls during a breeding season because some territories may not have been continuously occupied throughout the entire season (MacKenzie et al. 2006).

We first examined a priori model structures for detection probabilities (p). For the occupancy analyses, p represented the probability of detecting an owl during a survey when the territory was occupied. Note that for the mark-recapture analyses, p represented the probability of recapturing an individual during a given year. We modeled within-year p using two covariates, *initial* and *repro* (Tempel and Gutiérrez 2013). *Initial* specified a different p for all survey occasions subsequent to the first detection at a territory each year, and *repro* indicated whether owls attempted to nest at a territory that year. We then modeled annual p with the following temporal effects: linear, log-linear, quadratic, different for each year, and constant. We selected the model with the best-fitting time structure and then introduced covariates for vegetation class (57 and 67) relative to p and initial occupancy probability (ψ_1). Using the best model structure, we then followed the framework described previously to model the relationships between vegetation class and forest disturbance on territory extinction and colonization.

Sensitivity analyses

Life stage simulation.—We conducted life stage simulation analyses (LSA) to assess which covariates had the greatest influence on annual population growth rate (λ) of Spotted Owls by estimating the amount of variation in λ explained by each covariate that appeared in the top-ranked models of reproduction and survival (Wisdom et al. 2000). We used a stage-based, post-breeding census Lefkovich matrix model parameterized with reproductive and survival rates to represent changes in female population size:

$$\begin{bmatrix} N_{J,t+1} \\ N_{S1,t+1} \\ N_{S2,t+1} \\ N_{A,t+1} \end{bmatrix} = \begin{bmatrix} 0 & \phi_{S,t}b_{S,t} & \phi_{S,t}b_{A,t} & \phi_{A,t}b_{A,t} \\ \phi_{J,t} & 0 & 0 & 0 \\ 0 & \phi_{S,t} & 0 & 0 \\ 0 & 0 & \phi_{S,t} & \phi_{A,t} \end{bmatrix} \begin{bmatrix} N_{J,t} \\ N_{S1,t} \\ N_{S2,t} \\ N_{A,t} \end{bmatrix} \quad (1)$$

where $N_{J,t}$, $N_{S1,t}$, $N_{S2,t}$, and $N_{A,t}$ were the number of juvenile, first-year subadult, second-year subadult, and adult females at time t , respectively; $\phi_{J,t}$, $\phi_{S,t}$, and $\phi_{A,t}$ were the apparent survival rates of juvenile, subadult, and adult females from time t to $t + 1$, respectively; and $b_{S,t}$ and $b_{A,t}$ were the fecundity rates for subadult and adult females at time t , respectively. Fecundity was the number of female offspring produced per female in the population. We assumed a 1:1 sex ratio of offspring and divided the reproductive rate from our reproduction model by two. We estimated λ as the dominant eigenvalue of the matrix.

We expressed apparent survival and fecundity as functions of covariates and set the beta coefficients for all covariate effects equal to their estimated values from the top-ranked models for apparent survival and fecundity (Table 3). As an example, apparent survival was estimated as

$$\text{logit}(\phi) = \beta_0 + \beta_1 \times \text{sex} + \beta_2 \times \text{age} + \beta_3 \times \log(57) + \beta_4 \times \text{edge} \quad (2)$$

where sex is 0 for females and 1 for males, and age is 0 for subadults and 1 for adults. Thus, apparent survival for non-juvenile females was estimated as

$$\text{logit}(\phi) = -1.010 + 0.452 \times \text{age} + 1.004 \times \log(57) + 0.763 \times \text{edge}. \quad (3)$$

We allowed the vegetation covariates to vary between the minimum and maximum values observed within any territory during the 20-year study period (range for area of 57 is 0–332.8 ha; range for edge is 0–28.5 km). In addition, we lacked reliable estimates of juvenile survival for our study area, so we used the reported estimate from an insular population of California Spotted Owls ($\phi_{J,t} = 0.368$; LaHaye et al. 2004). We ran additional simulations in which we allowed juvenile survival to range from 0.318 to 0.418, and the results were nearly identical. We used SAS 9.3 (SAS Institute, Cary, North Carolina, USA) to conduct 1000 simulations in which we randomly generated sets of vegetation class covariate values from uniform probability distributions, estimated λ for each simulation, and regressed λ against each vegetation covariate for all 1000 simulations. The percentage of variation in λ that was explained by each vegetation covariate was a measure of the sensitivity of λ to changes in the vegetation covariate (Wisdom et al. 2000).

Occupancy.—Analogous to the LSA, we assessed which vegetation covariates had the greatest influence on the equilibrium territory occupancy (ψ_{Eq}) by estimating the variation in ψ_{Eq} explained by each covariate that appeared in our best-fitting dynamic

TABLE 3. Model results for analyses of California Spotted Owl reproduction (number of young fledged), apparent survival, territory extinction, and territory colonization at a 6-year time scale in the central Sierra Nevada, 1993–2012.

Model covariates	<i>k</i>	AIC	ΔAIC	<i>w_i</i>
Reproduction				
Female age + hardwoods + medium	8	1205.1	0.00	0.29
Female age + hardwoods	7	1205.6	0.50	0.23
Female age + hardwoods + high	8	1206.0	0.90	0.19
Female age + hardwoods + fire	8	1207.1	2.00	0.11
Female age + hardwoods + low	8	1207.4	2.30	0.09
Female age + hardwoods + understory	8	1207.5	2.40	0.09
Adult survival				
Sex + age + log(57) + edge	9	1311.11	0.00	0.32
Sex + age + log(57) + edge + medium	10	1312.82	1.71	0.14
Sex + age + log(57) + edge + understory	10	1313.07	1.96	0.12
Sex + age + log(57) + edge + high	10	1313.07	1.96	0.12
Sex + age + log(57) + edge + low	10	1313.10	1.99	0.12
Sex + age + log(57) + edge + fire	10	1313.11	2.00	0.12
Sex + age + log(57) + edge + medium + medium × log(57)	11	1314.39	3.28	0.06
Territory extinction				
57 + diversity(57) + high	39	3808.93	0.00	0.30
57 + diversity(57) + high + medium	40	3809.63	0.70	0.21
57 + diversity(57) + high + fire	40	3810.34	1.41	0.15
57 + diversity(57) + high + understory	40	3810.80	1.87	0.12
57 + diversity(57) + high + low	40	3810.85	1.92	0.11
57 + diversity(57) + high + high × 57	40	3810.92	1.99	0.11
57 + diversity(57)	38	3815.70	6.77	0.01
Territory colonization				
log(57) + diversity(57) + fire	39	3800.63	0.00	0.32
log(57) + diversity(57) + fire + medium	40	3802.25	1.62	0.14
log(57) + diversity(57) + fire + understory	40	3802.28	1.65	0.14
log(57) + diversity(57) + fire + low	40	3802.38	1.75	0.14
log(57) + diversity(57) + fire + fire × log(57)	40	3802.63	2.00	0.12
log(57) + diversity(57)	38	3803.02	2.39	0.10
log(57) + diversity(57) + high	39	3804.94	4.31	0.04

Notes: Shown are values for *k*, the number of model parameters; AIC, Akaike's information criterion; ΔAIC, the difference in AIC value from the top-ranked model; and *w_i*, AIC weight. See Table 2 for covariate definitions. Combined vegetation classes 5 and 7 (57) and classes 6 and 7 (67) are as defined in Table 2.

occupancy models. If local extinction (ϵ) and local colonization (γ) rates are constant, ψ_{Eq} can be calculated as $\gamma/(\gamma + \epsilon)$ (MacKenzie et al. 2006). This equation was equivalent to a mainland–island metapopulation model with no rescue effect (Hanski 1999), where each territory was a “subpopulation” within a larger population of Spotted Owl territories. Although owl territories were not strictly subpopulations, they represented breeding units within our study area because we defined them as locations where reproduction was observed at least once. The proportion of occupied territories probably never reached equilibrium during our study, so the actual values of ψ_{Eq} should be interpreted with caution. Nevertheless, we believe that our approach provided general insight into the importance of habitat and forest disturbance to occupancy dynamics of Spotted Owls.

We again set the beta coefficients for all covariate effects equal to their estimated values from the top-ranked models and allowed the vegetation covariates (except for the amount of wildfire, which we will discuss) to vary between their minimum and maximum observed values. As with the LSA, we used SAS 9.3 to conduct 1000 simulations, determined ψ_{Eq} for each simulation, and regressed ψ_{Eq} against each vegetation covariate for all 1000 simulations.

We handled the wildfire covariate, which appeared in the territory colonization model, in a more spatially explicit manner. The effect of wildfire on territory colonization was strongly negative due to a high-severity fire that occurred on our study area in 2001 and completely burned two territories, which subsequently were never colonized by owls. However, most owl territories were unaffected by wildfire because fire occurred within only 12 territories during our study. Therefore, we defined two types of territories, burned and unburned. For each simulation, we randomly varied the number of territories that burned from 1 to 12. For burned territories, we then randomly varied the amount of wildfire from 0 to 400 ha. We separately calculated γ and ψ_{Eq} for burned and unburned territories and calculated an overall ψ_{Eq} for the 74 territories as a weighted average of ψ_{Eq} . We regressed ψ_{Eq} against the average amount of wildfire in all 74 territories; for example, if 100 ha of wildfire occurred in six territories during a simulation, then the average amount of wildfire per territory was 8.1 ha (600/74). In addition, we conducted 1000 additional simulations in which we varied the number of burned territories from 1 to 24 to represent a scenario of increased wildfire activity.

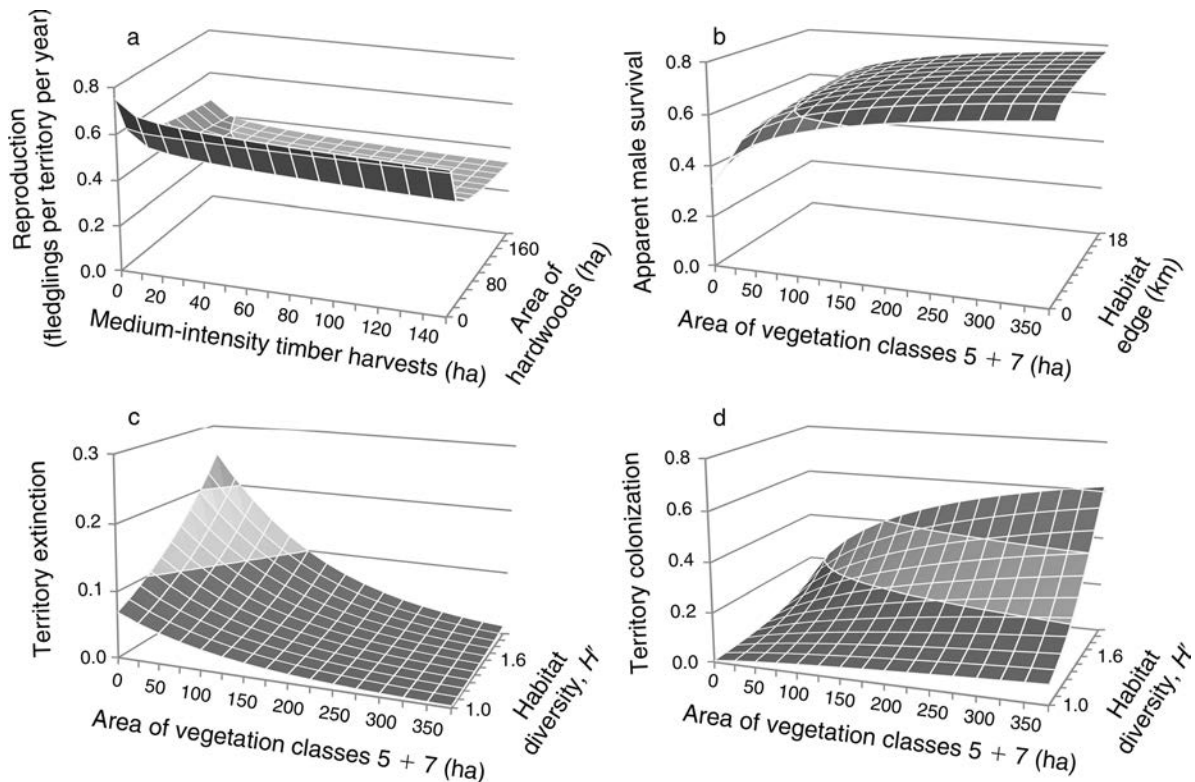


FIG. 2. Vital rates of California Spotted Owls in the central Sierra Nevada, California, 1993–2012, as a function of habitat, timber harvest, and wildfire covariates. We show (a) reproduction for adult females (number of young fledged per territory per year) vs. the total area of medium-intensity timber harvests in the previous 6 years and the area of hardwood forests within owl territories; (b) apparent survival for adult males vs. the total area of vegetation classes 5 and 7 and the amount of habitat edge within owl territories; (c) territory extinction (the probability that a territory occupied in year t becomes unoccupied in year $t + 1$); and (d) territory colonization (the probability that a territory not occupied in year t becomes occupied in year $t + 1$) as a function of the total area of classes 5 and 7 and habitat diversity (Shannon-Wiener index).

RESULTS

The results from the reproduction, survival, and occupancy analyses were similar for the three temporal scales (3, 6, and 9 years) used to calculate the timber harvest and wildfire covariates. Thus, we only present results for models containing timber harvest and wildfire covariates using the 6-year time frame, and we used this time frame for the sensitivity analyses as well. We present results for the 3- and 9-year time frames in Appendix C.

Reproduction

We assessed reproduction on 676 occasions at 70 territories, excluding territories with fewer than three reproductive observations and cases in which territories were occupied by a single owl. There were, on average, 0.612 ± 0.032 young fledged per territory per year (mean $\pm$ SE), and we detected 0, 1, 2, and 3 young on 62.1%, 14.8%, 22.8%, and 0.30% of the sampling occasions, respectively. The autoregressive variance-covariance structure was supported over the compound-symmetric ($\Delta\text{AIC} = 7.6$) or default ($\Delta\text{AIC} = 13.9$) variance-covariance structures. This structure indicated that reproduction in consecutive years was negatively corre-

lated ($\text{ARH1} = -0.148$, $\text{SE} = 0.048$) and was used in all subsequent modeling of fixed effects. The random year and territory effects were either statistically significant or nearly statistically significant (for year, $Z = 2.74$, $P = 0.003$; for territory, $Z = 1.28$, $P = 0.100$), so we retained both random effects when modeling fixed effects.

None of the vegetation covariates considered in step 1 (linear and nonlinear forms of 57 and 67) lowered the AIC value when added to a model containing only female age (Appendix C). The top-ranked model from step 2 included covariates for the area of hardwood forest within a territory and female age, and was 2.90 AIC units lower than the second-ranked model (Appendix C). The best overall model from step 3 contained a covariate for the area of medium-intensity timber harvests, but this model was only 0.50 AIC units lower than the best model from step 2 (Table 3). This model suggested a negative influence of medium-intensity (subscript “med”) timber harvests on reproduction of Spotted Owls, but we found only weak support for this effect based on the degree to which the 95% CI of the beta coefficient overlapped zero ($\beta_{\text{med}} = -0.065$, 95% CI = -0.145 to 0.016 ; Fig. 2a). In addition, adult females (subscript “ad”) had higher

reproduction than subadults ($\beta_{ad} = 0.335$, 95% CI = 0.136–0.533), and reproduction was negatively related to the area of hardwood (“hw”) forests ($\beta_{hw} = -0.123$, 95% CI = -0.219 to -0.027) (Fig. 2a).

Survival

We estimated apparent survival using 350 individual capture histories. The best structure for recapture probability contained covariates for age, sex, and survey effort. Recapture probability was higher for adults ($\beta_{ad} = 1.320$, 95% CI = 0.522–2.119) and males ($\beta_{male} = 0.571$, 95% CI = 0.121–1.022) and was positively correlated with annual survey effort (“eff”) ($\beta_{eff} = 1.607$, 95% CI = 0.342–2.872). We used this structure for recapture probability in all subsequent modeling of survival. Real values of recapture probability estimates were high. When annual survey effort was set equal to its mean value, recapture probability was estimated to be 0.92, 0.87, 0.75, and 0.63 for adult males, adult females, subadult males, and subadult females, respectively.

The top-ranked survival model in step 1 (Appendix C) contained covariates for sex, age, and the logarithm of the combined area of vegetation classes 5 and 7. The top-ranked model from step 2 also contained a covariate for the amount of habitat edge within a territory, and was 7.14 AIC units lower than the second-ranked model (Appendix C). None of the step 3 covariates (timber harvest, wildfire) lowered the AIC value when added to the best model from step 2. The second-ranked overall model ($\Delta AIC = 1.71$) contained a covariate for the area of medium-intensity timber harvests (Table 3), but this model was poorly supported, given that the maximum possible ΔAIC is 2 when an uninformative parameter is added (Arnold 2010). In the top-ranked model, adults ($\beta_{ad} = 0.452$, 95% CI = 0.016–0.889) and males ($\beta_{male} = 0.304$, 95% CI = 0.034–0.575) had higher survival rates than subadults and females, respectively. Survival was positively correlated with the area of 57 ($\beta_{\log(57)} = 1.004$, 95% CI = -0.337 to 2.345) (Fig. 2b) and the amount of edge ($\beta_{edge} = 0.763$, 95% CI = -0.104 to 1.629) (Fig. 2b), but the 95% CI for the beta coefficients overlapped zero. If we set the habitat covariates equal to their mean value for all territories, apparent survival was estimated to be 0.73, 0.66, 0.63, and 0.56 for adult males, adult females, subadult males, and subadult females, respectively.

Occupancy

We estimated territory extinction and colonization probabilities using 4907 survey occasions. The best model for detection probability (p) indicated that p was different for each year. Within years, p was higher at territories with reproducing owls ($\beta_{repr} = 1.566$, 95% CI = 1.339–1.794), at territories containing more forest dominated by large trees ($\beta_{67} = 0.017$, 95% CI = 0.000–0.033), and on surveys subsequent to the initial (“init”) detection of owls at a territory ($\beta_{init} = 1.185$, 95% CI = 1.011–1.359). The probability of initial occupancy (ψ_1) was not dependent on the amount of vegetation classes

57 or 67 within a territory (i.e., ψ_1 was constant). We used this structure for detection and initial occupancy probabilities for all subsequent modeling of territory extinction and colonization. Real values of detection probability estimates were high. When the area of forest with large trees was set equal to its mean value for all territories, detection probability was estimated to be 0.94, 0.83, 0.77, and 0.50 at territories with reproducing owls after the initial detection, territories with reproducing owls before the initial detection, territories with nonreproducing owls after the initial detection, and territories with nonreproducing owls before the initial detection, respectively.

Territory extinction.—The top-ranked model from step 1 (Appendix C) contained a covariate for the combined area of vegetation classes 5 and 7. The top-ranked model from step 2 included a covariate for habitat diversity in addition to the area of 57 and was 4.28 AIC units lower than the second-ranked model (Appendix C). The best overall model from step 3 also included the area of high-intensity timber harvests. In this model, territory extinction was negatively correlated with the area of 57 ($\beta_{57} = -0.117$, 95% CI = -0.189 to -0.044), such that occupied territories with greater amounts of 57 were less likely to become extinct (Fig. 2c). Surprisingly, territory extinction was also negatively correlated with the area of high-intensity timber harvests ($\beta_{high} = -0.776$, 95% CI = -1.327 to -0.224). Finally, territory extinction was positively correlated with habitat diversity ($\beta_{div} = 1.509$, 95% CI = 0.148–2.871) (Fig. 2c).

Territory colonization.—The top-ranked model from step 1 (Appendix C) contained a covariate for the logarithm of the combined area of vegetation classes 5 and 7. The top-ranked model from step 2 contained an additional covariate for habitat diversity and was 1.57 AIC units lower than the second-ranked model (Appendix C). The best overall model from step 3 included the area of wildfire that occurred within a territory. In this model, wildfire had a strong negative effect on territory colonization ($\beta_{fire} = -24.057$), but the standard error was unestimable because of the small number of territories that experienced fire. However, the value for β_{fire} was consistent across all of the models. Territory colonization was positively correlated with the area of 57 ($\beta_{\log(57)} = 1.299$, 95% CI = -0.857 to 3.456) (Fig. 2d) and habitat diversity ($\beta_{div} = 2.985$, 95% CI = -0.222 to 6.191) (Fig. 2d), but the beta coefficients had 95% CI's that overlapped zero, suggesting that these effects were relatively weak.

Sensitivity analyses

Life stage simulation.—Estimates of apparent survival from our simulations ($\hat{\phi}_A = 0.68$, 95% CI = 0.54–0.76; $\hat{\phi}_S = 0.58$, 95% CI = 0.42–0.67) were lower than those previously reported for this population (Blakesley et al. 2010) because we removed part of the capture histories for 14 individuals that relocated to different

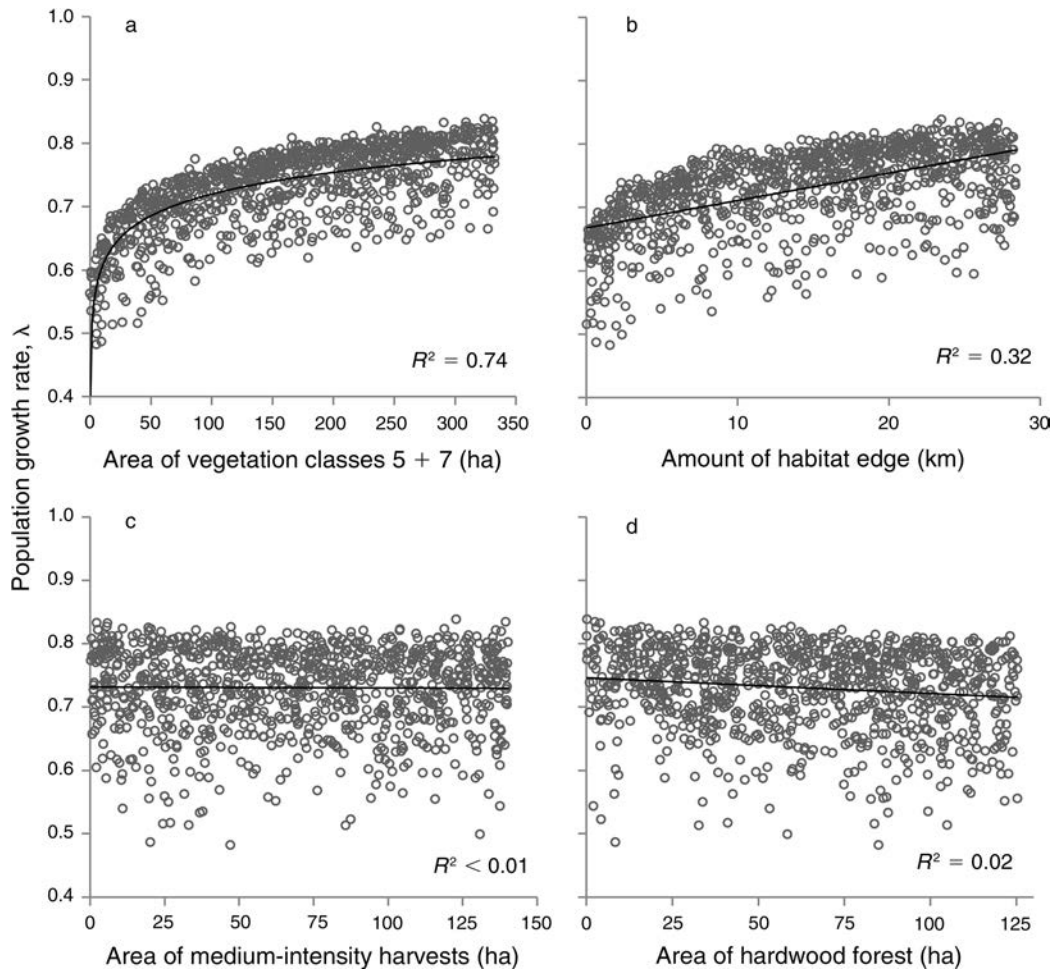


FIG. 3. Results of a life stage simulation analysis that we used to assess the sensitivity of annual population growth rate (λ) of California Spotted Owls to changes in forest vegetation conditions within owl territories. We generated 1000 λ values by randomly drawing (a) area of vegetation classes 5 and 7; (b) amount of habitat edge; (c) area of medium-intensity timber harvests; and (d) area of hardwood forest from a uniform distribution. Panel (a) is a best-fit logarithmic regression, and all other panels are best-fit linear regressions.

territories after a “missing” interval of one or more years (see *Methods: Sensitivity analyses*). Estimates of fecundity from our simulations were higher for adults ($\hat{b}_A = 0.22$ female offspring per female, 95% CI = 0.18–0.28) than for subadults ($\hat{b}_S = 0.05$ female offspring per female, 95% CI = 0.02–0.11), a pattern that has been previously reported for this study population (Blakesley et al. 2010).

Population growth rate was most sensitive (positive correlations) to the area of 57 and habitat edge, the two covariates that also best explained variation in apparent survival. We noted that population growth rate and the area of 57 were clearly related in a nonlinear fashion, so we calculated R^2 using a logarithmic relationship for this covariate; we specified a linear relationship for all other covariates. Population growth rate was positively correlated with the area of 57 ($R^2 = 0.74$; Fig. 3a) and habitat edge ($R^2 = 0.32$; Fig. 3b). In contrast, population growth rate was not sensitive to either of the covariates

used to model reproduction (for area of medium-intensity harvests, $R^2 < 0.01$; for area of hardwood forests, $R^2 = 0.02$; Fig. 3c, d). Population growth rate was always less than 1.0 ($\hat{\lambda} = 0.73$, 95% CI = 0.57–0.82), but we expected our matrix model to underestimate λ in the presence of immigration (Peery et al. 2006). Additionally, as we have noted, our apparent survival estimates were biased low. Nonetheless, changes in population growth rate allowed us to evaluate the relative importance of each covariate.

Occupancy.—Estimates of territory colonization from our simulations were strongly dependent upon the occurrence of wildfire during the previous six years ($\hat{\gamma}$ without fire = 0.21, 95% CI = 0.04–0.52; $\hat{\gamma}$ with fire = 0.00, 95% CI = 0.00–0.00) because we only observed three postfire colonization events at burned territories in the following six years. However, fire did not negatively affect territory occupancy in all cases. For example, the largest and most intense fire occurred on our study area

in 2001 and impacted nine owl territories. Five of these territories remained occupied every year after the fire, and thus, postfire colonization could not occur at these sites. Estimates of territory extinction were low ($\hat{\epsilon} = 0.03$, 95% CI = 0.00–0.12), which reflected the strong site fidelity displayed by Spotted Owls (e.g., Blakesley et al. 2005, Seamans and Gutiérrez 2007a).

Equilibrium occupancy was most sensitive (positive correlation) to the area of 57 within a territory. We again noted a nonlinear relationship between equilibrium occupancy and the area of 57 and calculated R^2 using a logarithmic relationship for this covariate ($R^2 = 0.87$; Fig. 4a). Equilibrium occupancy was not sensitive to changes in habitat diversity ($R^2 = 0.02$; Fig. 4b) or high-intensity timber harvests ($R^2 = 0.01$; Fig. 4c). Equilibrium occupancy was weakly negatively correlated with wildfire when it occurred at the same frequency as during our study ($R^2 = 0.02$; Fig. 4d). However, when we doubled the frequency of wildfire to represent a future scenario of increased fire activity, we found a stronger negative association between the area burned and equilibrium occupancy ($R^2 = 0.11$; Fig. 4e). As a result, equilibrium occupancy was higher under the scenario with fewer fires ($\hat{\psi} = 0.78$, 95% CI = 0.37–0.96) than the scenario with more fires ($\hat{\psi} = 0.72$, 95% CI = 0.36–0.94).

DISCUSSION

We characterized associations between territory-scale changes in forest conditions and demographic rates in a declining population of California Spotted Owls to assess the potential consequences of implementing landscape-scale fuel treatments in the Sierra Nevada. Although the correlative nature of our study posed constraints on inferences, we used 20 years of data on owl demography, forest treatments, and detailed changes in forest conditions. Our study differed from most previous, long-term Spotted Owl studies in that we quantified habitat within owl territories on an annual basis, rather than assuming that habitat was static over time. Thus, we believe that the relationships that we detected can help to guide forest management intended to balance reductions in high-severity fires with the needs of a key old-forest-associated species in the Sierra Nevada, as well as provide insight into mechanisms responsible for observed declines in California Spotted Owls in this region.

The amount of forest with high (>70%) canopy cover dominated by medium- or large-sized trees was the most important predictor of variation in demographic rates; this variable occurred in the top-ranked models for survival, territory extinction, and territory colonization rates, and explained far more variation in population growth rate and equilibrium occupancy than other covariates based on our simulations. This result is consistent with previous studies of Northern and California Spotted Owls that found a strong correlation between the area of high-canopy-cover forest and adult

survival, and in some cases, reproduction and occupancy of territories (Franklin et al. 2000, Blakesley et al. 2005, Dugger et al. 2005, Seamans and Gutiérrez 2007a). We also found that forests with large trees and a lower threshold of canopy cover (>30%) were not a significant predictor of owl vital rates. This finding suggested that high canopy cover was a more important habitat component than large trees, although forests containing both were probably the highest quality habitat. The specific reasons for why high-canopy-cover forests are important for California Spotted Owls are unknown, but prey availability, predator avoidance, or microclimate may all be important factors (Verner et al. 1992). Nevertheless, consistent positive associations between demographic rates of Spotted Owls and forest with high canopy cover across studies and subspecies indicate the importance of these forest conditions for Spotted Owl populations.

The positive association between owl demographic rates and high-canopy-cover forest, coupled with the average loss of 10.6 ha (7.4%) of high-canopy-cover forest within territories on the DSA from 1993–2012 (Fig. 5a), suggests that habitat loss may have been at least partially responsible for the observed ~30% decline in abundance and territory occupancy in our study population (Tempel and Gutiérrez 2013). We were unable to assess the potential lag effects associated with habitat change prior to 1993, when more stringent harvesting guidelines were implemented on public land (USFS 1993); thus, observed declines could also reflect the historic legacy of timber harvesting. Nevertheless, many factors not considered here such as predation, prey availability, and disease, also could have contributed to population declines. Associations between high-canopy-cover forest and both population growth and equilibrium occupancy were nonlinear such that further loss of habitat could lead to relatively rapid declines in abundance and occupancy (Figs. 3a and 4a). For example, 26 owl territories currently contain between 100 and 150 ha of high-canopy-cover forest (Fig. 5b). If the average amount of high-canopy-cover forest within territories were reduced from 150 to 100 ha, the estimated decrease in population growth rate ($\lambda_{150\text{ha}} = 0.740$, $\lambda_{100\text{ha}} = 0.720$) would lead to a significant difference in realized population change when extrapolated over long time periods. We expected our estimates of population growth rate to be biased low, but the importance of forest with high canopy cover nevertheless can be assessed by relative changes in population growth rate.

As predicted, medium-intensity timber harvests characteristic of proposed fuel treatments were negatively related to reproduction of Spotted Owls in our study. Reproduction appeared sensitive to modest amounts of medium-intensity harvests, and was predicted to decline from 0.54 to 0.45 when 20 ha were treated (assuming the mean area of hardwoods in territories, 60 ha). Greater areas harvested in this manner only resulted in slightly

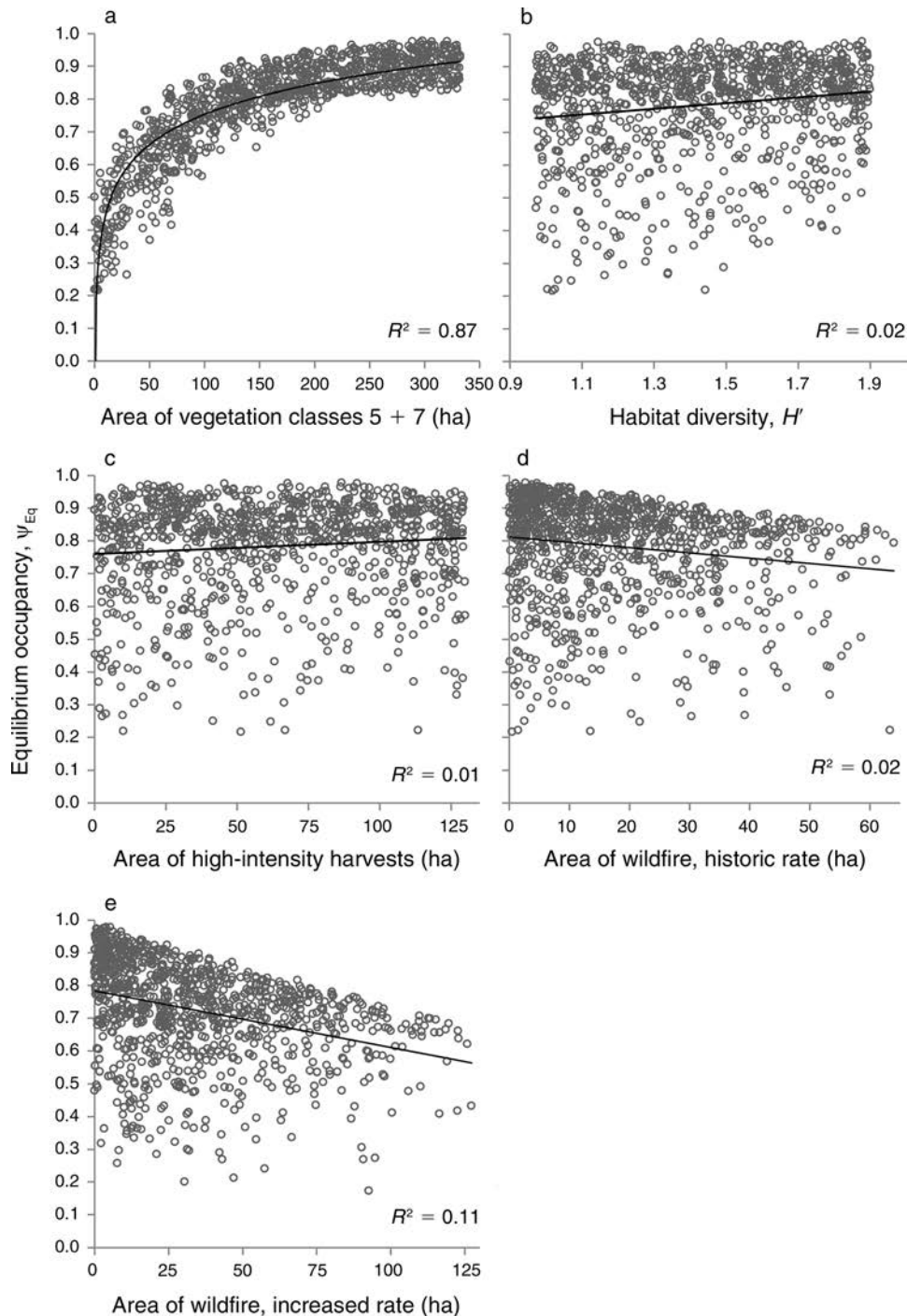


FIG. 4. Assessment of the sensitivity of equilibrium occupancy (ψ_{Eq}) of California Spotted Owl territories to changes in forest vegetation conditions within owl territories. We generated 1000 ψ_{Eq} values by randomly drawing: (a) area of vegetation classes 5 and 7; (b) habitat diversity (Shannon-Wiener index); and (c) area of high-intensity timber harvests from a uniform distribution. Panels (d) and (e) were generated under two different wildfire scenarios: a maximum of 12 territories burned (the observed number during our study) and a maximum of 24 territories burned (representing the potential for increased fire frequency in the future), respectively. Panel (a) is a best-fit logarithmic regression, and all other panels are best-fit linear regressions.

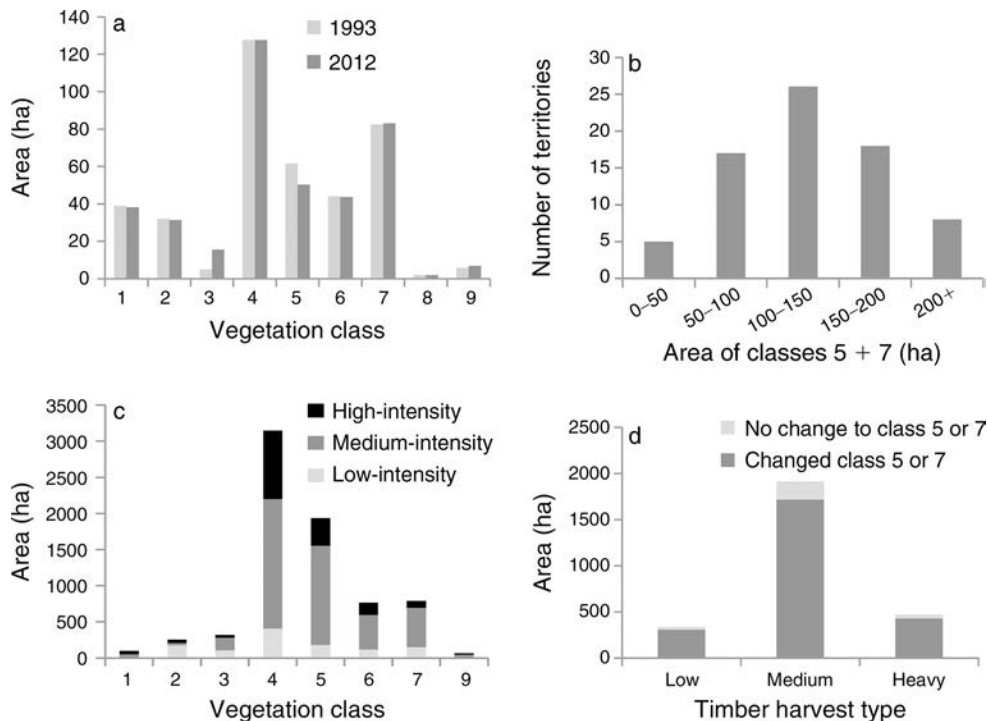


FIG. 5. Vegetation conditions within California Spotted Owl territories on our study area in the central Sierra Nevada, California, as represented by (a) the area of each vegetation class in owl territories on the Density Study Area in 1993 and 2012; (b) the number of owl territories containing different areas of vegetation classes 5 and 7 in 2012; (c) the area of low-, medium-, and high-intensity timber harvests that occurred in each vegetation class from 1993–2012 (class 8, water or barren rock, was omitted here as no timber harvest was possible); and (d) the area of low-, medium-, and high-intensity timber harvests occurring in vegetation classes 5 and 7 that did or did not result in a change in vegetation class from 1993 to 2012.

larger declines in reproduction (Fig. 2a). The mechanism linking medium-intensity timber harvests to declines in reproduction is not entirely clear, but the thinning practices characteristic of medium-intensity harvests typically reduce the vertical forest structure and understory complexity that are believed to be important characteristics of foraging conditions used by Spotted Owls (Verner et al. 1992). Although we detected an overall effect of medium-intensity timber harvests on reproduction, we did not detect an effect of understory removal independent of modifications to the overstory for medium-intensity harvests. Understory removal is generally an important component of fuel-reduction strategies, but we caution that medium-intensity harvesting with understory treatments occurred on only 5.2% of the total area within owl territories, which could have limited our power to detect effects.

Unlike reproduction, we did not detect a relationship between the area of medium-intensity harvests and apparent survival or territory occupancy. The absence of an association is perhaps not surprising, given the Spotted Owl's "bet-hedging" life history strategy in which individuals have evolved long life spans and forgo reproduction when environmental conditions are unfavorable without compromising lifetime reproductive success (Seamans and Gutiérrez 2007b). In addition, only

42.8% of medium-intensity harvests occurred in forests with high canopy cover; thus, over half of these harvests occurred in habitats that might be less important to Spotted Owls (Fig. 5c). When medium-intensity harvests were implemented within high-canopy-cover forests, they reduced the canopy sufficiently for mapped polygons to be reclassified into a lower-canopy-cover vegetation class in 90.1% of these treated areas (Fig. 5d). As we described previously, such changes were associated with reductions in survival and territory colonization rates, as well as increases in territory extinction rates. As a result, we believe that the most appropriate inference about the influence of medium-intensity harvesting practices is that they appear to reduce reproductive potential, and when implemented in forests with high canopy cover, are likely to reduce survival and territory occupancy as well.

Contrary to our prediction, the probability of a territory going extinct was reduced in proportion to the area harvested with high-intensity practices such as clear-cutting and shelterwood harvest. In principle, harvesting prescriptions creating small gaps might promote brushy habitat suitable for prey species such as woodrats and increase prey availability for Spotted Owls along the edges of forested habitats (Sakai and Noon 1997). Similarly, we found that owl survival and population growth were positively associated with the

amount of habitat edge between shrubs/saplings and forests dominated by trees ≥ 30.5 cm dbh, so the juxtaposition of owl and prey habitat could be important, as suggested by Franklin et al. (2000). Nevertheless, these associations are largely speculative without direct evidence of foraging by owls and elevated prey availability along ecotones. Moreover, high-intensity treatments occurred on only 5.4% of the total area within our owl territories and larger scale implementation of heavy harvesting could have adverse impacts on Spotted Owls. Finally, flying squirrels are the most important prey by biomass within our study area (R. J. Gutiérrez, *unpublished data*), and intensive harvesting practices are believed to negatively impact this species (Waters and Zabel 1995, Manning et al. 2012). Thus, while detailed studies of prey availability and Spotted Owl foraging near brush habitat are merited, we believe it would be premature to implement such timber-harvesting practices as a tool for managing prey availability for California Spotted Owls.

Although our results suggested that fuel treatments can have negative and direct impacts on Spotted Owl habitat quality in the short term, comprehensive assessments must consider the potential long-term benefits of reduced wildfire risk. Long-term benefits will depend on both the risk that fire poses to Spotted Owls and the extent to which fuel treatments reduce high-severity fires. We detected a large decline in territory colonization following wildfire, but not all burned territories were negatively affected by fire. Several burned territories remained occupied in all years after a fire (see *Results: Sensitivity analyses*); as a result, colonization could not occur, by definition. Thus, while our results were somewhat consistent with other studies that detected adverse impacts of high-severity fires on Spotted Owls, particularly when coupled with salvage logging (Clark et al. 2013, Lee et al. 2013), the effect of wildfire on Spotted Owls and their habitat is undoubtedly complex (Bond et al. 2009, 2013). Nonetheless, because equilibrium occupancy declined more under a scenario of increased fire activity (Fig. 4e), which is projected under some climate change scenarios (Liu et al. 2013), we believe a valid need exists to reduce the risk of wildfire to Spotted Owls. Previous modeling efforts indicated that the benefits of reducing habitat loss from high-severity fires outweighed the impacts of fuel treatments on forest conditions used by Spotted Owls (Lee and Irwin 2005, Ager et al. 2007). However, these studies were either conducted for Northern Spotted Owls in another physiographic province (Ager et al. 2007) or did not assess the immediate effects of fuel treatments on California Spotted Owl demographic rates using empirical data (Lee and Irwin 2005). Thus, additional research is needed to determine the long-term trade-offs between direct reductions in owl habitat from fuel treatments vs. habitat loss from increased fire frequency or severity.

We suggest the following caveats from our study when considering the impact to Spotted Owls from forest fuel

treatments and wildfire. First, our study was observational, not experimental, and thus observed relationships between covariates and owl demographic rates were correlative and not directly attributable to cause and effect. Second, a broad range of timber harvests occurred within owl territories during our study, which may have confounded our ability to assess specific management practices (e.g., fuel-reduction treatments following current management prescriptions; USFS 2004). Nevertheless, proposed fuel-reduction treatments have effects on forest structure similar to those in our medium-intensity timber harvest category (Appendix B). Third, we used aerial photos to compile our vegetation map, which required us to subjectively categorize vegetation classes into relatively coarse bins. Thus, we were unable to assess the potential effects of small (e.g., 10%) reductions in canopy cover that did not result in changes in vegetation class. Our mapping approach also precluded the inclusion of potentially important habitat elements such as large, residual trees and understory structure. Large trees are known to be important components of nesting and roosting conditions used by Spotted Owls (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997), and the high-canopy-cover forest that we found to be highly correlated with owl demographic rates included vegetation class 7 (trees with dbh ≥ 76.2 cm). Finally, the potential effects of habitat, forest treatments, and wildfire within owl territories were probably confounded with differences in individual quality, which can be an important source of variation in avian demographic rates (e.g., Goodburn 1991, Espie et al. 2004, Sergio et al. 2009). Despite these caveats, we identified several reasonable predictors of Spotted Owl demographic parameters supported by prior knowledge of Spotted Owl environmental requirements that we believe can contribute to forest management.

Conclusions

Our results suggest that reductions in the area of high-canopy-cover forest resulting from either logging or high-severity wildfire could reduce the viability of California Spotted Owl populations and may be contributing to ongoing declines in abundance and territory occupancy (Conner et al. 2013, Tempel and Gutiérrez 2013). Nevertheless, our results also suggest that fuel treatments that occur in forests with lower canopy cover ($< 70\%$) or do not significantly reduce canopy in high-canopy-cover forests are less likely to have adverse impacts on Spotted Owls. While such a constraint may seem restrictive because fuel-reduction treatments necessarily target dense, fire-prone stands, we note that 50.7% of all medium-intensity harvests implemented from 1993 to 2012 occurred in medium-sized forest with low canopy cover (vegetation class 4 = 40.1%) or large-sized forest with low canopy cover (vegetation class 6 = 10.6%; Fig. 5c). Moreover, fuel treatments in dense stands can emphasize thinning from below while maintaining sufficient canopy cover and some vertical stand structure (Verner et al. 1992).

Zielinski et al. (2013) recently concluded that it may be possible to implement fuel-reduction treatments that achieve fire-reduction goals without affecting occupancy by fishers, another species associated with older forests in the Sierra Nevada. However, they did not distinguish among different types of timber harvest, nor did they assess where timber harvests occurred with respect to preexisting vegetation types. We recommend that landscape-scale fuel treatments intended to reduce fire risk in the Sierra Nevada proceed with caution to reduce the chance of impacting old-forest-associated species, particularly in high-canopy-cover forests. Specifically, we recommend that fuel treatments focus on ladder fuels and reduction in tree density while maintaining relatively high canopy cover. Given the uncertain relationship between timber harvest and demography of Spotted Owls, we suggest that landscape-scale fuel treatments be accompanied by a rigorous monitoring program.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: <http://dx.doi.org/10.1890/13-2192.1.sm>

Evaluating short- and long-term impacts of fuels treatments and simulated wildfire on an old-forest species

DOUGLAS J. TEMPEL,^{1,†} R. J. GUTIÉRREZ,² JOHN J. BATTLES,³ DANNY L. FRY,³ YANJUN SU,⁴ QINGHUA GUO,⁴ MATTHEW J. REETZ,¹ SHEILA A. WHITMORE,¹ GAVIN M. JONES,¹ BRANDON M. COLLINS,⁵ SCOTT L. STEPHENS,³ MAGGI KELLY,³ WILLIAM J. BERIGAN,¹ AND M. ZACHARIAH PEERY¹

¹Department of Forest and Wildlife Ecology, 1630 Linden Drive, University of Wisconsin-Madison, Madison, Wisconsin 53706 USA

²Department of Fisheries, Wildlife and Conservation Biology, 1980 Folwell Avenue,
University of Minnesota, St. Paul, Minnesota 55108 USA

³Ecosystem Sciences Division, Department of Environmental Science, Policy, and Management, 130 Mulford Hall,
University of California, Berkeley, California 94720-3114 USA

⁴Sierra Nevada Research Institute, School of Engineering, University of California,
5200 North Lake Road, Merced, California 95343 USA

⁵USDA Forest Service, Pacific Southwest Research Station, 1731 Research Park Drive, Davis, California 95618 USA

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Abstract. Fuels-reduction treatments are commonly implemented in the western U.S. to reduce the risk of high-severity fire, but they may have negative short-term impacts on species associated with older forests. Therefore, we modeled the effects of a completed fuels-reduction project on fire behavior and California Spotted Owl (*Strix occidentalis occidentalis*) habitat and demography in the Sierra Nevada to assess the potential short- and long-term trade-offs. We combined field-collected vegetation data and LiDAR data to develop detailed maps of forest structure needed to parameterize our fire and forest-growth models. We simulated wildfires under extreme weather conditions (both with and without fuels treatments), then simulated forest growth 30 years into the future under four combinations of treatment and fire: treated with fire, untreated with fire, treated without fire, and untreated without fire. We compared spotted owl habitat and population parameters under the four scenarios using a habitat suitability index developed from canopy cover and large-tree measurements at nest sites and from previously derived statistical relationships between forest structure and fitness (λ) and equilibrium occupancy at the territory scale. Treatments had a positive effect on owl nesting habitat and demographic rates up to 30 years after simulated fire, but they had a persistently negative effect throughout the 30-year period in the absence of fire. We conclude that fuels-reduction treatments in the Sierra Nevada may provide long-term benefits to spotted owls if fire occurs under extreme weather conditions, but can have long-term negative effects on owls if fire does not occur. However, we only simulated one fire under the treated and untreated scenarios and therefore had no measures of variation and uncertainty. In addition, the net benefits of fuels treatments on spotted owl habitat and demography depends on the future probability that fire will occur under similar weather and ignition conditions, and such probabilities remain difficult to quantify. Therefore, we recommend a landscape approach that restricts timber harvest within territory core areas of use (~125 ha in size) that contain critical owl nesting and roosting habitat and locates fuels treatments in the surrounding areas to reduce the potential for high-severity fire in territory core areas.

Key words: California Spotted Owl; fuels treatment; habitat; Sierra Nevada; *Strix occidentalis occidentalis*; territory fitness; territory occupancy; wildfire.

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† **E-mail:** dtempel@wisc.edu

INTRODUCTION

The management of fire-adapted forests in the western U.S. is increasingly challenged by the need to consider the ecological impacts of wildfire and fuels-reduction treatments intended to modify wildfire behavior (Stephens et al. 2013). Historic fire regimes in many of these forests were characterized by fires burning at intervals of less than 20 years and having primarily low- and moderate-severity fire effects but interspersed with some areas of high-severity effects (Agee 1993, Skinner and Chang 1996), and some high-severity fire apparently occurred with regularity (Collins and Stephens 2010, Hanson and Odion 2014). This type of fire regime resulted in highly heterogeneous landscapes in which vegetation conditions were governed by complex interactions between topography, site productivity, and disturbance (Collins et al. 2015, Stephens et al. 2015). However, decades of fire exclusion have disrupted historic fire regimes, altered forest structure and landscape vegetation patterns, increased forest fuel loads, and led to increases in the frequency of large fires (Westerling et al. 2006), as well as increases in proportions and patch sizes of high-severity fire (Miller et al. 2009, Miller and Safford 2012). In addition, further increases in fire activity are expected under most climate change scenarios (Westerling and Bryant 2008, Liu et al. 2013). High-severity fire effects (defined by >75% mortality of overstory trees) can impact ecosystem processes such as erosion rates, stream sedimentation, and carbon sequestration (Benavides-Solorio and MacDonald 2001, Breshears and Allen 2002), as well as modify forest structure and wildlife habitat. While some wildlife species become more abundant after high-severity fire (Smucker et al. 2005, Fontaine and Kennedy 2012), other species, particularly those associated with older forests, may be negatively impacted by habitat loss resulting from large patches of high-severity fire (e.g., Lee et al. 2013). Old-forest species with large home ranges are typically rare and preventing their

populations from reaching critically small sizes is widely regarded as an important policy objective (e.g., National Forest Management Act of 1976), in part because meeting the habitat needs of such species might protect broader old-forest communities (Temple 1997).

To reduce the potential for large patches of high-severity fire, forest managers are implementing fuels-reduction treatments in many western U.S. forests (e.g., USFS 2004). Fuels-reduction treatments primarily remove duff, downed wood, shrubs, and smaller trees (i.e., surface and ladder fuels), and fire models suggest that these treatments can reduce potential fire spread and intensity across landscapes (Ager et al. 2007, Finney et al. 2007). However, these treatments also reduce canopy cover and vertical forest structure, which could have negative short-term impacts on old-forest-associated species such as the spotted owl (*Strix occidentalis*). Hypothetically, such short-term negative impacts would be outweighed by the longer-term benefits from reductions in the amount of habitat lost during future wildfires, as has been suggested by previous simulations (Ager et al. 2007, Roloff et al. 2012). Similarly, the current management plan for the national forests in the Sierra Nevada posits that fuels-reduction treatments will result in long-term increases in the amount of suitable California Spotted Owl (*S. o. occidentalis*) habitat while acknowledging the potential for short-term negative impacts (USFS 2004). Indeed, a recent study found that fuels-reduction treatments can negatively impact spotted owl populations over shorter time frames (<10 years) if they reduce the amount of high-canopy-cover ($\geq 70\%$) forest dominated by trees ≥ 30.5 cm diameter at breast height (dbh) within owl territories (Tempel et al. 2014a). However, whether short-term impacts of fuels treatments to spotted owls and their habitat in the Sierra Nevada will be offset by long-term gains resulting from reductions in high-severity fire is unknown.

Here, we used fire and forest-growth models to simulate how fuels treatments might alter the

effects of fire on spotted owl habitat and demographic rates at the “fireshed” scale over a 30-year period in the Sierra Nevada. Firesheds are contiguous areas with similar fire histories and have been identified by the U.S. Forest Service as useful landscape units for fuels-treatment planning and effective fire suppression (Bahro et al. 2007, North et al. 2015). Firesheds are commonly delineated by sub-watershed boundaries and range in size from ~3,200 to 16,200 ha within the Sierra Nevada (North et al. 2015). We chose this spatial scale because of its management relevance (i.e., project planning) and because our field-based vegetation sampling would not have been feasible at larger spatial scales. In contrast to previous studies that relied upon simulated treatments (Ager et al. 2007, Roloff et al. 2012; but see Stephens et al. 2014), our study involved actual fuels-reduction treatments implemented by the U.S. Forest Service and was intended to assess the efficacy of existing management guidelines governing forest management at a bio-regional scale. We intensively sampled the vegetation within field plots before and after the implemented treatments and coupled this fine-scale vegetation data with LiDAR data to quantify changes in forest structure and parameterize fire and forest-growth models. Finally, we linked spotted owl demographic rates to changes in vegetation conditions resulting from fuels treatments and wildfire using data from a long-term demography study, as few previous studies have simulated the short- versus long-term trade-offs of fuel treatments on wildlife population dynamics (however, see Scheller et al. 2011). We specifically considered two demographic parameters at the scale of an owl territory: (1) fitness, which we defined as the population growth rate (λ) conferred on resident owls by habitat conditions within the territory (Franklin et al. 2000); and (2) equilibrium occupancy, which is the level at which occupancy probability at a territory will stabilize when colonization and extinction probabilities remain constant (MacKenzie et al. 2006).

We hypothesized that fuels treatments would result in a short-term loss of owl habitat, but in the event of simulated wildfire, these treatments would result in a long-term increase in owl habitat (relative to the untreated landscape) by reducing owl habitat loss to fire. Thus, if a fire

was simulated under extreme weather conditions shortly after treatment implementation, we predicted the treatments to reduce the amount of habitat lost during the fire and to result in greater habitat amounts 30 years post-fire because forest growth would be insufficient to compensate for the loss of overstory trees during this timeframe. If no fire was simulated after treatment implementation, we expected that the amount of habitat would initially decline, but that similar amounts would be present on treated and untreated landscapes after 30 years because of forest regrowth (Collins et al. 2011). Because owl demographic rates are strongly and positively correlated with the amount of high-canopy-cover ($\geq 70\%$) forest within owl territories (Tempel et al. 2014a), we predicted that owl demographic rates would follow similar patterns as habitat amount. Thus, we hypothesized that fuels treatments would reduce territory fitness and occupancy in the short-term, but result in higher fitness and occupancy after 30 years in the event of simulated fire.

MATERIALS AND METHODS

Study area

Our 13,482-ha Last Chance Study Area (LCSA) was located within the Tahoe National Forest in the central Sierra Nevada, California (Fig. 1). Elevations ranged from 600 to 2,200 m. The vegetation was primarily mixed-conifer forest dominated by white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), incense-cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), ponderosa pine (*Pinus ponderosa*), and California black oak (*Quercus kelloggii*), with lesser amounts of other forest types and montane chaparral. The LCSA had a Mediterranean climate with an average of 1,182 mm of precipitation, most of which fell as snow, from 1990 to 2008 (Hell Hole Remote Automated Weather Station). The historic fire regime in this region mainly consisted of frequent, low-to moderate-severity fire occurring every 5–15 years (Stephens and Collins 2004).

As part of the experimental design for SNAMP, the study area was composed of a central treatment fireshed (4,293 ha) and two adjacent watersheds to the north and south that together served as a control ‘fireshed’ (5,658 ha; Fig. 1). We further expanded the study area by an

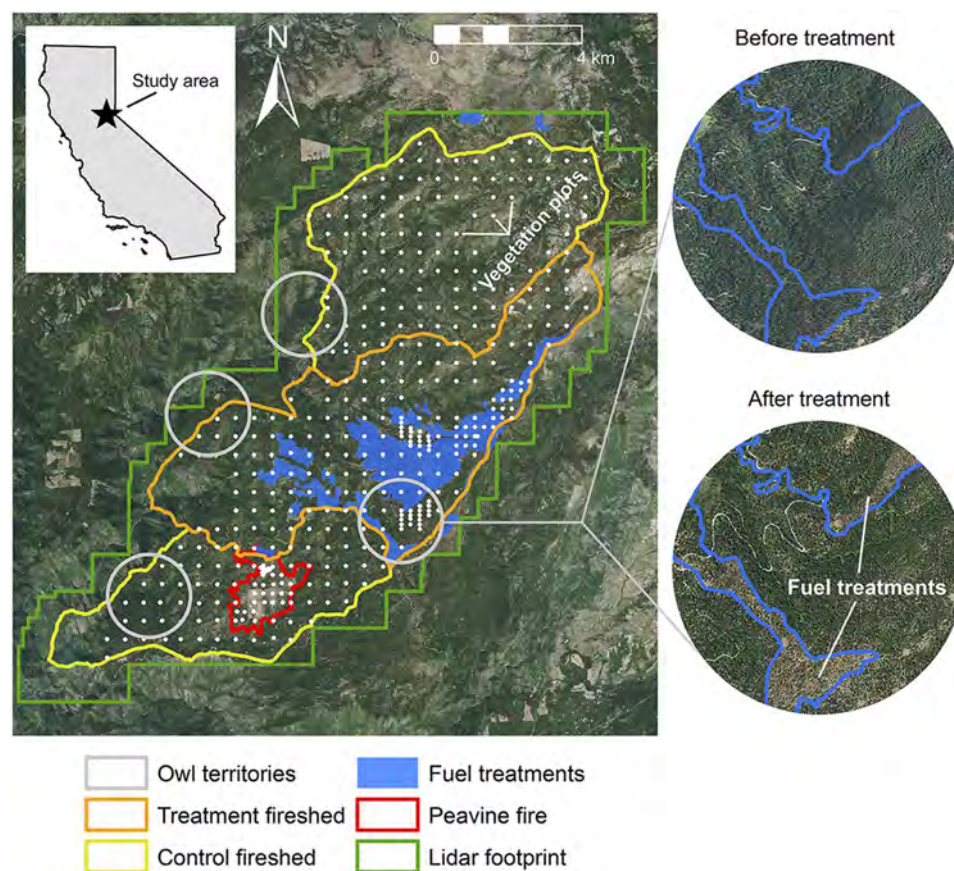


Fig. 1. Map of the Last Chance Study Area in the central Sierra Nevada, California, showing the delineation of treatment and control firesheds, the locations of four California Spotted Owl (*Strix occidentalis occidentalis*) territories used in our demographic analyses, fuel treatments conducted in 2011–2012, the plot network for ground-based sampling of forest vegetation before and after the fuel treatments, and an aerial overview of part of the treated area before and after the fuel treatments.

additional 3,531 ha of untreated landscape covered by the LiDAR footprint to incorporate additional owl territories (Fig. 1). Fuels-reduction treatments were implemented within the treatment fireshed by the U.S. Forest Service during 2011–2012 as part of the Sierra Nevada Adaptive Management Project (SNAMP; Sierra Nevada Adaptive Management Project 2014). The fuels treatments, also known as Strategically Placed Landscape Area Treatments (SPLATs), followed the guidelines specified in the 2004 management plan for national forests in the Sierra Nevada (USFS 2004). The management plan specified that no trees ≥ 76.2 cm can be harvested, at least 40% canopy cover must be retained, and at least 40% of a stand's basal area must be retained.

Treatments were implemented on 942 ha (7.0% of the total study area) as follows: 561 ha of mechanical thinning (tractor and cable), 247 ha of prescribed fire, and 134 ha of mastication of shrubs and small trees. Although no treatments were implemented in the control fireshed, the 2008 Peavine Fire burned 268 ha within the southern unit of the control fireshed (Fig. 1). Collins et al. (2011) modeled treatments and hazardous fire potential in the same study area, but focused on the treatment fireshed only.

Development of vegetation map

We developed a pre-treatment vegetation map using a combination of LiDAR, high-resolution digital color-infrared (CIR) aerial imagery, and an

intensive network of field plots. First, we used LiDAR and CIR data to create an initial polygon-based map where the polygons represented areas of homogeneous vegetation in terms of species, vertical structure, basal area, and canopy cover. The mean polygon size was 9.4 ha (range = 0.9–72.6 ha). We collected the LiDAR and CIR data before the fuels-reduction treatments, and we sampled vegetation at the field plots before and after treatment. We then used the field-plot data to impute detailed attributes (e.g., tree lists and fuels models) for each polygon. Thus, we derived two different maps (with and without treatment), which we used in fire and forest-growth modeling. We used field-plot data to assess the accuracy of the pre-treatment and post-treatment maps in terms of canopy cover and large tree density, which were the variables we used to identify spotted owl habitat (see *Materials and methods: Assessing effects of fuels treatments and fire on spotted owl habitat*). We found that values for percent canopy cover and large tree density were similar for field plots and their associated map polygon, although on average the field plot values were slightly lower than the map values. For percent canopy cover, the average difference for the pre-treatment map was –5.42% canopy cover (SE = 1.12), and for the post-treatment map the average difference was –2.05% canopy cover (SE = 1.21; Appendix A). For large tree density, the average difference for the pre-treatment map was –7.05 large trees per hectare (SE = 1.51), and for the post-treatment map the average difference was –4.30 large trees per hectare (SE = 1.55; Appendix A).

We contracted with the National Center for Airborne LiDAR Mapping (National Center for Airborne Laser Mapping 2011) to collect small-footprint, multiple-return airborne LiDAR data with a point density of 6–10 points/m² in September 2008, and we obtained 1 × 1 m² resolution CIR data collected by the National Agriculture Imagery Program (NAIP) in 2005. After initial processing of the LiDAR and CIR data, we used an object-based segmentation approach to delineate polygons of homogeneous vegetation types. We then applied an unsupervised classification strategy to label the different vegetation types based on the Bayesian Information Criterion algorithm, which is used to automatically determine the optimized number

of vegetation groups. We identified 8 vegetation types on our study area—low shrub, high shrub, open true fir, pine forest, cedar forest, young mixed-conifer forest, and mature mixed-conifer forest. The dominant vegetation type on the study area was mixed-conifer forest (56% mature, 19% young); the other forest types were present in lesser amounts (13% cedar, 7% pine, 4% open true fir). Chaparral (low and high shrubs) covered only 1% of the study area. Post-treatment LiDAR was collected in 2013 and was used to delineate actual treatment areas based on a change-detection algorithm to identify where forest structure noticeably changed between the two LiDAR acquisitions. This approach was employed because there can be inconsistencies between agency-generated treatment polygons and actual treatment extent on the ground.

We sampled forest vegetation at field plots that were spaced at 500-m intervals across the LCSA, except the southwest corner of the LCSA where extreme topography precluded sampling (Fig. 1). We sampled more intensively at 125- and 250-m spacing around instrument locations for a separate hydrological study. In August 2008, we also intensively sampled the area burned by the Peavine Fire. In total, we sampled 408 plots in 2007–2008 (pre-treatment) and 369 plots in 2013 (post-treatment). We briefly summarize the vegetation sampling here, but refer the reader to Collins et al. (2011) for greater detail. We sampled within 0.05-ha circular plots and recorded information on individual trees using three different sampling intensities based on tree size: (1) throughout the entire plot for trees ≥19.5 cm dbh; (2) within a random one-third of the plot (167 m²) for trees 5.0–19.4 cm dbh; and (3) along a random belt transect (76 m²) for trees <5.0 cm dbh. We recorded tree species, vigor, crown position, dbh, total height, and height to live crown base (live trees only) for all trees in the upper two size classes, and species and dbh for trees in the smallest size class. In addition, we sampled downed wood, litter, duff fuels, and woody shrub cover on three randomly chosen transects within each plot. We used the line-intercept method to sample downed woody fuels (van Wagner 1968, Brown 1974), and we recorded percent cover and average height for woody shrubs intersecting each transect.

We then used the field-plot data to impute

detailed vegetation attributes for each polygon of the vegetation map for use in the fire and forest-growth modeling. We developed an imputation procedure to assign three field plots to each map polygon based on their similarity in “gradient space” (Ohmann and Gregory 2002). We performed a multivariate analysis of the plot data to define the gradient space. The definition of the gradient nearest neighbors for each polygon (*sensu* Ohmann and Gregory 2002) included topographic variables (e.g., slope, aspect, elevation), canopy structure (percent canopy cover and an index of large tree density), and vegetation type. To maintain some of the fine-scale heterogeneity observed in the field, we identified all plots in the 95th percentile in terms of nearest neighbor distance for each stand and then randomly assigned three of those plots to the stand. Our pre-treatment map represented conditions after the Peavine Fire occurred (see *Materials and methods: Study area*) because we collected the remotely sensed data and sampled additional field plots within the burned area after the fire. The treatment scenario differed from the no treatment scenario in what field-plot data were used to impute vegetation attributes for polygons where treatments occurred. For the treatment scenario, we used post-treatment tree lists from treated plots ($n = 49$) for polygons that experienced noticeable structural change based on LiDAR change detection or were confirmed on-the-ground to have been burned by prescribed fire.

Modeling forest dynamics and fire

We considered four scenarios when modeling forest dynamics and wildfire: (1) with treatments and with fire; (2) without treatments and with fire; (3) with treatments and without fire; and (4) without treatments and without fire. For the “with fire” scenarios, we used FARSITE (Finney 1998) to simulate a single fire for both the treated and untreated landscape based on the weather conditions during the 2001 Star Fire, which burned 6,817 ha, including 314 ha on the northeast edge of our study area (Fig. 2). Approximately 39% of this fire burned at high severity (www.mtbs.gov; accessed on 4 February 2015). FARSITE is a spatially explicit fire-growth model that uses several topographic, forest-structure, and fuel-model map layers to project

fire behavior parameters over a complex landscape. Topographic inputs such as slope, aspect, and elevation were obtained from the LiDAR-derived surface elevation model at 30-m resolution. We derived forest structure map layers for canopy cover, canopy bulk density, canopy base height, and canopy height using the imputation procedure previously described. We calculated fuel-model assignments using a selection logic based on surface fuels and forest structure measured at the plots (Collins et al. 2011, 2013). This approach has proven sufficient at assigning fuel models based on actual fuel loads rather than relying on the Forest Vegetation Simulator (FVS; Dixon 2002), which has been shown to use fuel models that underestimate fire behavior (Collins et al. 2013). This approach for assigning fuel models was different for treated and untreated stands. For untreated stands, we used a regression tree analysis with several response variables representing surface fuels: shrub cover, litter, 1- to 100-hour woody fuels, and 1000-hour woody fuels. Forest structure and stand vegetation classification were used as independent variables. Model fits were moderate ($R^2 = 0.3$ – 0.6), but given the known variability in surface fuels in mixed-conifer forests (Lydersen et al. 2015), we deemed the assignments to be sufficient in describing the generalized fuel conditions represented by surface fuel models (Collins et al. 2011, 2013). For treated stands, post-treatment fuel models were based on treatment type and post-treatment fuel measurements. Prescribed-burn plots were assigned a moderate-load timber-litter fuel model (Scott and Burgan 2005). We assigned a low-load, timber-understory model to initial post-treatment masticated stands based on observed fire behavior from Knapp et al. (2011). There were two types of tree-harvest treatments: thinning and cable logging. Prescriptions for the cable-logging units indicated that the slash was to remain on site, so we used a moderate-load, timber-slash model followed by timber-understory models. Thinning treatments used whole-tree removal in which slash typically was removed, so we used the same selection logic for these treatments that we used for untreated stands.

We obtained weather information from the Duncan Remote Automatic Weather Station, limited to the active burning period of the Star

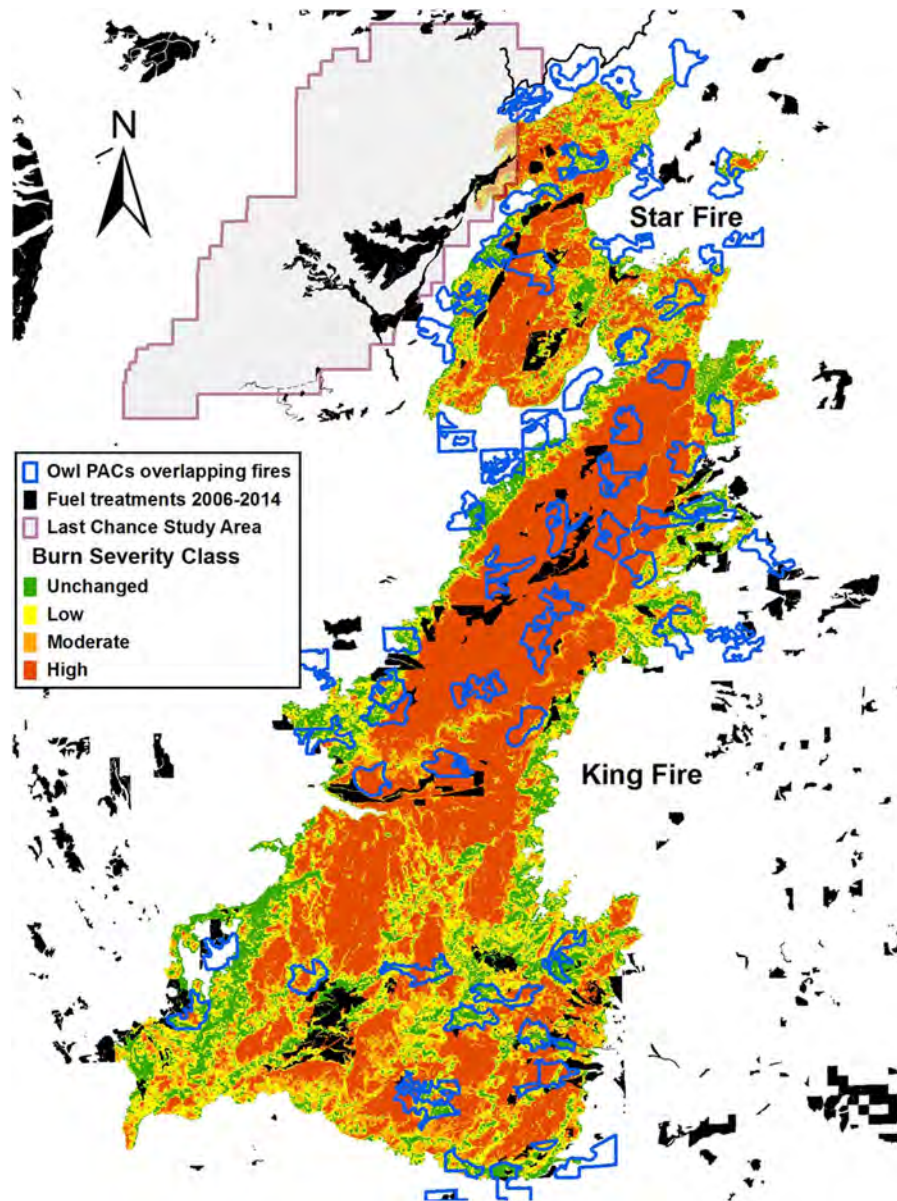


Fig. 2. Burn-severity map of the 2001 Star Fire and 2014 King Fire that burned near the Last Chance Study Area in the central Sierra Nevada, California. The burn-severity maps were created by the U.S. Forest Service (USFS) as detailed in Finco et al. (2012). We also show the spotted owl Protected Activity Centers (PACs) that were affected by these fires, and fuels-reduction treatments that were implemented by the USFS from 2006 to 2014.

Fire (August–September 2001), which served as the basis of our fire modeling. Moisture content for live and dead woody fuels and live herbaceous fuels used in the model were equivalent to 97th percentile weather conditions. Winds were generally easterly in the morning, switching to southwest to west during the day, with an

average of 8 km h^{-1} (range = $0\text{--}15 \text{ km h}^{-1}$). Our ignition location was established in the northeast corner of the study area where the Star Fire perimeter overlapped our study area boundary. There were other wildfires that burned into the study area (2008 Peavine Fire, 2013 American Fire), but the 2001 Star Fire location and the

conditions it burned under yielded the highest potential to burn a large portion of our study area, and in doing so impact more known owl sites. The simulation duration was set to allow the fire perimeter to expand through the entire study area.

We used the tree list databases associated with the 2008 pre-treatment field plots when simulating fire under the “no treatment” scenario, and we used the 2013 post-treatment field plots when simulating fire under the “treatment” scenario. Stand average flame lengths and proportion burned by fire type (surface fire, conditional crown fire, and active crown fire) were calculated for both scenarios and used as inputs for fire effects simulation using the keyword SIMFIRE in FVS with the Fire and Fuels Extension (FFE; Reinhardt and Crookston 2003).

For all four scenarios, we then simulated 30 years of forest growth on the study area in 10-year time steps using FVS with FFE. The simulations were performed using the integrated platform ArcFuels (Ager et al. 2006, Vaillant et al. 2011), which runs FVS-FFE to produce the forest structure inputs needed for FARSITE. We used the western Sierra variant of FVS to simulate forest dynamics over the simulation periods. Because this variant does not include a “full-establishment model,” users must set parameters for tree regeneration by identifying number, species, and frequency of establishment. Following the methods of Collins et al. (2011, 2013), we used a random-number generator, within defined bounds, to set the number of seedlings at each time step in FVS while regulating height-growth rates to simulate realistic conditions in a mixed-conifer forest.

Assessing effects of fuels treatments and fire on spotted owl habitat

We identified canopy cover and large trees as the most important predictors of spotted owl habitat because nest locations were characterized by greater amounts of these elements in the central Sierra Nevada (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997, Williams et al. 2011). To determine a biologically meaningful definition of a large tree, we examined 101 spotted owl nest trees on the nearby Eldorado Demography Study Area (EDSA). The size distribution of these nest trees was not significantly different from a

normal distribution at $\alpha = 0.05$ (Shapiro-Wilk test, $p = 0.052$), so we estimated the standard deviation of the 101 nest tree diameters and used the 10% quantile value of a normal distribution to identify the minimum size of a large tree as 71.3 cm dbh. Thus, 90% of owl nest trees on our study area were expected to be ≥ 71.3 cm dbh. We then performed a logistic regression (Hosmer et al. 2013) of owl nesting habitat as a function of canopy cover and large tree density using data collected by Bond et al. (2004) within 0.02-ha plots at 25 nest trees and 36 random locations within potentially suitable owl nesting habitat on the EDSA (Fig. 3). We identified the following logistic regression equation for canopy cover (CC; percent) and large tree density (LT; ha⁻¹) using SAS (SAS Institute, Cary, North Carolina, USA):

$$\begin{aligned} \text{logit}(Pr[\text{nesting habitat}]) = & -4.141 \\ & + 0.026 \times CC \\ & + 0.052 \times LT. \quad (1) \end{aligned}$$

The parameter estimate for large tree density was statistically significant at $\alpha = 0.05$ ($p < 0.01$, Wald chi-squared test statistic [Q_W] = 8.71, df = 1), but the parameter estimate for canopy cover was not ($p = 0.19$, $Q_W = 1.72$, df = 1). However, we elected to include CC in the model given that canopy cover is known to be an important component of spotted owl nesting habitat (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997).

We used Eq. 1 to estimate the probability that each forest stand (i.e., map polygon) on our study area contained suitable owl nesting habitat under each of the four treatment/wildfire scenarios at four points in simulated time (years 0, 10, 20, and 30). Using the values for canopy cover and large tree density from each map polygon, we calculated the probability that the polygon contained suitable nesting habitat and obtained an average probability (weighted by the area of each map polygon) for the entire study area, which we refer to hereafter as the habitat suitability index. We also obtained separate habitat suitability indices for the control and treatment firesheds within the study area (see *Materials and methods: Study area*) because we expected the direct and indirect (i.e., through modification of fire behavior) effects of fuels treatments to be more pronounced near the treatments.

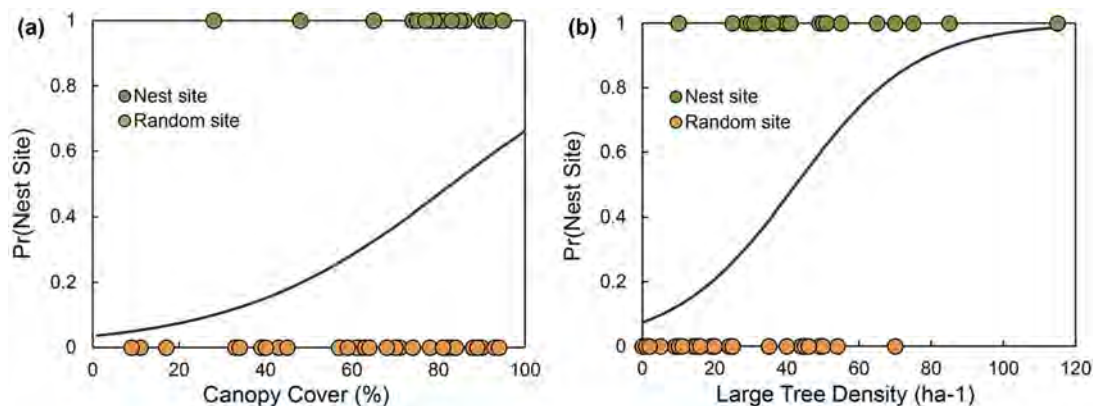


Fig. 3. Comparison of (a) canopy cover (percent) and (b) large tree density (≥ 71.3 cm dbh; ha^{-1}) for 25 California Spotted Owl (*Strix occidentalis occidentalis*) nest locations and 36 random locations in potentially suitable owl nesting habitat on the Eldorado National Forest in the central Sierra Nevada, California. These data were used to develop a logistic regression model to estimate the probability of forest being suitable as spotted owl nesting habitat; best-fit logistic regression lines are shown on each graph.

Assessing effects of fuels treatments and fire on spotted owl demography

Under each of the four treatment/wildfire scenarios, we projected how changes in owl habitat were expected to affect fitness and equilibrium occupancy (ψ_{Eq}) at the spatial scale of a spotted owl territory. We defined an owl territory as the area contained within a 1,128-m radius (400-ha) circle around each owl territory center; this radius was equal to one-half the mean nearest neighbor distance between owl territory centers on the EDSA (Tempel et al. 2014a). We estimated the territory center as the geometric mean of the most informative owl location(s) from each year that the territory was occupied. We used a nest location if one was located that year; otherwise we used the mean of the roost locations for that year. We located nests and roost sites during surveys conducted annually from 2007 to 2013 during the spotted owl breeding season (April–August; see Tempel et al. [2014a]), and we found no barred owls (*Strix varia*) on our study area. We limited this analysis to four spotted owl territories that were largely within our study area ($\geq 80\%$ of the 400-ha territory). Three of the territories were occupied by an owl pair every year from 2007 to 2013, and the other was occupied in all but one of those years. For the demographic analyses, we defined owl habitat as high-canopy-cover forest dominated

by trees ≥ 30.5 cm dbh because previous analyses showed that this vegetation type had a strong positive relation with λ and ψ_{Eq} (Tempel et al. 2014a). On the 2008 pre-treatment map, forest stands with $\geq 70\%$ canopy cover always contained a substantial number of trees ≥ 30.5 cm dbh (mean density = 55.8 ha^{-1} , range = 16.0 – 130.7 ha^{-1}), so we considered all of these stands to be dominated by trees ≥ 30.5 cm dbh. Although our inferences were limited by the small sample size of four territories, the amount of high-canopy-cover forest within these territories (mean = 154 ha, range = 102–207 ha) was typical of the amount found in 70 other territories near our study area (mean = 132 ha; Tempel et al. 2014a).

To assess how changes in the amount of high-canopy-cover forest impacted fitness and ψ_{Eq} at each of the four territories, we used the habitat maps developed under each scenario at four points in simulated time (years 0, 10, 20, and 30) to quantify the proportion of each territory consisting of high-canopy-cover forest. We estimated territory fitness and equilibrium occupancy following the methods of Tempel et al. (2014a). For fitness, where we used a stage-based, Lefkovich matrix model parameterized with fecundity and survival rates to represent changes in the female population size

$$\begin{bmatrix} N_{J,t+1} \\ N_{S1,t+1} \\ N_{S2,t+1} \\ N_{A,t+1} \end{bmatrix} = \begin{bmatrix} 0 & \varphi_{S,t}b_{S,t} & \varphi_{S,t}b_{A,t} & \varphi_{A,t}b_{A,t} \\ \varphi_{J,t} & 0 & 0 & 0 \\ 0 & \varphi_{S,t} & 0 & 0 \\ 0 & 0 & \varphi_{S,t} & \varphi_{A,t} \end{bmatrix} \begin{bmatrix} N_{J,t} \\ N_{S1,t} \\ N_{S2,t} \\ N_{A,t} \end{bmatrix}$$

where $N_{J,t}$, $N_{S1,t}$, $N_{S2,t}$ and $N_{A,t}$ were the number of juvenile, first-year subadult, second-year subadult, and adult females at time t , respectively; $\varphi_{J,t}$, $\varphi_{S,t}$ and $\varphi_{A,t}$ were the apparent survival rates of juvenile, subadult, and adult females from time t to $t + 1$, respectively; and $b_{S,t}$ and $b_{A,t}$ were the fecundity rates for subadult and adult females at time t , respectively. Fecundity was the number of female offspring produced per female in the population, assuming a 50:50 sex ratio for fledged owls. Based on previous analyses in Tempel et al. (2014a), we estimated survival at each territory as a function of female age and the logarithm of the hectares of high-canopy-cover forest (HCF)

$$\logit(\varphi) = -0.005 + 0.557 \times \text{age} + 0.497 \times \log([HCF/10] + 1) \quad (2)$$

where $\text{age} = 0$ for subadults and 1 for adults, and we divided the amount of HCF by 10 to facilitate model fitting. However, we estimated fecundity solely as a function of female age because high-canopy-cover forest was not a significant predictor of reproductive output,

$$b = 0.153 + 0.178 \times \text{age} \quad (3)$$

where $\text{age} = 0$ for subadults and 1 for adults. Using the territory-specific estimates of survival and fecundity, we then computed a territory-specific fitness (i.e., λ) as the dominant eigenvalue of the matrix. As noted in Tempel et al. (2014a), we expected our estimates of fitness to be biased low because (1) we did not incorporate immigration into the projection matrix, and (2) if an individual was not resighted for one or more years and was then resighted on a new territory, we removed the portion of its capture history at the original territory (which lowered the estimates of annual survival) to avoid making assumptions about the owl's location during the intervening period. Nevertheless, differences in fitness allowed us to evaluate the relative simulated effects of fuels treatments and wildfire.

We calculated equilibrium occupancy (ψ_{Eq}) from the territory extinction (ε) and colonization (γ) rates at each territory where $\psi_{Eq} = \gamma/(\gamma + \varepsilon)$

(MacKenzie et al. 2006). Again, based on previous analyses in Tempel et al. (2014a), we estimated extinction probability at each territory as a linear function of the hectares of HCF

$$\logit(\varepsilon) = -1.944 - 0.058 \times (HCF/10), \quad (4)$$

and we estimated colonization as a function of the logarithm of the hectares of HCF

$$\logit(\gamma) = -3.528 + 2.149 \times \log([HCF/10] + 1). \quad (5)$$

As we did when estimating survival, we divided the amount of HCF by 10 to facilitate model fitting.

RESULTS

Effects of fuels treatments on forest structure

We compared pre- and post-treatment measurements at 49 field plots located within the fuels-treatment network (Table 1). Fuels treatments reduced the mean canopy and woody shrub cover by ~10% and reduced mean total tree density from 540.8 to 263.6 trees/ha. Mean large tree density increased slightly from 20.8 to 22.8 trees/ha, perhaps because of tree growth during the five years that elapsed between pre- and post-treatment measurements. Fuels treatments decreased the amount of 1–1000 hour woody fuels from 31.5 to 24.9 Mg/ha, whereas duff fuels increased from 64.2 to 67.2 Mg/ha.

Fire modeling

The simulated fire spread across nearly all of the study area for both scenarios (with and without treatment) because of the prevailing winds (Fig. 4). Fuels treatments reduced the intensity of the fire, as evidenced by the predicted flame lengths, with the greatest reductions occurring within treated areas. Overall, when fire occurred on the untreated landscape, 70.2%, 16.6%, 9.3%, and 3.9% of the study area experienced flame lengths of <2, 2–4, 4–8, and >8 m, respectively. In contrast, when fire occurred on the treated landscape, 76.2%, 14.3%, 6.8%, and 2.7% of the study area burned at these flame lengths. Collins et al. (2011) noted that flame lengths >2 m often corresponded to areas with crown fire initiation (i.e., torching). Differences in fire behavior between the two scenarios (i.e., a greater proportion of the fire

Table 1. Comparison of pre- and post-treatment canopy cover (percent), total tree density (ha^{-1}), large tree density (≥ 71.3 cm dbh; ha^{-1}), shrub cover (percent), duff fuels (Mg/ha), and woody fuels (1–1000 hour; Mg/ha) at 49 field plots located within a fuels-treatment network on the Last Chance Study Area in the central Sierra Nevada, California. Standard errors are shown in parentheses.

Vegetation attribute	Pre-treatment	Post-treatment
Canopy cover	56.6 (3.2)	45.8 (2.7)
Total tree density	540.8 (31.6)	263.6 (21.1)
Large tree density	20.8 (4.4)	22.8 (4.6)
Shrub cover	31.6 (4.0)	22.2 (3.3)
Duff fuels	64.2 (5.4)	67.2 (5.6)
Woody fuels	31.5 (4.9)	24.9 (4.1)

burned at < 2 m after fuels treatments) also generally held true for the land encompassed by the four owl territories. Interestingly, the one territory where this pattern did not hold true was at the territory located within the fuels-treatment network (the territory in the southeastern part of the study area; Fig. 4) where 29.3% of the

territory burned at flame lengths > 2 m under the treatment scenario compared to 19.7% under the no treatment scenario. This result may have been influenced by differences in the direction of fire spread and time-of-day that the territory burned, which would influence burning conditions via fuel moisture, relative humidity, and air temperature.

Effects of fuels treatments and fire on spotted owl habitat

When we applied Eq. 1 to the habitat maps under the four treatment/wildfire scenarios, we found that fuels treatments had a persistent, slightly negative effect on the owl habitat suitability index for the entire study area when no wildfire occurred (Fig. 5). Implementing fuels treatments immediately decreased the habitat suitability index (0.25 for 2008 pre-treatment map compared to 0.23 for 2013 post-treatment map), and this small difference was still present after 30 years of simulated forest growth (0.37 without treatment versus 0.36 with treatment). Conversely, we found that fuels treatments had a

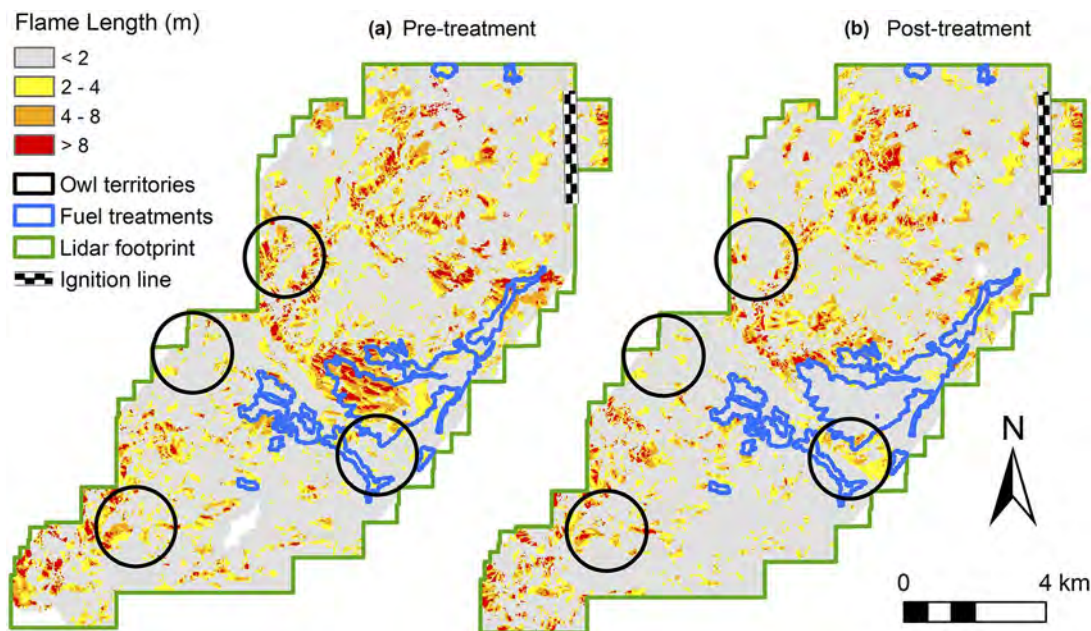


Fig. 4. Flame lengths (m) of simulated fires on the Last Chance Study Area under two scenarios: (a) on an untreated landscape; and (b) after implementation of fuels treatments. We show the location of treatment polygons in (a) for ease of comparison, but treatments were not implemented in (a). Four California Spotted Owl (*Strix occidentalis occidentalis*) territories within the study area are also shown. Fire occurred in all areas within the “ < 2 m” category (gray shading).

persistent, slightly positive effect on the owl habitat suitability index for the entire study area after wildfire was simulated (Fig. 5). After 30 years of simulated forest growth following fire, the habitat suitability index under the treatment scenario was 0.20 compared to 0.17 under the no treatment scenario. The results were very similar when we summarized habitat suitability indices separately for the control and treatment fireshed (Appendix B).

Effects of fuels treatments and fire on spotted owl demography

We estimated that fuels treatments had a slight, persistent negative effect on fitness at four spotted owl territories within our study area when no wildfire occurred (Fig. 6). The mean fitness of owls at the four territories using the 2013 post-treatment map was 0.825 (SE = 0.012) compared to 0.839 (SE = 0.007) using the 2008 pre-treatment map. This difference was still present after 30 years of simulated forest growth (fitness with treatments = 0.850, SE = 0.008; fitness with no treatments = 0.856, SE = 0.005). In contrast, the simulations suggested that fuels treatments had a larger positive effect on

territory fitness after wildfire (Fig. 6). Thirty years after the occurrence of fire, the simulations projected the mean territory fitness with treatments to be 0.796 (SE = 0.009) versus 0.776 (SE = 0.008) with no treatments.

The general patterns for equilibrium occupancy were similar to those for territory fitness, but there was greater variation in ψ_{Eq} under the different scenarios (Fig. 6). Fuels treatments again had a slight negative effect if fire did not occur, but they had a larger positive effect if simulated fire did occur. When fire did not occur, the projected mean equilibrium occupancy for the four territories after 30 years was 0.883 (SE = 0.037) with fuels treatments and 0.911 (SE = 0.023) with no fuels treatments. In contrast, the projected mean equilibrium occupancy 30 years after fire was 0.577 (SE = 0.053) with treatments compared to 0.468 (SE = 0.042) with no treatments.

DISCUSSION

Several studies have investigated the short-term and long-term impacts of fuel treatments on habitat availability for old-forest species using various treatment simulations (Lee and Irwin 2005, Ager et al. 2007, Thompson et al. 2011, Roloff et al. 2012), but ours was unique in several respects. First, we simulated the effects of actual (as opposed to hypothetical) fuels treatments that reflected an actual implementation of a region-wide strategy to reduce landscape-level fire spread and intensity on U.S. Forest Service lands, while conserving key forest structural attributes associated with old-forest species (i.e., large trees, high canopy cover; USFS 2004). Second, we combined field-collected vegetation data and LiDAR data to develop a detailed map of forest structure used to parameterize our fire and forest-growth models. The LiDAR data provided information on vertical structure that was unattainable with other sources of remotely sensed data (Lefsky et al. 2002) and allowed us to determine the actual extent of treatments. While the full potential of LiDAR data was not demonstrated here (e.g., the mapping of individual trees; Li et al. 2012, Jakubowski et al. 2013), the LiDAR data were critical in developing a more detailed and accurate vegetation map for use in fire modeling than what could have been

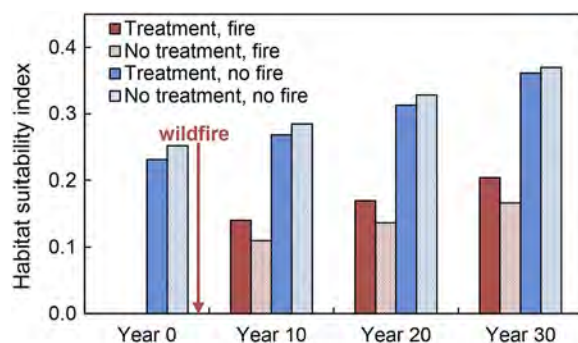


Fig. 5. California Spotted Owl (*Strix occidentalis*) habitat suitability index for a 13,482-ha study area in the Sierra Nevada under four scenarios: (1) no fuel treatments and no wildfire; (2) fuel treatments and no wildfire; (3) no fuel treatments and wildfire; and (4) fuel treatments and wildfire. Year 0 for the “no treatment” scenarios was 2008, and year 0 for the “treatment” scenarios was 2013 (i.e., after fuels treatments were implemented). Simulated fires occurred in year 0 for both the “no treatment” and “treatment” scenarios, and post-fire effects were first assessed in year 10.

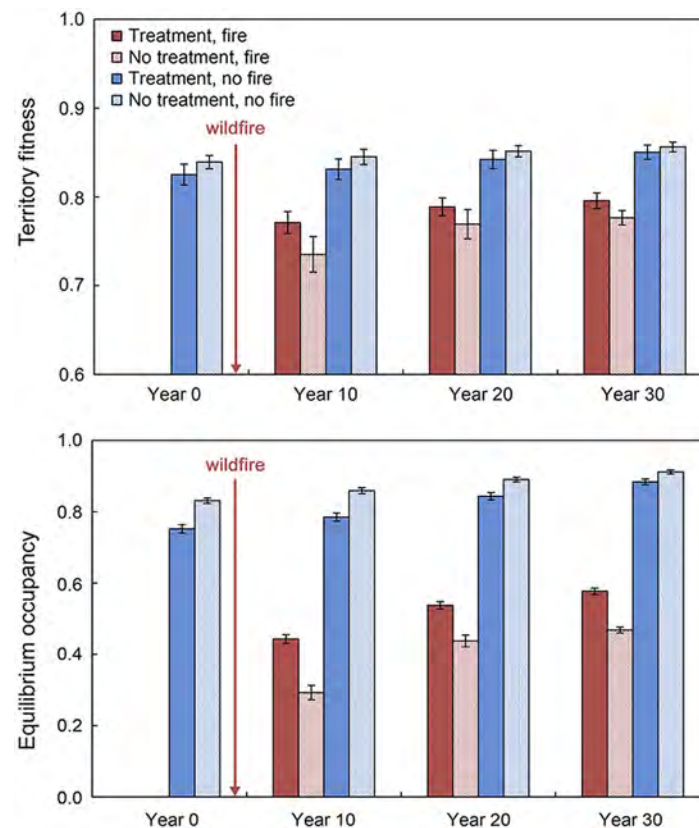


Fig. 6. The average territory fitness and equilibrium occupancy with standard errors at four California Spotted Owl (*Strix occidentalis occidentalis*) territories on a 13,482-ha study area in the Sierra Nevada under four scenarios: (1) no fuel treatments and no wildfire; (2) fuel treatments and no wildfire; (3) no fuel treatments and wildfire; and (4) fuel treatments and wildfire. Year 0 for the “no treatment” scenarios was 2008, and year 0 for the “treatment” scenarios was 2013 (i.e., after fuels treatments were implemented). Simulated fires occurred in year 0 for both the “no treatment” and “treatment” scenarios, and post-fire effects were first assessed in year 10.

solely achieved with lower-resolution satellite or optical imagery. Finally, in addition to projecting changes in habitat over time, we linked vegetation conditions under the different scenarios to territory fitness and occupancy within our study area using previously modeled relationships between forest structure and owl demography (Tempel et al. 2014a). For these reasons, we believe our study provided a rigorous simulation of the effects of fuels-reduction treatments on an old-forest species that has regional-scale implications for forest management.

We modeled the behavior of a fire (both with and without fuels treatments) parameterized using actual conditions during the 2001 Star Fire; this fire burned large areas at high severity (2,677 of 6,817 total ha; Fig. 2). We then simulated forest

growth 30 years into the future under four landscape scenarios: treated/fire, untreated/fire, treated/no fire, and untreated/no fire. As predicted, we projected that fuels-reduction treatments had a negative short-term impact on spotted owl habitat and demographic rates in the absence of fire, but contrary to our expectations, a very slight negative effect was still evident after 30 years. Conversely, treatments had a projected long-term positive effect on owls up to 30 years later when we simulated a fire that burned 30% of our study area at high severity (i.e., >2 m flame length). Thus, our findings were in general agreement with previous modeling efforts for the Northern Spotted Owl (*S. o. caurina*) in the Pacific Northwest where treated landscapes contained more owl habitat after simulated fire than

untreated landscapes, either immediately afterwards (Ager et al. 2007) or up to 75 years later (Roloff et al. 2012).

The observed differences in owl habitat and demographic rates under the different scenarios were modest. For example, the habitat suitability index on our study area 30 years after simulated fire was 0.20 and 0.17 for the treated and untreated landscapes, respectively. Within the four owl territories 30 years after fire, we estimated the mean territory fitness to be 0.796 and 0.776 for the treated and untreated landscapes, respectively. Only 7% of the study area was treated because we expanded our study area to include additional owl territories (Fig. 1), but previous fire modeling studies suggested that at least 20% of the landscape should be treated to significantly reduce fire spread and intensity (e.g., Ager et al. 2007, Finney et al. 2007, Moghaddas et al. 2010). Thus, our finding of fairly modest differences in predicted flame lengths outside of the “treatment” fireshed for the treated and untreated scenarios (Fig. 4) was likely related to the low overall proportion of the study area treated. Based on the original study design, 18% of the area (i.e., the treatment fireshed) was treated, which was shown to be effective at reducing hazardous fire potential across the treatment fireshed (Collins et al. 2011). Although the projected effects on owl fitness are relatively small, even small reductions in annual growth rates (a function of fitness parameters) can translate into large population declines over longer time periods (Tempel et al. 2014b). For example, if the annual growth rate is 1.00, then the population size remains unchanged after 30 years. In contrast, if the annual growth rate is 0.98, then population size would decline by 45% after 30 years. Importantly, California Spotted Owl populations have already declined by up to 50% throughout the Sierra Nevada in the past 20 years (Conner et al. 2013, Tempel et al. 2014b), and any further declines could jeopardize their long-term persistence.

We linked spotted owl demography to fuels treatments and fire behavior via their effects on high-canopy-cover forests because relationships between owl territory fitness/occupancy and this forest type have been well-established in the Sierra Nevada (Blakesley et al. 2005, Tempel et al. 2014a). Moreover, previous studies have shown

that large (>50 ha) areas of high-severity fire within owl territories may reduce territory occupancy (Lee et al. 2013). In addition, territory extinction has been positively correlated with the combined area of early-seral forests, high-severity burn, and post-fire salvage logging within owl territories (Clark et al. 2013). As such, a reasonable ecological basis exists for inferring that simplification or elimination of high-canopy-cover forests by fuels treatments or high-severity fire will adversely affect spotted owl populations. However, the effects of wildfire on spotted owls are undoubtedly complex and owls may benefit from the presence of a mosaic of habitat types promoted by mixed-severity fire, and particularly from shrub patches and early-seral forests that harbor diverse prey assemblages (Roberts et al. 2015). For example, Bond et al. (2009) found that spotted owls in the southern Sierra Nevada selectively foraged in burned areas, even those that burned at high severity. We further note that not all previous studies of spotted owls have found reduced occupancy rates in burned areas relative to unburned areas (Roberts et al. 2011, Lee et al. 2012). Therefore, to the extent that low- or moderate-severity fire may benefit owls, the modeled declines in territory fitness and occupancy in our fire scenarios might be overestimated, and by extension the long-term (30-year) benefits of fuels reduction treatments overly optimistic. Clearly, additional empirical work is needed to assess the complex effects of wildfire on spotted owls, particularly longer-term studies of marked individuals in landscapes that have experienced a range of fire severities (with and without existing fuel treatment networks on the landscape) and that are not confounded by the effects of salvage logging.

Other Sierra Nevada species of conservation concern have similar habitat needs as the spotted owl (i.e., mature forests with high canopy cover), particularly the Pacific fisher (*Pekania pennanti*) and Northern Goshawk (*Accipiter gentilis*; Greenwald et al. 2005, Davis et al. 2007). Thus, similar forest-management trade-offs may exist for these species such that fuels-reduction treatments may reduce available habitat in the short-term but result in greater, long-term habitat amounts if fire occurs. Indeed, Thompson et al. (2011) performed an analogous study to ours, in which they modeled fire and forest growth under

treatment and no treatment scenarios and assessed fisher habitat suitability in the southern Sierra Nevada. They projected that fuels treatments had slight negative effects on fisher habitat in the absence of fire, but provided significant positive benefits up to 37 years after simulated fire. Truex and Zielinski (2013) suggested that less fisher resting habitat was present immediately after mechanical fuels treatments were implemented in the Sierra Nevada. However, fishers consistently used areas in the southern Sierra Nevada where some timber harvest had occurred, so it may be possible to implement fuels-reduction treatments at an extent and rate that achieves fire-hazard-reduction goals (Zielinski et al. 2013). Therefore, we believe that our results, although specific to the spotted owl, have broader applicability to other species of management concern in the Sierra Nevada that selectively use forests characterized by large trees and high canopy cover.

We note, however, several caveats from our study when assessing the long-term effects of fuels treatments and wildfire on spotted owls. First, our projections were based on a single simulated fire for each treatment scenario (with and without treatment), and additional fire simulations may have suggested alternative fire patterns with differing effects on the components of owl habitat that we considered (canopy cover, large tree density). We used FARSITE to simulate a single fire in order to obtain specific predictions on how fire would impact forest structure via tree mortality, as opposed to probabilistic predictions on fire occurrence at a specific location (e.g., Ager et al. 2007). By having spatially explicit predictions of fire effects on forest structure, we were able to track the impacts of fire on owl habitat and make more direct assessments of owl demography over time. Second, our simulation was conducted at the relatively fine spatial scale of the fireshed (10s of km²) because of its management relevance (North et al. 2015) and the difficulty of collecting detailed vegetation data for improved parameterization of fire models at larger spatial scales. However, conducting simulations such as ours at a larger spatial scale would increase the sample size of owl territories used to assess the potential effects of fire and fuels treatments on spotted owls. Future studies should carefully weigh the

trade-off between collecting more accurate vegetation data at smaller spatial scales, and therefore deriving more accurate inputs for fire modeling, and increasing the number of owl territories by using larger spatial scales. Third, both of our simulated fires exhibited burn patterns that were substantially different than the burn patterns of the 2001 Star Fire that we attempted to simulate and the large 2014 King Fire (39,545 ha) that burned near our study area (cf. Figs. 2 and 4). Whereas our simulations resulted in relatively small, evenly distributed patches of high-severity fire, the Star Fire and King Fire burned large, contiguous areas at high severity. Indeed, our past experience suggests that existing fire models are generally incapable of replicating the burn patterns seen in the most extreme real fires. Thus, improved fire models are needed to more reliably assess how fuels treatments modify fire behavior and effects on forest structure especially under extreme conditions. Fourth, we did not simulate post-fire salvage logging (which often occurs after fires) on the habitat suitability of burned areas, and post-fire salvage logging has been shown to negatively affect spotted owl occupancy rates (Clark et al. 2013, Lee et al. 2013). Finally, the net effect of fuels treatments on spotted owls depends upon the true, but unknown, probability that high-severity fire effects will occur within individual owl territories. If individual territories have a low probability of experiencing high-severity fire effects, a relatively small portion of the owl population would accrue the long-term benefits of fuels reductions, whereas a greater portion of the population would experience the unfavorable short-term impacts. However, it is difficult to estimate spatially explicit, future probabilities for specific fire behaviors (e.g., crown-fire initiation) on specific areas of the landscape, and it is thus difficult to quantify trade-offs associated with fuel treatments on large spatial scales and in absolute terms (Finney 2005). We note, however, that the area burned by high-severity fire in the Sierra Nevada has increased in the past 30 years (Miller et al. 2009, Miller and Safford 2012) and may increase further in upcoming years because of climate change (Westerling and Bryant 2008, Liu et al. 2013). In addition, several fires on or near our study area have burned large areas of the

landscape in the last 15 years (2001 Star Fire [6,817 ha], 2013 American Fire [11,305 ha], 2014 King Fire [39,545 ha]) and provide circumstantial evidence that a significant probability of large-scale, high-severity fire effects can be expected, at least in this region of the north-central Sierra Nevada. All three of these fires were human-ignited, which further complicates the estimation of future fire probabilities. In sum, future research on the short- versus long-term benefits of fuels treatments would benefit from a greater understanding of the probability of fire under various climate change scenarios, and linking replicated fire and forest-growth simulations to spotted owl population dynamics at landscape scales using spatially explicit population models.

In conclusion, our results suggest that fuels-reduction treatments, as currently implemented by the U.S. Forest Service in the Sierra Nevada, have the potential to provide long-term (30-year) benefits to spotted owls in the event of fire under extreme weather conditions, but can have long-term negative effects on owls if fire does not occur. Furthermore, major uncertainties remain (e.g., What is the future probability that high-severity fire effects will occur within individual owl territories?). In conjunction with the observed population declines in the last 20 years (Conner et al. 2013, Tempel et al. 2014b), we believe these uncertainties warrant an informed approach to landscape fuels management that explicitly balances the seemingly conflicting goals of providing habitat for owls and reducing hazardous fire potential. Specifically, we recommend that the U.S. Forest Service continue its current policy that restricts timber harvest within spotted owl Protected Activity Centers (PACs), which contain ~125 ha of the best habitat that owls use for nesting and roosting over long time periods (up to 24 years; Berigan et al. 2012). Furthermore, fuels-treatment arrangements should be designed to limit the potential for high-severity fire to spread into PACs.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

Appendices A and B are available online: <http://dx.doi.org/10.1890/ES15-00234.1.sm>

Meta-analysis of California Spotted Owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: Habitat associations and their implications for forest management

Author(s): Douglas J. Tempel , John J. Keane , R. J. Gutiérrez , Jared D. Wolfe , Gavin M. Jones , Alexander Koltunov , Carlos M. Ramirez , William J. Berigan , Claire V. Gallagher , Thomas E. Munton , Paula A. Shaklee , Sheila A. Whitmore , and M. Zachariah Peery

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RESEARCH ARTICLE

Meta-analysis of California Spotted Owl (*Strix occidentalis occidentalis*) territory occupancy in the Sierra Nevada: Habitat associations and their implications for forest management

Douglas J. Tempel,¹ John J. Keane,² R. J. Gutiérrez,^{3a} Jared D. Wolfe,⁴ Gavin M. Jones,¹ Alexander Koltunov,^{5,6} Carlos M. Ramirez,⁵ William J. Berigan,¹ Claire V. Gallagher,² Thomas E. Munton,⁷ Paula A. Shaklee,² Sheila A. Whitmore,¹ and M. Zachariah Peery^{1*}

¹ Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, Wisconsin, USA

² Pacific Southwest Research Station, USDA Forest Service, Davis, California, USA

³ Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota, USA

⁴ Pacific Southwest Research Station, USDA Forest Service, Arcata, California, USA

⁵ Remote Sensing Laboratory, USDA Forest Service, Sacramento, California, USA

⁶ Center for Spatial Technologies and Remote Sensing (CSTARS), University of California, Davis, California, USA

⁷ Pacific Southwest Research Station, USDA Forest Service, Fresno, California, USA

^a Current address: McKinleyville, California, USA

* Corresponding author: mpeery@wisc.edu

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ABSTRACT

We assessed the occupancy dynamics of 275 California Spotted Owl (*Strix occidentalis occidentalis*) territories in 4 study areas in the Sierra Nevada, California, USA, from 1993 to 2011. We used Landsat data to develop maps of canopy cover for each study area, which we then used to quantify annual territory-specific habitat covariates. We modeled the relationships between territory extinction and colonization using predictor variables of habitat, disturbance (logging, fire), climate, and elevation. We found that forests with medium (40–69%) and high ($\geq 70\%$) canopy cover were the most important predictors of territory occupancy in all study areas, and that both canopy cover categories were positively correlated with occupancy. We used analysis of deviance to estimate the amount of variation explained by the habitat covariates (primarily medium and high canopy cover) and found that these covariates explained from 35% to 67% of the variation in occupancy. Climatic covariates were not correlated with occupancy dynamics and explained little of the variation in occupancy. We also conducted a post hoc analysis in which we partitioned canopy cover into 10% classes, because our original partitioning into 3 classes may have lacked sufficient resolution to identify canopy cover levels where occupancy changed abruptly. In this post hoc analysis, occupancy declined sharply when territories contained more area with $<40\%$ canopy cover, and the amount of 50–59% and 60–69% canopy cover had a more positive association with occupancy than did 40–49% canopy cover. Our results suggest that some fuels treatments intended to reduce fire risk and improve forest resilience could be located within Spotted Owl territories without adversely impacting territory occupancy if such treatments do not consistently reduce canopy cover below 50%. We suggest that future work quantify components of forest structure (e.g., large tree density, vertical complexity) known to be selected by owls and relate these characteristics to occupancy and fitness metrics.

Keywords: California Spotted Owl, canopy cover, forest management, occupancy, Sierra Nevada, *Strix occidentalis occidentalis*

Meta análisis de la ocupación de territorios de *Strix occidentalis occidentalis* en la Sierra Nevada: asociaciones de hábitat y sus implicaciones para el manejo forestal

RESUMEN

Determinamos la dinámica de ocupación de 275 territorios de *Strix occidentalis occidentalis* en 4 áreas de estudio en la Sierra Nevada, California, entre 1993 y 2011. Usamos datos de Landsat para desarrollar mapas de cobertura del dosel para cada área de estudio, que usamos luego para cuantificar covariables de hábitat anuales específicas de cada territorio. Modelamos la relación entre la extinción y la colonización de los territorios usando variables predictoras de hábitat, disturbio (tala, incendios), clima y elevación. Encontramos que los bosques con cobertura de dosel media (40–69%) y alta ($\geq 70\%$) fueron los predictores más importantes de la ocupación de los territorios en todas las áreas de estudio, y ambas categorías de cobertura de dosel se correlacionaron positivamente con la ocupación. Usamos análisis de desviación para estimar la cantidad de variación explicada por las covariables del hábitat (principalmente cobertura de dosel media y alta) y encontramos que estas covariables explican entre 35.1% y 67.1% de la variación en la

ocupación. Las covariables del clima no se correlacionaron con la dinámica de ocupación y explicaron poco de la variación en ocupación. También hicimos un análisis post-hoc en el que hicimos particiones de la cobertura del dosel en clases de 10% porque nuestra partición original en 3 clases podría no tener suficiente resolución para identificar los niveles de cobertura del dosel en los que la ocupación cambia abruptamente. En este análisis post-hoc, la ocupación disminuyó fuertemente cuando los territorios contenían menos de 40% de cobertura de dosel, y las clases de cobertura entre 50–59% y 60–69% presentaron una asociación más positiva con la ocupación de lo que la tuvo la clase de cobertura entre 40–49%. Nuestros resultados sugieren que algunos tratamientos con la intención de reducir el riesgo de incendios y mejorar la resiliencia de los bosques podrían ser ubicados dentro de los territorios de *S. o. occidentalis* sin afectar seriamente la ocupación de los territorios si tales tratamientos no reducen la cobertura del dosel por debajo del 50%. Sugerimos que trabajos futuros cuantifiquen los componentes de la estructura del bosque (e.g. densidad de árboles grandes, complejidad vertical) que se sabe son seleccionados por los búhos y relacionen estas características con la ocupación y medidas de aptitud.

Palabras clave: cobertura del dosel, manejo forestal, ocupación, Sierra Nevada, *Strix occidentalis occidentalis*

INTRODUCTION

The range of the California Spotted Owl (*Strix occidentalis occidentalis*) extends from the southern Cascade Range, USA, to northern Baja California, Mexico, but most of its population is found in the Sierra Nevada, California, USA (Verner et al. 1992, Gutiérrez et al. 1995). For nesting and roosting, it selectively uses economically valuable, older forests that have been affected by timber harvesting for more than a century (Gutiérrez et al. 1995). Although it is the only Spotted Owl subspecies not protected under the U.S. Endangered Species Act, management guidelines developed to retain important Spotted Owl habitat in Sierra Nevada forests have been in place for >20 yr (Verner et al. 1992, USDA Forest Service 2004), and Spotted Owl habitat remains a central component of forest management in the Sierra Nevada (USDA Forest Service 2016).

Management of Spotted Owl habitat in the Sierra Nevada is complicated by changing fire regimes that are largely the result of decades of fire suppression, which has allowed uncharacteristic accumulation of fuel loads on the landscape (Stephens et al. 2015). Whereas historical fire regimes were typified by relatively frequent fires that burned mainly at low and moderate severity (Skinner and Chang 1996), the relative proportion and patch sizes of high-severity fires have increased within the past 30 yr (Miller et al. 2009, Miller and Safford 2012). High-severity fire is often characterized by $\geq 75\%$ mortality of overstory trees and can result in habitat loss for species associated with older forests. In fact, large patches of high-severity fire have been shown to negatively affect occupancy of Spotted Owl territories after controlling for postfire timber harvest (Lee et al. 2013, Jones et al. 2016a). In addition, climate change is expected to increase the incidence of extreme fire behavior in California (Westerling and Bryant 2008, Liu et al. 2013).

As a result, forest managers in the Sierra Nevada modify forest vegetation structure (i.e. implement “forest treatments”), primarily by removing surface and ladder fuels

(Finney 2001, USDA Forest Service 2004), in attempts to reduce wildfire intensity, size, and rate of spread. Although concern exists that these treatments may adversely impact Spotted Owl habitat in the short term (5–10 yr), it is possible that they may provide long-term benefits by reducing future habitat loss as a result of high-severity fire (Tempel et al. 2015). Thus, reconciling forest restoration and Spotted Owl habitat conservation is important because owl populations in the Sierra Nevada have declined by up to 50% in the past 20 yr (Conner et al. 2013, Tempel et al. 2014a). Furthermore, managers are now considering recommendations to modify forest treatments to emphasize forest heterogeneity at the spatial scales of the forest stand and the landscape (North et al. 2009, North 2012). Under these recommendations, forest treatments would be less uniform and tailored to local conditions (e.g., topography, soil, aspect), resulting in a range of stand conditions (tree density, canopy cover) on the landscape (North et al. 2009). This approach also is believed to increase forest resilience to ecological stressors such as high-severity fire, warming temperatures, or extended drought (e.g., Asner et al. 2016).

To assess the potential effects of forest management on Spotted Owls, we related territory occupancy dynamics to canopy cover using presence–absence data collected from 1993 to 2011 in 4 long-term demographic study areas in the Sierra Nevada. We also evaluated the relationship between annual climatic variables and territory occupancy dynamics because changing climatic conditions could affect occupancy dynamics (Jones et al. 2016b). To quantify forest structure within owl territories, we used Landsat imagery to develop raster-based maps of forest canopy cover for each study area and assigned canopy cover into categories. We hypothesized that high ($\geq 70\%$), medium (40–69%), and low ($< 40\%$) canopy cover would be biologically meaningful for Spotted Owls in different ways, because forests with $\geq 70\%$ canopy cover are selected by owls for nesting and roosting (Moen and Gutiérrez 1997), whereas forests with 40–69% canopy cover may be used for foraging, and forests with $< 40\%$ canopy cover are often

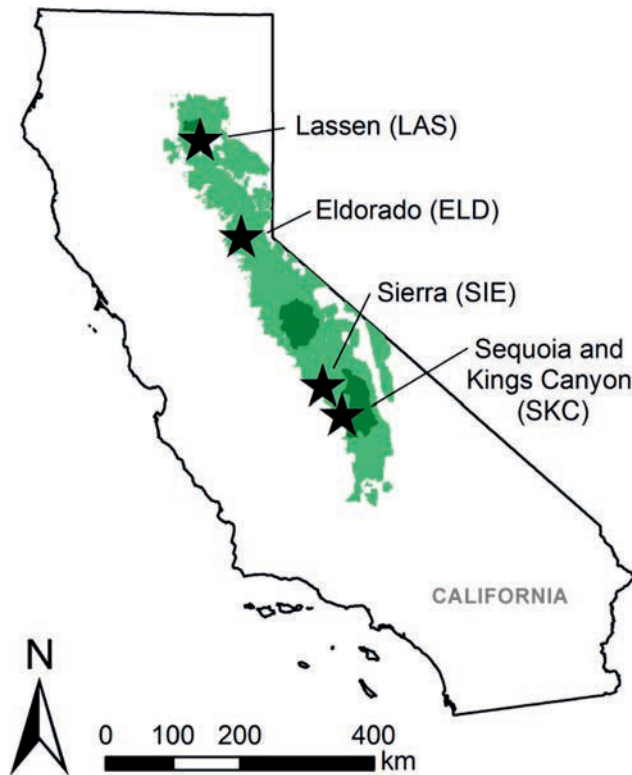


FIGURE 1. Locations of 4 study areas for California Spotted Owls, 1993–2011. Light shading indicates national forests; dark shading indicates national parks.

avoided (Call et al. 1992). We were unable to accurately estimate other important Spotted Owl habitat features (e.g., large trees, snags, vertical structure) with Landsat, and these variables were omitted from our analyses. We also tested whether spatially explicit metrics of forest structure, such as the spatial dispersion of high-canopy-cover forest and heterogeneity in canopy-cover conditions, were related to territory occupancy dynamics.

METHODS

Study Areas

Our long-term demographic study areas were situated on a north–south axis from the southern Cascades to the southern Sierra Nevada, California, USA (Figure 1). The Lassen study area (LAS) was in the southern Cascades, but was managed by the USDA Forest Service as part of the Sierra Nevada province, and the owls here are more likely to be California Spotted Owls than Northern Spotted Owls (*Strix occidentalis caurina*; USDA Forest Service 2004, Barrowclough et al. 2011). The Lassen, Eldorado (ELD), and Sierra (SIE) study areas consisted mainly of public land managed by the Forest Service, but also contained some privately owned land. **Most private land within the Lassen study area was not surveyed for owls**, but some owl

territories on private land adjacent to the Lassen National Forest were included. The Eldorado and Sierra study areas contained 37% and 8% private land, respectively. The Sequoia–Kings Canyon (SKC) study area was entirely within 2 national parks of the same name. Barred Owls (*Strix varia*) were not present in any of the study areas until the last several years of our study, and they were either uncommon (Lassen) or extremely rare (≤ 3 individuals each in the Eldorado, Sierra, and Sequoia–Kings Canyon sites). Most precipitation in each study area fell as rain or snow during winter and early spring. Summers in all study areas were hot and dry. Additional detailed climatic information is described in Franklin et al. (2004).

The Lassen study area was located in the Lassen National Forest between Mineral and Susanville, California, at 1,200 m to 2,100 m elevation, and encompassed 2,200 km². The primary vegetation type in this study area was mixed-conifer forest dominated by sugar pine (*Pinus lambertiana*), ponderosa pine (*P. ponderosa*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), and incense cedar (*Calocedrus decurrens*). California black oak (*Quercus kelloggii*) and Pacific dogwood (*Cornus nuttallii*) occurred in the understory, and red fir (*A. magnifica*) was present at higher elevations as pure stands or mixed with white fir.

The Eldorado site was located in the Eldorado and Tahoe national forests east of Georgetown, California, between 300 and 2,500 m elevation, and encompassed 818 km². Mixed-conifer forest was the primary vegetation type in this study area, and was dominated by sugar pine, ponderosa pine, white fir, Douglas-fir, and incense cedar. California black oak, canyon live oak (*Q. chrysolepis*), tanoak (*Notholithocarpus densiflorus*), and bigleaf maple (*Acer macrophyllum*) were common understory species. Red fir and lodgepole pine (*Pinus contorta*) occurred at the higher elevations.

The Sierra study site was located in the Sierra National Forest east of Fresno, California, between 300 and 2,900 m elevation, and encompassed 693 km². This study area contained 3 major vegetation types. Oak woodland (26% of the study area) dominated by blue oak (*Q. douglasii*), interior live oak (*Q. wislizeni*), canyon live oak, and California foothill pine (*Pinus sabiniana*) occurred at lower elevations. Mixed-conifer forest (61%) dominated by sugar pine, ponderosa pine, white fir, incense cedar, black oak, red fir, and Jeffrey pine (*P. jeffreyi*) occurred at middle elevations. Conifer forest (13%) dominated by red fir, lodgepole pine, and western white pine (*P. monticola*) occurred at higher elevations.

The Sequoia–Kings Canyon study area was located in Sequoia and Kings Canyon national parks northeast of Visalia, California, at elevations ranging from 425 to 3,050 m and encompassed 343 km². This study area consisted of 3 major vegetation types. Oak woodlands (24% of the study

area) containing blue oak, interior live oak, canyon live oak, and California foothill pine were present at lower elevations. Mixed-conifer forest (67%) dominated by sugar pine, ponderosa pine, white fir, and incense cedar occurred at middle elevations. Ten giant sequoia (*Sequoiadendron giganteum*) groves (7%) were found within the mixed-conifer zone. Conifer forests dominated by red fir, lodgepole pine, and western white pine occurred at higher elevations.

Spotted Owl Surveys

We conducted Spotted Owl surveys annually across each study area from 1993 to 2011 during the breeding season. All study areas consisted of a core study area that we surveyed completely in each year of the study (i.e. both the areas containing owl territories and all areas not containing owls within the core area were surveyed every year). In addition, we added some owl territories over time, either as an expansion of the core area (Lassen) or as individual satellite territories to increase owl sample sizes for demographic analysis (Lassen and Eldorado), and we deleted a portion of the Sequoia–Kings Canyon site in 2006. We accounted for these changes in our analyses. We surveyed all satellite sites used in our occupancy analyses for a minimum of 3 yr; most territories in the core areas were surveyed for ≥ 15 yr. We conducted surveys from April 1 to August 31 in the Lassen and Eldorado study areas and from March 1 to September 30 in the Sierra and Sequoia–Kings Canyon sites. However, no surveys were conducted in the Sequoia–Kings Canyon study site in 2005 because of a temporary suspension of funding.

We imitated Spotted Owl vocalizations at designated survey stations or while walking survey routes through historical owl territories or between survey stations. We determined a responding owl's sex by the pitch of its 4-note territorial call; males have a lower-pitched call than females (Forsman et al. 1984). If owls were detected during nocturnal surveys, we conducted diurnal surveys to band unmarked owls, resight marked owls, assess reproduction, locate roosting areas, and band fledglings (Franklin et al. 1996). We included both nocturnal and diurnal surveys in our occupancy analyses.

Canopy Cover Map Development

We developed annual, raster-based canopy cover maps at 30×30 m spatial resolution using Landsat 5 Thematic Mapper satellite images from 1990 to 2011 acquired during July or August of each year. In each of these images, we estimated the fractional tree cover (in 1% increments) in a pixel using the Mixed Stratified Spectral Mixture Analysis method (MixSSMA; Koltunov et al. 2014, Koltunov and Ramirez 2015; see [Supplemental Material Appendix A](#) for complete details). To test the accuracy of the canopy cover maps, we compared them to 2

independent sets of canopy cover data obtained from airborne LiDAR (Light Detection and Ranging) and by double-blind visual interpretation of multitemporal high-resolution imagery from Google Earth (Google, Mountain View, California, USA) and the National Agriculture Imagery Program (NAIP; USDA Farm Service Agency, Salt Lake City, Utah, USA). The LiDAR data were acquired at a density of ~ 8 – 10 points m^{-2} during 2009–2012, but were available only for parts of 2 study areas, Lassen and Sierra. We selected a stratified random sample of 3×3 pixel (90×90 m) polygons with no overlap (550 polygons for the Lassen study site, 376 for Sierra; [Supplemental Material Figure S1](#)) and compared the Landsat-derived canopy cover for 2010 with the fraction of LiDAR returns above 3 m. The mean ($\pm$ SD) absolute differences in canopy cover were $8.4 (\pm 8.8)$ for Lassen and $9.5 (\pm 9.5)$ for Sierra, and the pseudo r^2 values were 0.83 for Lassen and 0.71 for Sierra ([Supplemental Material Figure S2](#)). The test set based on high-resolution imagery was developed for all 4 study areas in 2005 and 2010. We selected 3×3 pixel (90×90 m) polygons with no overlap (195 to 600+ polygons per study area; [Supplemental Material Figure S1](#)), and again compared the Landsat-derived canopy cover with the values based on high-resolution imagery. The mean absolute differences in canopy cover ranged between 9.7 and 15.5, and the pseudo r^2 values ranged between 0.33 and 0.80 ([Supplemental Material Table S1](#)).

Canopy cover at the pixel scale was grouped into one of 3 classes ($<40\%$, 40 – 69% , $\geq 70\%$) to minimize the effect of map error on inference. Although our classes were relatively coarse, they were less subject to mapping error than classes with a narrower range of values, and thus more likely to yield robust relationships between canopy cover and territory occupancy. Furthermore, previous Spotted Owl occupancy studies have used similar or identical canopy cover classes to these 3 classes (Blakesley et al. 2005, Seamans and Gutiérrez 2007b, Tempel et al. 2014b). However, forest managers could benefit from finer resolution as to how occupancy is related to canopy cover levels within these classes (e.g., the difference that might be expected if forest treatments reduce canopy cover from 70% to 40% vs. 70% to 60%). Thus, we performed a post hoc analysis using 10% canopy cover classes (see Statistical Analysis—Model selection). **It is important, however, to recognize that canopy cover conditions are mapped with lower accuracy in this analysis and that inferences are more likely influenced by map uncertainty. As such, we did not make explicit predictions, for example, of how much forest with 70–80% canopy cover would be needed to achieve a specific target goal of territory occupancy. Rather, we searched for broad patterns across study areas in the directionality of relationships between the area of forest within 10% canopy cover classes and Spotted Owl territory occupancy metrics.**

Statistical Analysis

We used the annual survey data to identify Spotted Owl territories and construct occupancy histories for our analyses. We identified owl territories as sites where at least 1 owl was detected during diurnal hours in ≥ 3 yr, where diurnal hours occurred between dawn and dusk based on civil twilight times (http://aa.usno.navy.mil/data/docs/RS_OneYear.php). For the purpose of quantifying habitat covariates within Spotted Owl territories, we first calculated the geometric center of each territory as the average spatial coordinates of all nest and roost locations in the territory. We then calculated the mean nearest-neighbor distance among territory centers for each study area as the average distance between each territory center and the center of its nearest neighboring territory, and we defined the spatial extent of a “territory” as a circle around each territory center with a radius of half of the mean nearest-neighbor distance. The resulting territory size for each study area decreased along a north–south gradient: Lassen = 639.4 ha (1,427-m radius), Eldorado = 399.5 ha (1,128-m radius), Sierra = 301.6 ha (980-m radius), and Sequoia–Kings Canyon = 254.3 ha (900-m radius). This process nearly eliminated spatial overlap among adjacent territory circles. We did not include nocturnal detections outside a territory circle when compiling occupancy histories to eliminate potential spurious detections of owls from nearby territories or nonterritorial, floater owls. A survey in which no owls were detected needed a total duration of ≥ 30 min to be included in the occupancy history.

We used a multiple-season, robust-design occupancy model to assess territory occupancy dynamics in each study area separately, in which the statistical model contained parameters for initial occupancy (ψ_1), territory extinction (ϵ_t), territory colonization (γ_t), and detection probability ($p_{t,j}$; MacKenzie et al. 2003). Our primary sampling periods (t) were breeding seasons (i.e. years), and our secondary sampling periods (j) were bimonthly periods within each breeding season (March 1–15, March 16–31, April 1–15, April 16–30, etc.). Thus, the Lassen and Eldorado study areas had 10 secondary periods each year, and the Sierra and Sequoia–Kings Canyon study areas had 14 secondary periods each year. If multiple surveys were conducted within the same secondary period, we assigned a “0” to the survey history if no owls were detected during any survey and a “1” if at least 1 owl was detected during any survey. When fitting the models for Sequoia–Kings Canyon, we fixed all 2005 detection probabilities and ϵ and γ from 2004 to 2005 at 0 because no surveys were conducted in 2005. We used program PRESENCE 10.2 (USGS Patuxent Wildlife Research Center, Laurel, Maryland, USA) to fit models and estimate parameters for individual models that contained covariates (Table 1) that we hypothesized would affect

detection probability, initial occupancy, territory colonization, and territory extinction.

Model covariates. We hypothesized that within-year detection probability would be higher on survey occasions subsequent to the survey when owl(s) were initially detected at a territory (*initial*) because surveyors might intensify their efforts to relocate detected birds in order to resight or capture them and to assess reproduction (Riddle et al. 2010, Tempel and Gutiérrez 2013). We expected nesting owls (*repro*; value equal to 1 for all surveys in a territory in a given year if reproduction was detected during any survey) to be more easily detected than nonnesting owls because nesting owls defend their territories more aggressively or spend more time near the territory center (MacKenzie et al. 2009, Tempel and Gutiérrez 2013). We also considered linear (T), logarithmic ($\ln T$), and quadratic (TT) time trends for within-year detection probability, and that $p_{t,j}$ could be different during each bimonthly sampling period (*survey*). We hypothesized that among-year detection probability would vary in a linear (T), logarithmic ($\ln T$), or quadratic (TT) time trend, or that $p_{t,j}$ would be different for each year of the study (*year*; Tempel and Gutiérrez 2013).

We used the raster-based canopy cover maps to quantify annual, territory-specific vegetation covariates that could have affected occupancy. We first used ArcMap 10.1 (ESRI, Redlands, California, USA) to calculate the proportion of each owl territory that contained forest (i.e. pixels) with $\geq 70\%$ canopy cover (*highCC*) and forest with canopy cover between 40% and 69% (*mediumCC*). Previous studies have shown that California Spotted Owls select high-canopy-cover forest for nesting and roosting (Bias and Gutiérrez 1992, Moen and Gutiérrez 1997) and that territory occupancy is positively correlated with the amount of high-canopy-cover forest (Blakesley et al. 2005, Tempel et al. 2014b). Forests with intermediate amounts of canopy cover may function as Spotted Owl nesting or roosting habitat if large, residual trees are present (Moen and Gutiérrez 1997, Hunter and Bond 2001), or might be used by foraging owls (Call et al. 1992).

We then used FRAGSTATS 4.2 (McGarigal et al. 2012) to calculate 3 annual covariates that represented the spatial arrangement or distribution of *highCC* and/or *mediumCC* within a territory. We hypothesized that the density of edge (*edge*) between *highCC* and any vegetation type with $< 40\%$ canopy cover would be positively correlated with occupancy because these edges could increase the availability of prey such as dusky-footed woodrats (*Neotoma fuscipes*) and other rodents (Sakai and Noon 1997). Similarly, we hypothesized that owls would experience improved foraging conditions if *highCC* was spatially dispersed throughout the territory, rather than being aggregated into large patches. Therefore, we calculated the area-weighted clumpiness index for *highCC* within a territory

TABLE 1. Covariates used to model detection probability ($p_{t,j}$), initial occupancy (ψ_1), territory extinction (ε_t), and territory colonization (γ_t) for California Spotted Owls in 4 study areas in the Sierra Nevada, California, USA, 1993–2011. The predicted effects were: positive correlation between covariate and parameter (+), negative correlation (–), and no specific prediction (x). The covariate was not modeled for a parameter if the predicted effect is blank.

Covariate	Definition	Predicted effect on parameter			
		$p_{t,j}$	ψ_1	ε_t	γ_t
<i>initial</i>	Different p in surveys after initial detection of owls.	+			
<i>repro</i>	Reproductive status of owls (0 = not nesting, 1 = nesting).	+			
<i>survey</i>	Different p for each survey within a year.	x			
<i>year</i>	Year-specific variation in parameter value.	x		x	x
<i>T</i>	Linear temporal trend.	x			
<i>lnT</i>	Logarithmic temporal trend.	x			
<i>TT</i>	Quadratic temporal trend.	x			
<i>highCC</i>	Proportion of owl territory containing forest with $\geq 70\%$ canopy cover.	x	+	–	+
<i>mediumCC</i>	Proportion of owl territory containing forest with canopy cover between 40% and 69%.	x	+	–	+
<i>edge</i>	Edge density (m m^{-2}) between <i>highCC</i> and any vegetation type with $< 40\%$ canopy cover.			–	+
<i>clump</i>	Clumpiness index for <i>highCC</i> , a measure of its spatial aggregation.			+	–
<i>even</i>	Shannon's evenness index for <i>highCC</i> , <i>mediumCC</i> , and $< 40\%$ canopy cover.			–	+
<i>logging</i>	Proportion of owl territory within which canopy cover was reduced by at least 10% in the previous 3 yr from logging (or other causes in SKC ^a).			+	–
<i>fire</i>	Proportion of owl territory within which canopy cover was reduced by at least 10% in the previous 3 yr due to fire.			+	–
<i>Rxfire</i>	Proportion of owl territory affected by prescribed fire in the previous 3 yr.			–	+
<i>Pwinter</i>	Total precipitation (cm) from November to March averaged across all territories in each study area.			+	–
<i>Twinter</i>	Mean of daily minimum temperatures ($^{\circ}\text{C}$) from November to March averaged across all territories in each study area.			–	+
<i>Pnest</i>	Total precipitation (cm) from April to May averaged across all territories in each study area.			+	–
<i>Tnest</i>	Mean of daily minimum temperatures ($^{\circ}\text{C}$) from April to May averaged across all territories in each study area.			–	+
<i>Tsummer</i>	Mean of daily maximum temperatures ($^{\circ}\text{C}$) from July to August averaged across all territories in each study area.			+	–
<i>elev</i>	Average elevation (m) of owl territory.			x	x

^a SKC = Sequoia–Kings Canyon study area.

(*clump*), which provided an index of fragmentation of *highCC* (McGarigal et al. 2012). Finally, we hypothesized that owls would benefit when *highCC*, *mediumCC*, and any vegetation type with $< 40\%$ canopy cover were present in equal proportions within a territory because each class may fulfill different requirements of the owl's life history. For example, *highCC* may provide optimal nesting and roosting sites, as well as habitat for northern flying squirrels (*Glaucomys sabrinus*; Waters and Zabel 1995), which can be an important prey item for Spotted Owls. Conversely, areas containing shrubs and pole-sized timber ($< 40\%$ canopy cover) may be source habitat for woodrats (Sakai and Noon 1993). Thus, we calculated Shannon's evenness index (*even*) for these 3 classes within each territory.

We also quantified annual habitat disturbance covariates that we attributed either to fire or to timber harvest. First, we used ArcMap 10.1 to identify each pixel on our annual canopy cover maps where canopy cover declined by at least 10% during the previous 3 yr. We then obtained shapefiles from the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (<http://frap.cdf.ca.gov/>) of the perimeters of all California fires, including prescribed burns, that occurred during 1990–2011. We overlaid the fire perimeters on the annual canopy cover maps and attributed $> 10\%$ canopy cover loss to fire if the pixel was located where a fire had occurred during the previous 3 yr. For pixels located where fire had not occurred during the previous 3 yr, we attributed $> 10\%$ canopy cover loss to timber harvest (except in the

Sequoia–Kings Canyon study area, where no timber harvest occurred) because no large-scale tree mortality from sources other than fire (e.g., disease, insect outbreaks) occurred in the Lassen, Eldorado, and Sierra study sites. Thus, we calculated annual habitat disturbance covariates for fire (*fire*) or timber harvest (*logging*) within territory circles during the previous 3 yr. We chose a 3-yr timeframe because most logging projects were implemented over a period of 2 to 3 yr and postfire tree mortality often occurred for several years after wildfire. We acknowledge that canopy cover loss from fire and postfire salvage logging were confounded in the *fire* covariate for Lassen, Eldorado, and Sierra, and that the *logging* covariate for Sequoia–Kings Canyon represented canopy cover loss that was the result of disease or insect outbreaks, not timber harvest. Although prescribed fire was essentially nonexistent in the Lassen and Eldorado study areas, prescribed burns were frequently conducted in the Sierra and Sequoia–Kings Canyon study areas. We hypothesized that Spotted Owls may have benefited from managed fires that mimicked historical fires (Roberts et al. 2011). Thus, in the Sierra and Sequoia–Kings Canyon study areas, we included a covariate for the proportion of an owl territory that was affected by prescribed fire in the previous 3 yr (*Rxfire*).

Finally, we calculated annual climate covariates for each study area that may have affected Spotted Owl survival rates and thus indirectly affected occupancy. We hypothesized that cold, wet conditions during winter (November–March) would be energetically stressful for owls and hinder their ability to hunt for prey (Seamans et al. 2002, Seamans and Gutiérrez 2007a). Thus, we predicted that winters with greater precipitation (*Pwinter*) and colder temperatures (*Twinter*) than average would negatively affect occupancy in the following breeding season; for example, that precipitation from November 2003 to March 2004 would affect territory colonization and extinction rates between the 2003 and 2004 breeding seasons. Similarly, we hypothesized that cold, wet conditions during the nesting season (April–May) would be energetically stressful for both female and male owls (Seamans et al. 2002, LaHaye et al. 2004). Once nesting has been initiated, males bring food to incubating females, and after young fledge both males and females hunt for prey to feed their offspring. In this case, we hypothesized that greater precipitation (*Pnest*) and colder temperatures (*Tnest*) would negatively affect occupancy in the following year; for example, that precipitation during April and May 2004 would affect territory colonization and extinction rates between the 2004 and 2005 breeding seasons. We hypothesized that high summer temperatures (July–August; *Tsummer*) would negatively affect owls through heat stress because Spotted Owls appear to be cold-adapted (Weathers et al. 2001). Therefore, we predicted

that hot summer temperatures during July and August 2004 would affect territory colonization and extinction rates between the 2004 and 2005 breeding seasons. We extracted all climatic data (1992–2011) from PRISM (PRISM Climate Group, Oregon State University, Corvallis, Oregon, USA) at 4-km spatial resolution using ArcMap 10.1. We first extracted the climate covariate values for each territory (see Jones et al. 2016b), and then calculated annual values for each study area as the average of all territory values. We used annual climatic means rather than territory-specific values because temperature and precipitation were highly correlated with elevation at the territory level ($r > 0.8$; Jones et al. 2016b). We felt that it was more important to treat elevation as a territory-specific covariate given that managers can employ different management practices at different elevations. Despite variation among territories in climatic variables, mean study area values are often correlated with Spotted Owl demographic rates and capture broad-scale variation in weather conditions (e.g., wet vs. dry years). We estimated average elevation at each territory (*elev*; m) using 30-m resolution digital-elevation models in ArcMap 10.1.

Model selection. We used a hierarchical, multistage framework to evaluate our occupancy models because we had many covariates and wished to avoid fitting an excessive number of models, which could result in spurious relationships by chance. We examined correlations between covariates appearing in the same models, and none of these covariates were highly correlated ($r < 0.65$). At each stage, we compared candidate models using Akaike's Information Criterion (AIC; Burnham and Anderson 2002), and then used the best model (i.e. lowest AIC value) from a given stage as the base model for the next stage (see [Supplementary Material Tables S2–S5](#) for all modeling results). The stages in our modeling framework were:

- (1) We assessed within-year, survey-specific variation in detection probability using the following covariates: *repro*, *initial*, *survey*, *T*, *lnT*, *TT*, and constant value (i.e. the null model and indicated by '.'). In this stage, we included general year effects for the other model parameters including among-year variation in detection probability: $\psi_1(\cdot)$, $\varepsilon(\text{year})$, $\gamma(\text{year})$, $p(\text{year})$.
- (2) We assessed among-year variation in detection probability using the following covariates: *year*, *T*, *lnT*, *TT*, constant, *highCC*, and *mediumCC*. We included *highCC* and *mediumCC* to ensure that any correlation between these habitat covariates and ε or γ was not simply the result of their effect on detection probabilities. We used the best structure for within-year variation in detection probability from stage 1 and included general year effects for the other model parameters: $\psi_1(\cdot)$, $\varepsilon(\text{year})$, $\gamma(\text{year})$.

- (3) We examined potential covariate effects on initial occupancy probability at a territory using the following covariates: *highCC*, *mediumCC*, and constant. Furthermore, we considered linear, logarithmic, and quadratic relationships between the habitat covariates (*highCC*, *mediumCC*) and ψ_1 . We used the best structure for within-year and among-year variation in p from the previous modeling stages and included general year effects for territory extinction and colonization rates: $\varepsilon(\text{year})$, $\gamma(\text{year})$.
- (4) We examined the potential effects of our primary habitat covariates (*highCC*, *mediumCC*) on territory extinction and colonization because we expected these covariates to have the strongest association with occupancy dynamics (e.g., Tempel et al. 2014b). We again considered linear, logarithmic, and quadratic relationships between these covariates and ε and γ because previous Spotted Owl studies have found evidence for nonlinear relationships (Dugger et al. 2005, Forsman et al. 2011, Tempel et al. 2014b). We also included a model with an interaction term between *highCC* and *mediumCC*. We modeled habitat effects on ε and γ separately. When we modeled extinction probability, we included a general year effect for colonization ($\gamma[\text{year}]$). When we modeled colonization probability, we included a general year effect for extinction ($\varepsilon[\text{year}]$).
- (5) We next assessed the potential effects of covariates related to the spatial arrangement of habitat and habitat disturbance from logging or fire: *edge*, *clump*, *even*, *logging*, *fire*, and *Rxfire* (the latter for Sierra and Sequoia–Kings Canyon study areas only). We modeled ε and γ separately. We also included a model with interaction terms between *highCC* and/or *mediumCC* (if either covariate was still in the model) and any covariates from this stage that appeared in the top-ranked model.
- (6) Then we assessed 10 models that represented different combinations of our climate covariates (*Pwinter*, *Twinter*, *Pnest*, *Tnest*, and *Tsummer*). We again modeled ε and γ separately. We also included a model with interaction terms between *highCC* and/or *mediumCC* (if either covariate was still in the model) and any covariates from this stage that appeared in the top-ranked model.
- (7) Finally, we modeled the potential effects of *elev* on ε and γ separately. We also included a model with interaction terms between *highCC* and/or *mediumCC* (if either covariate was still in the model) and *elev*, as well as a model with interaction terms between climate covariates (if any were still in the model) and *elev*.

Furthermore, we included interactions between *highCC*, *mediumCC*, and other covariates under the hypothesis that

territories containing more Spotted Owl habitat would be more resilient to disturbance (Seamans and Gutiérrez 2007b) or adverse climatic conditions (Jones et al. 2016b). We included interactions between *elev* and climate because territories located at higher elevations were expected to have colder temperatures and more precipitation than territories at lower elevations. We did not retain a model if the standard errors for any beta coefficients were inestimable, which frequently occurred for models with interaction terms.

We assessed the importance of covariates in the top-ranked occupancy model for each study area in 2 ways. First, we calculated equilibrium occupancy (ψ_{eq}) from the territory colonization and extinction rates as $\gamma/(\gamma + \varepsilon)$ (MacKenzie et al. 2006). When using this equation, one assumes that γ and ε are stable over time, which was not likely to be true for some of our study areas. Therefore, we did not interpret ψ_{eq} as an expected long-term proportion of occupied territories within each study area, but rather we used ψ_{eq} to assess the relative importance of covariates in the top model by examining how occupancy varied over a range of typical values for these covariates. Second, we used the analysis of deviance (ANODEV) test in Program MARK (White and Burnham 1999) to estimate how much variation in occupancy was explained by the habitat and climate covariates in the top-ranked models. The ANODEV test compares the amount of deviance explained by the covariates in a model with the amount of deviance not explained by these covariates and thus provides an estimate of r^2 for the model (Skalski et al. 1993). The global model for each study area that we used for the ANODEV test consisted of the top-ranked model with additional annual effects for γ and ε , and the constant model consisted of the best structure for detection probability with constant values for γ and ε .

Finally, because *mediumCC* and *highCC* encompassed a relatively large range in canopy cover, we performed a post hoc analysis in which we grouped canopy cover into 10% classes and evaluated whether occupancy changed abruptly between levels of canopy cover. For each study area, we successively replaced any habitat covariates for extinction and colonization in the top-ranked model with a covariate for the proportion of a territory containing 0–9% canopy cover, a covariate for 10–19% canopy cover, etc., up to 90–100% canopy cover. For example, the top-ranked model for Lassen was $\psi_1(\cdot)$, $\varepsilon(\text{highCC} + \text{mediumCC} + \text{Tsummer})$, $\gamma(\text{highCC} + \text{Twinter} + \text{elev})$, $p(\text{year}, \text{repro} + \text{initial})$, so we fit the model $\psi_1(\cdot)$, $\varepsilon(0\text{--}9\% \text{ canopy cover} + \text{Tsummer})$, $\gamma(0\text{--}9\% \text{ canopy cover} + \text{Twinter} + \text{elev})$, $p(\text{year}, \text{repro} + \text{initial})$, then fit the model $\psi_1(\cdot)$, $\varepsilon(10\text{--}19\% \text{ canopy cover} + \text{Tsummer})$, $\gamma(10\text{--}19\% \text{ canopy cover} + \text{Twinter} + \text{elev})$, $p(\text{year}, \text{repro} + \text{initial})$, etc. We then used the beta coefficients for extinction and colonization from each model to iteratively compute ψ_{eq} for each 10% canopy

TABLE 2. Mean values (SD) for the habitat, climate, and elevation covariates used to assess California Spotted Owl territory occupancy dynamics in 4 study areas in the Sierra Nevada, California, USA, 1993–2011. Study site abbreviations: LAS = Lassen, ELD = Eldorado, SIE = Sierra, and SKC = Sequoia–Kings Canyon. Covariate definitions are provided in Table 1.

Covariate	Study area			
	LAS	ELD	SIE	SKC
<i>highCC</i> ^a	0.26 (0.12)	0.37 (0.19)	0.24 (0.12)	0.29 (0.18)
<i>mediumCC</i> ^a	0.33 (0.05)	0.24 (0.06)	0.40 (0.08)	0.37 (0.08)
<i>edge</i> (m m ⁻²)	43.6 (13.1)	50.6 (16.6)	41.5 (19.4)	26.8 (16.2)
<i>clump</i> ^b	0.33 (0.08)	0.41 (0.15)	0.23 (0.08)	0.33 (0.09)
<i>even</i> ^b	0.94 (0.06)	0.88 (0.14)	0.92 (0.07)	0.90 (0.09)
<i>logging</i> ^a	0.008 (0.020)	0.008 (0.015)	0.010 (0.016)	0.007 (0.024)
<i>fire</i> ^a	0.004 (0.032)	0.006 (0.053)	0.011 (0.055)	0.012 (0.040)
<i>Rxfire</i> ^a	—	—	0.011 (0.055)	0.030 (0.098)
<i>Pwinter</i> (cm)	91.5 (31.1)	118.3 (37.7)	73.4 (27.2)	78.4 (26.7)
<i>Pnest</i> (cm)	18.7 (10.1)	24.5 (12.6)	14.5 (9.4)	14.9 (9.4)
<i>Twinter</i> (°C)	−3.4 (0.7)	0.4 (0.5)	−0.5 (0.6)	−1.7 (0.7)
<i>Tnest</i> (°C)	0.4 (1.1)	3.7 (1.3)	3.1 (1.6)	1.8 (1.4)
<i>Tsummer</i> (°C)	26.9 (1.2)	29.0 (1.1)	28.1 (0.9)	26.8 (0.9)
<i>elev</i> (m)	1732.7 (160.0)	1441.0 (205.3)	1643.5 (562.0)	1783.4 (385.2)

^a Covariate values are the proportion of an owl territory.

^b Unitless index.

cover class when the covariate value for the class was equal to 0.25 (i.e. 25% of the territory consisted of vegetation in that 10% canopy cover class).

RESULTS

Survey Results and Environmental Conditions during the Study Period

We identified 90, 74, 66, and 45 owl territories in the Lassen, Eldorado, Sierra, and Sequoia–Kings Canyon study areas, respectively. Eldorado was the only study area in which the mean proportion of *highCC* within owl territories was greater than *mediumCC* (0.37 vs. 0.24), but *highCC* varied more than *mediumCC* in all 4 study areas (Table 2). Logging (tree disease in Sequoia–Kings Canyon) or fire generally affected <1% of any given owl territory annually, regardless of study area (Table 2). Wildfires that occurred from 1990 to 2011 affected a small number of territories in each study area (12 in Lassen, 14 in Eldorado, 3 in Sierra, and 14 in Sequoia–Kings Canyon), although some of these territories were greatly affected by high-severity fire (>50% of the territory). In contrast, prescribed fire was more common than wildfire in the 2 southern study areas, as 20 territories were affected by prescribed burns in Sierra and 22 in Sequoia–Kings Canyon. The Sierra and Sequoia–Kings Canyon study areas were drier than the 2 northern study areas; Eldorado was the wettest and warmest study area (Table 2).

The covariate *highCC* exhibited more spatial variation (spatial CV ranged from 0.47 to 0.61) than *mediumCC* (spatial CV ranged from 0.13 to 0.24). Temporal variation was much lower than spatial variation for both *highCC*

(temporal CV ranged from 0.01 to 0.03) and *mediumCC* (temporal CV ranged from 0.02 to 0.05). The variation in climate covariates shown in Table 2 was due solely to temporal variation because we calculated a single value for these covariates within a study area during each year of our study (see Statistical Analysis—Model covariates).

Estimates of Parameters

Within each study area we estimated annual extinction and colonization probabilities and bimonthly detection probabilities using the model $\psi_1(\cdot)$, $\varepsilon(\text{year})$, $\gamma(\text{year})$, and the most parsimonious structure for $p_{j,t}$ within a given study area. Additionally, we derived annual estimates of territory occupancy probability from ψ_1 , ε , and γ . Territory occupancy declined over time in the Lassen, Eldorado, and Sierra study areas as the result of declining colonization and increasing extinction rates, but increased over time in the Sequoia–Kings Canyon study site (Figure 2). Initial territory occupancy probabilities were high for all study areas (Lassen = 1.00, Eldorado = 1.00, Sierra = 0.96, Sequoia–Kings Canyon = 0.91), and these rates were not due to a sampling artifact (i.e. pseudo-increase in early years of sampling associated with a learning curve) because all territories within the core study areas were surveyed in 1993. Territory occupancy probabilities in 2011 (Lassen = 0.85, Eldorado = 0.73, Sierra = 0.71, Sequoia–Kings Canyon = 1.00) were lower than at the beginning of the study in all study areas except Sequoia–Kings Canyon. Owl densities (i.e. number of occupied territories) in Lassen, Eldorado, and Sierra appeared to be at or near their maximum values in 1993 and slowly declined over time as some territories became unoccupied and were not

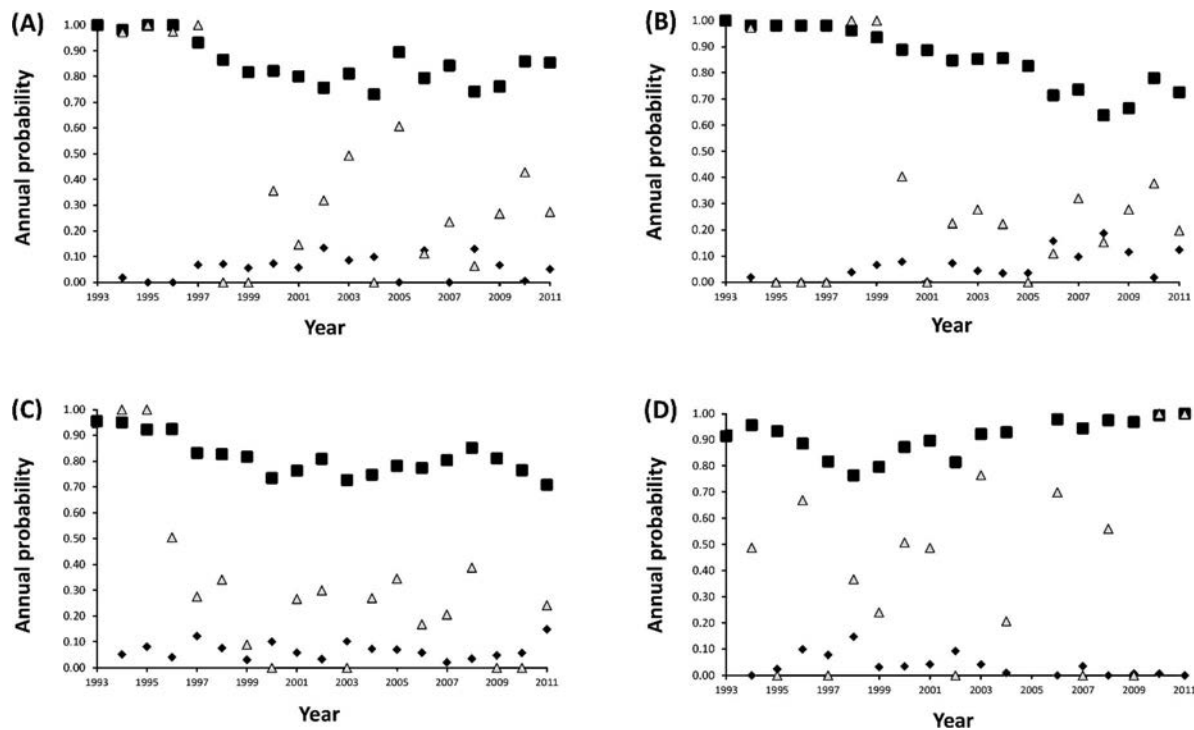


FIGURE 2. Annual estimates of occupancy (■), extinction (◆), and colonization (Δ) probabilities for California Spotted Owl territories in 4 study areas in the Sierra Nevada, California, USA, 1993–2011, calculated using the dynamic occupancy model with annual variation in extinction and colonization probabilities and the best detection probability structure for each study area. Annual occupancy estimates were derived from the extinction and colonization estimates. The study areas are: (A) Lassen, (B) Eldorado, (C) Sierra, and (D) Sequoia–Kings Canyon. Note that no surveys were conducted in the Sequoia–Kings Canyon site in 2005.

recolonized, a pattern which has previously been reported for Eldorado (Tempel and Gutiérrez 2013). Detection probabilities during bimonthly sampling periods were higher for Eldorado (average = 0.68, range = 0.51–0.91), Sierra (average = 0.70, range = 0.35–0.90), and Sequoia–Kings Canyon (average = 0.71, range = 0.49–0.82) than for Lassen (average = 0.56, range = 0.39–0.70).

Model Selection Results

Detection probability. The reproductive status of birds at a territory, *repro*, was positively correlated with p in all 4 study areas (i.e. nesting owls were more likely to be detected than nonnesting owls; Table 3; see also complete model-selection results [stages 1–7] for each study area in Supplemental Material Appendix B). For within-year variation in detection probability, *initial* was positively correlated with p in the Lassen and Eldorado study sites; thus, owls were more likely to be detected during surveys subsequent to the initial detection at a territory in a given year (Table 3). For Sierra and Sequoia–Kings Canyon, within-year detection probability followed a quadratic relationship (TT), so that p increased gradually during the survey season before dropping off sharply in August and September (Table 3). In Lassen, Eldorado, and Sierra,

the best model for annual variation in detection probability contained year-specific parameter estimates (*year*). However, the best model for annual variation in p in Sequoia–Kings Canyon suggested that p was positively correlated with forest conditions (*highCC*, *mediumCC*) within a territory (Table 3).

Occupancy. We have provided the complete model-selection results (stages 1–7) for each study area in Supplemental Material Appendix B. In the Lassen study area, the top-ranked occupancy model was $\psi_1(\cdot)$, $\epsilon(\text{highCC} + \text{mediumCC} + T_{\text{summer}})$, $\gamma(\text{highCC} + T_{\text{winter}} + \text{elev})$. As predicted, territory extinction was negatively correlated with both *highCC* and *mediumCC*, and colonization was positively correlated with *highCC*. With respect to climate covariates, T_{summer} had a positive relationship with ϵ , and T_{winter} was positively related to γ (i.e. territories were more likely to be colonized following warmer winters). In addition, colonization was positively related to *elev*. Although the covariates in the top-ranked occupancy model were supported in model selection, the 95% confidence intervals for the beta coefficients overlapped zero for all terms except $\epsilon(\text{highCC})$ and $\gamma(\text{elev})$.

In the Eldorado study area, the top-ranked model was $\psi_1(\cdot)$, $\epsilon(\ln[\text{highCC}] + \ln[\text{mediumCC}] + \text{logging} + \text{edge})$,

TABLE 3. Beta coefficients (SE) for covariate effects on model parameters in the top-ranked California Spotted Owl territory occupancy models for 4 study areas in the Sierra Nevada, California, USA, 1993–2011. Covariate definitions are provided in Table 1. Blank cells denote that a covariate did not affect a given parameter, and + indicates that there are separate beta coefficients for each year that we do not list to save space. Bold font indicates that the 95% confidence interval did not overlap zero.

Covariate	Beta coefficients		
	Detection ($p_{t,j}$)	Extinction (ε_t)	Colonization (γ_t)
Lassen:			
year	+		
repro	1.49 (0.09)		
initial	0.85 (0.07)		
highCC		−9.94 (2.58)	2.98 (2.98)
mediumCC		−5.27 (3.74)	
Tsummer		0.26 (0.15)	
Twinter			0.83 (0.45)
elev			4.78 (2.36)
Eldorado:			
year	+		
repro	1.53 (0.12)		
initial	1.23 (0.09)		
ln(highCC)		−6.48 (1.86)	
ln(mediumCC)		−7.07 (5.34)	8.24 (3.35)
logging		−42.28 (21.61)	
edge		4.22 (1.80)	
Sierra:			
year	+		
repro	1.42 (0.12)		
T	1.81 (0.71)		
TT	−3.09 (0.59)		
highCC		−2.39 (1.56)	0.94 (1.94)
mediumCC		−5.25 (1.99)	9.96 (3.15)
edge		3.63 (0.90)	−2.61 (1.04)
Pwinter		0.41 (0.26)	
Sequoia–Kings Canyon:			
repro	1.29 (0.11)		
highCC	0.78 (0.25)	−16.13 (10.64)	−33.05 (11.85)
(highCC) ²			61.06 (21.38)
mediumCC	2.26 (0.58)	−16.09 (8.68)	
highCC*mediumCC		44.88 (30.67)	
T	0.66 (0.80)		
TT	−1.60 (0.68)		
fire		−40.57 (34.40)	
Rxfire			−8.68 (6.77)
Twinter			0.01 (0.65)
elev			−2.10 (1.00)
elev*Twinter			5.26 (2.06)

$\gamma(\ln[\text{mediumCC}])$. Again, territory extinction was negatively related to both *highCC* and *mediumCC*, but colonization was positively correlated only with *mediumCC*. Contrary to our expectations, *logging* was negatively correlated with ε , whereas *edge* was positively related to ε . No climate covariates or *elev* were found in the best model. The 95% confidence intervals for the beta coefficients did not include zero for $\varepsilon(\ln[\text{highCC}])$, $\varepsilon(\text{edge})$, and $\gamma(\ln[\text{mediumCC}])$.

In the Sierra study area, the top-ranked model was $\psi_1(\cdot)$, $\varepsilon(\text{highCC} + \text{mediumCC} + \text{edge} + \text{Pwinter})$, $\gamma(\text{highCC} + \text{mediumCC} + \text{edge})$. Territory extinction was negatively correlated with both *highCC* and *mediumCC*, and territory

colonization was positively related to both *highCC* and *mediumCC*. In contrast, *edge* was positively related to extinction and negatively related to colonization, so it had a negative association with territory occupancy. Territory extinction was also positively correlated with *Pwinter* (i.e. territories were more likely to become unoccupied following wetter winters). The 95% confidence intervals for the beta coefficients of $\varepsilon(\text{mediumCC})$, $\varepsilon(\text{edge})$, $\gamma(\text{mediumCC})$, and $\gamma(\text{edge})$ did not overlap zero.

In the Sequoia–Kings Canyon study area, the top-ranked model was $\psi_1(\cdot)$, $\varepsilon(\text{highCC} + \text{mediumCC} + \text{highCC}*\text{mediumCC} + \text{fire})$, $\gamma(\text{highCC} + [\text{highCC}]^2 + \text{Rxfire} + \text{Twinter} + \text{elev} + \text{elev}*\text{Twinter})$; thus, Sequoia–Kings

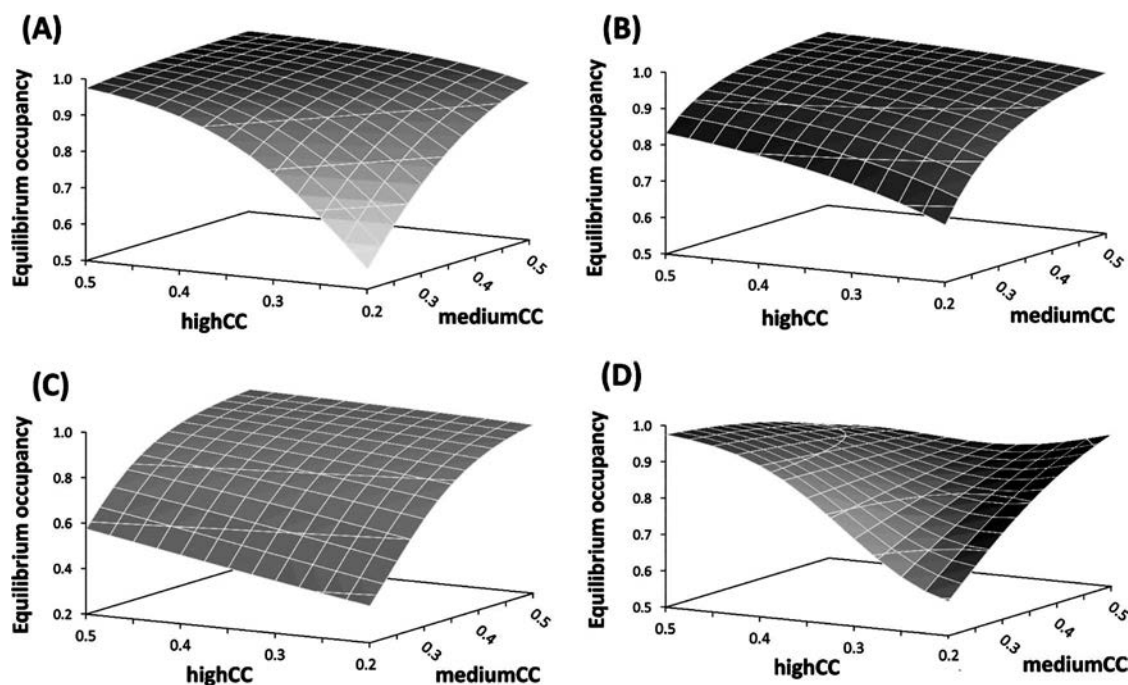


FIGURE 3. Equilibrium occupancy for California Spotted Owl territories in 4 study areas in the Sierra Nevada, California, USA, 1993–2011. Occupancy is plotted against the proportion of owl territories containing forest with $\geq 70\%$ canopy cover (*highCC*) and forest with 40–69% canopy cover (*mediumCC*). We used the beta coefficients from the top-ranked extinction and colonization models in each study area: (A) Lassen, (B) Eldorado, (C) Sierra, and (D) Sequoia–Kings Canyon.

Canyon was the only study area for which interaction terms appeared in the best model. The extinction beta coefficients for *highCC* and *mediumCC* were both negative, but their interaction was positive. Furthermore, the colonization coefficient was negative for *highCC* and positive for $(\text{highCC})^2$, so that colonization was lowest at intermediate amounts of *highCC*. Territory extinction was negatively related to *fire*, and colonization was negatively related to *Rxfire*. Although *Twinter* had a weak association with colonization, *elev* had a negative association, and their interaction was positive. This suggested that territories at higher elevations were less likely to be colonized except after warmer winters. All of the 95% confidence intervals for the extinction beta coefficients overlapped zero, but they did not do so for $\gamma(\text{highCC})$, $\gamma([\text{highCC}]^2)$, $\gamma(\text{elev})$, and $\gamma(\text{elev} * \text{Twinter})$.

The only covariates that were consistently important for all 4 study areas were *highCC* and *mediumCC*, so we calculated equilibrium occupancy for each study area while varying these 2 covariates from 0.2 to 0.5, which encompassed the typical range of values in the study areas (Table 2). When doing so, we included all covariates and their corresponding beta coefficients that appeared in the top-ranked model for a study area. For covariates other than *highCC* and *mediumCC*, we either used their average value across the study area (all climate covariates, *elev*, and

edge) or set their value to zero (*logging*, *fire*, *Rxfire*). For all 4 study areas, equilibrium occupancy reached its lowest value when both *highCC* and *mediumCC* were minimized at 0.2 and reached its highest value (or near it in the case of Sequoia–Kings Canyon) when both were maximized at 0.5 (Figure 3). Furthermore, in Eldorado and Sierra, *mediumCC* was more positively correlated with occupancy than *highCC* (Figure 3). The amounts of *highCC* and *mediumCC* within owl territories were clearly important because the analyses of deviance showed that the habitat covariates explained much of the variation in occupancy in all of the study areas—41% in Lassen, 47% in Eldorado, 67% in Sierra, and 35% in Sequoia–Kings Canyon. In contrast, the climate covariates explained much less variation in occupancy—7% in Lassen, 4% in Sierra, and 4% in Sequoia–Kings Canyon (no climate covariates were included in the top-ranked model for Eldorado).

The post hoc analysis in which we categorized canopy cover into 10% classes suggested that thresholds existed at 30% or 40%, depending on the study area; equilibrium occupancy declined sharply when below these thresholds (Figure 4). In addition, we observed that occupancy for the 40–49% canopy cover class was always lower than occupancy for the 50–59% and 60–69% canopy cover classes, and that occupancy was lower for the 90–100% class in 2 study areas (Figure 4).

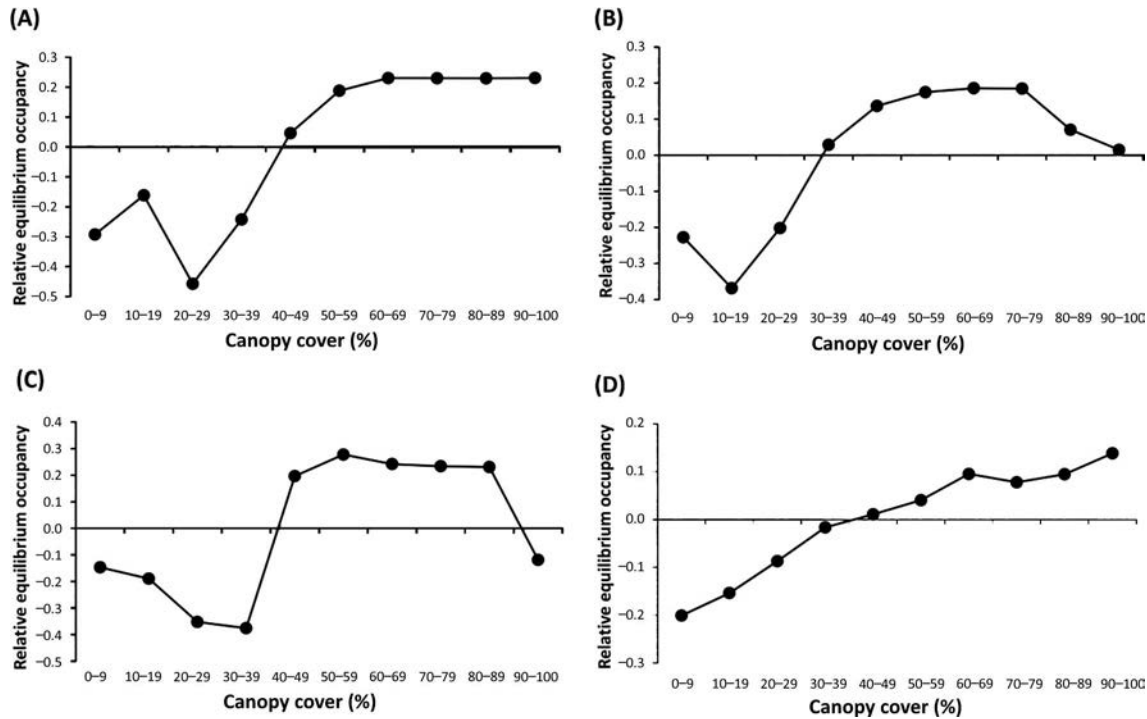


FIGURE 4. Equilibrium occupancy (relative to the mean value) for California Spotted Owl territories in 4 study areas in the Sierra Nevada, California, USA, 1993–2011. Relative occupancy is plotted against the proportion of owl territories containing canopy cover in 10% classes. We used the beta coefficients from the extinction and colonization models to estimate equilibrium occupancy for each canopy cover class, then calculated the “relative” occupancy by subtracting the mean equilibrium occupancy of all 10 canopy cover classes. The study areas are: (A) Lassen, (B) Eldorado, (C) Sierra, and (D) Sequoia-Kings Canyon.

DISCUSSION

We modeled the territory occupancy dynamics of California Spotted Owl populations in 4 study areas which were large in spatial extent and spanned the length of the Sierra Nevada. As such, we believe that our results have implications for forest management throughout this region. One of our key findings was the consistently positive association between both medium (40–69%) and high ($\geq 70\%$) canopy cover forests and territory occupancy metrics (i.e. increased colonization and decreased extinction) and that these vegetation variables explained a high proportion of variance in occupancy. By extension, and as suggested by our post hoc analysis, forests having $<40\%$ canopy cover were not Spotted Owl habitat, which supports a long history of such findings from habitat studies of California Spotted Owls (see below). **In contrast, we did not consistently find strong support for associations between occupancy and fire, logging, habitat configuration, or climate.**

The positive association that we detected between Spotted Owl territory occupancy and the amount of forest with $\geq 70\%$ canopy cover for each study area is consistent with a previous occupancy–habitat study using Eldorado data only (Tempel et al. 2014b). Notably, the 2 studies used

different and independent vegetation data sources (Landsat with verification based on other remote sensing techniques vs. aerial-photo interpretation with ground verification); collectively, they strengthen the inference that high-canopy-cover forests promote territory occupancy by Spotted Owls. Furthermore, other studies have shown that forest with $\geq 70\%$ canopy cover serves as important nesting and roosting habitat for owls (Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004). **In contrast, the positive association between California Spotted Owl occupancy and forest with medium (40–69%) canopy cover is a novel finding.**

The proportion of area within owl territories having $<40\%$ canopy cover was negatively related to territory occupancy in 3 study areas and nearly so in the fourth (Figure 4), and such forests thus do not appear to constitute suitable Spotted Owl habitat. It has been suggested that much of the Sierra Nevada historically consisted of forests having low tree density with $<40\%$ canopy cover (Collins et al. 2015) and, by extension, that such forests were suitable for owls in the past. A possible explanation for this dichotomy is that existing areas of $<40\%$ canopy cover that have resulted from forest management or disturbance may not be ecologically equivalent to historical areas of low canopy cover,

particularly if they lack larger trees. However, the negative relationship between occupancy and forests with <40% canopy cover in the Sequoia–Kings Canyon study area, where the vegetation presumably more closely reflected historical conditions under which Spotted Owls evolved (Lydersen and North 2012), suggests that forests with <40% canopy cover may not have constituted suitable Spotted Owl habitat in the Sierra Nevada historically either. Moreover, the relationship with occupancy continued to strengthen as canopy cover increased in Sequoia–Kings Canyon, suggesting that forests with $\geq 70\%$ canopy cover may have been important to the owls prior to the recent period of fire suppression. However, owl territories in Sequoia–Kings Canyon did not contain appreciably less high-canopy-cover forest than the other study areas (Table 2) and may not have fully reflected “reference conditions” prior to changes associated with fire suppression. Thus, additional work is needed to understand how closely forest characteristics at owl sites in Sequoia–Kings Canyon reflect or do not reflect conditions prior to fire suppression.

We had expected the amount of edge between high-canopy-cover forest and areas with <40% canopy cover to have positive associations with Spotted Owl occupancy via increased prey availability (Franklin et al. 2000), but edge was negatively related to occupancy in 2 of the study areas (Eldorado, Sierra). In addition, our other measures of spatial heterogeneity (evenness, clumpiness) were not supported in the occupancy models for any of the study areas. These spatial metrics may have been relatively unimportant for territory occupancy, although prior research has suggested that habitat heterogeneity and fire history have important effects on Spotted Owl prey abundance and diversity (Roberts et al. 2015). However, we measured habitat heterogeneity at a different spatial scale than Franklin et al. (2000), who mapped forest stands with a minimum size of 2 ha (as opposed to 0.09-ha pixels) and found an edge relationship between old forest and “other” cover types (i.e. not specifically <40% canopy cover as we hypothesized). In addition, habitat configuration may influence Spotted Owl fitness, as demonstrated by Franklin et al. (2000), but not necessarily occupancy, as in our present study. Finally, other aspects of habitat heterogeneity that we did not quantify may have more biological significance for Spotted Owls.

Logging was associated with occupancy in only one study area (Eldorado), where it unexpectedly had a positive association with territory colonization. However, we may have underestimated the amount of logging in the Lassen, Eldorado, and Sierra study areas as evidenced by the low values of our logging covariate within these study areas (Table 2). We used the criterion of a 10% reduction in canopy cover to infer logging activity and, therefore, omitted potential logging activities that reduced canopy

cover by <10%, which can occur. Furthermore, we examined logging events within a relatively short time-frame, and the cumulative effects of logging activities over decades could still adversely impact Spotted Owl territories. Three of the study areas had a history of timber harvest in the 20th century, which undoubtedly left a historical legacy in terms of the distribution of forest with high canopy cover and large trees within the individual study areas. The Sequoia–Kings Canyon study site did not have this logging history and it had the only study population that did not show a decline in occupancy. This spatial variation in forest conditions among territories was important in these study areas, as evidenced by the strong positive correlation between territory occupancy and forest with medium or high canopy cover.

The relationship between Spotted Owls and fire is complex and likely depends upon the overall severity of the specific fire and the proportion and patch sizes affected by high-severity fire. Some studies have found that fire had no discernible negative impact on Spotted Owl territory occupancy (Roberts et al. 2011, Lee et al. 2012, Lee and Bond 2015). However, other studies of large, contiguous areas affected by high-severity fire have reported negative effects on Spotted Owl territory occupancy after controlling for postfire salvage logging (Lee et al. 2013, Jones et al. 2016a). In our study, fire effects were included in the top-ranked model for only 1 study area (Sequoia–Kings Canyon); few territories were affected by fire in the other 3 study areas, which reduced our statistical power to detect any potential effects. Although Tempel et al. (2014b) reported that fire was negatively related to territory colonization in the Eldorado study area over a similar time period (1993–2012), their model failed to estimate a standard error for the beta coefficient of the fire covariate. We also were unable to estimate a standard error for the fire effect on territory colonization within Eldorado, so we chose to exclude the fire covariate from further modeling stages (see Statistical Analysis—Model selection). In the Sequoia–Kings Canyon study area our results were mixed, in that fire (either wildfire or prescribed fire) that reduced canopy cover by >10% reduced the probability of territory extinction, but the amount of prescribed fire within a territory reduced colonization (Table 3). The mixed results for Sequoia–Kings Canyon suggest that fire may affect owl occupancy in different ways. For example, Southern and Lowe (1968; see also Hiron 1985) suggested that Tawny Owls (*Strix aluco*) could survive poor years because they could mitigate bad years owing to their accumulated experience and intimate knowledge of territories. Under this hypothesis, if fire creates prey habitat by opening canopy and allowing shrubs to grow, it might increase foraging opportunities for established owls that have acquired knowledge of their territory. Alternatively, if fire has negative effects, resident owls might simply shift

foraging areas because they have experience with other potential foraging areas within their territory (i.e. they might mitigate the negative impact). On the other hand, new owls attempting to colonize an area that had experienced some fire (e.g., controlled burns in Sequoia–Kings Canyon in our case) would not have the accumulated territory knowledge (i.e. experience) to avoid areas affected by fire, and thus fire would reduce their incentive to colonize an unoccupied, but available, area.

Our climate covariates were not strongly correlated with Spotted Owl territory occupancy dynamics, but we modeled annual climate covariates to control for potential sources of variation in occupancy dynamics separately from habitat change. Associations between climate and occupancy, however, may be reflected over longer time periods or after time lags (Jones et al. 2016b). For example, if favorable weather conditions result in a year with high reproduction, the effects of these conditions on territory occupancy may not become apparent for several years, until the birds of that cohort have had the opportunity to colonize vacant territories. In addition, bad weather may lead to individual mortality, but no territory extinction will be observed if at least one member of an owl pair survives or if a new individual colonizes the territory before the next breeding season. Thus, occupancy may be relatively insensitive to weather conditions.

Although territory occupancy dynamics were clearly influenced by canopy cover conditions within Spotted Owl territories, we observed declining occupancy rates in 3 study areas as the result of increased extinction and decreased colonization rates in individual territories (Figure 2). These declines occurred despite relatively constant canopy cover conditions over the duration of our study. Additional components of forest structure (e.g., density of large old trees and snags, vertical complexity) undoubtedly make important contributions to owl habitat selection, territory occupancy, and fitness. We did not have the data to accurately quantify these elements at the required large spatial scales over nearly 2 decades or to determine changes in these elements that occurred prior to our study but that could have had lasting effects on owls, but the development of such datasets could significantly advance our understanding of habitat effects on Spotted Owl demography. Interestingly, the one study area (Sequoia–Kings Canyon) in which territory occupancy did not decline was located within a national park, rather than a national forest interspersed with varying amounts of private land. The different occupancy trajectory in Sequoia–Kings Canyon may have been related to different forest management practices, the presence of giant sequoia groves in this study area, a different proportion of oak woodlands, or some combination of these factors (Blakesley et al. 2010).

Management Implications

Recent proposals to revise forest management practices in the Sierra Nevada emphasize increasing forest resilience to fire, climate change, and drought (i.e. the capacity of the forest to return to its predisturbance state while maintaining characteristic ecosystem processes; Allen et al. 2002) by promoting within-stand and landscape heterogeneity (North et al. 2009, North 2012). Fuels and restoration treatments that reduce tree density and canopy cover are considered important tools in this effort (Stephens and Moghaddas 2005, Stephens et al. 2009, Stevens et al. 2014). Thus, a key management consideration involves the degree to which canopy cover can be reduced without causing significant impacts on old-forest species such as Spotted Owls that depend on forests characterized by high canopy cover. When considering the implications of our results, we stress that our study relied on Landsat imagery to quantify canopy cover, whereas forest managers typically use the Forest Vegetation Simulator (FVS; Dixon 2002) to produce canopy cover estimates when planning management activities. **Because FVS generally underestimates canopy cover, especially at higher values (Fiala et al. 2006), our canopy cover data should be calibrated against the source data used during planning. We also reiterate that we estimated equilibrium occupancy under the assumption of stable extinction and colonization rates, a condition that was not true for 3 of our study areas (Figure 2), and thus that the values of ψ_{eq} in Figure 3 should not be construed as the expected long-term proportion of occupied territories under different habitat conditions.** Nonetheless, we believe that these values can be used to assess the relative importance of the canopy cover covariates on occupancy dynamics, particularly because these covariates exhibited low temporal variation in all study areas.

Collectively, our study suggests that fuels and restoration treatments could be used to reduce canopy cover below 70% in some high-canopy-cover forest within Spotted Owl territories without having a significant impact on expected occupancy rates. **Specifically, treatments within a territory comprised of 50% high- and 50% mid-canopy-cover forest (i.e. the peaks in Figures 3A–3C) that convert some high-canopy-cover forest into mid-canopy-cover forest are predicted to incur a relatively modest cost to expected occupancy rates in the 3 national forest study areas (note the modest slope of the declines along the back right edges of the surfaces in Figures 3A–3C). Similarly, treatments within a territory comprised of 50% high-canopy-cover forest and 20% mid-canopy-cover forest that reduce high-canopy-cover forest to 30% of the territory, and where these altered stands also remain at >40% canopy cover, are not predicted to experience major reductions in occupancy.** In fact, a slight increase in occupancy would be expected in the Eldorado study area

and a greater increase would be expected in the Sierra study area. **However, our study also indicates that territory occupancy rates are likely to be negatively affected if canopy cover is consistently reduced to 40%, as evidenced by the lowest predicted occupancy rates occurring in the bottom right corners of Figures 3A–3D (i.e. where only 20% of a territory is in the high- and mid-canopy-cover classes, and 60% is in the low-canopy-cover class).** Moreover, our post hoc analysis, in which we partitioned canopy cover into 10% classes, showed that forest with 50–69% canopy cover was more strongly and positively correlated with occupancy than forest with 40–49% canopy cover. Finally, we caution that forest with 40–69% canopy cover cannot simply be substituted for forest with $\geq 70\%$ canopy cover. The importance of $\geq 70\%$ canopy cover forests as nesting and roosting habitat for California Spotted Owls has been well documented (Bias and Gutiérrez 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004). Indeed, few territories contained $< 20\%$ of high-canopy-cover forest, and as a result our study does not provide a reliable means of assessing the effects of reducing high-canopy-cover forest—and thus nesting and roosting habitat—below this level. In conjunction with declining numbers of large trees (i.e. suitable nest trees) in the Sierra Nevada over the past century (Smith et al. 2005, Lutz et al. 2009), sufficiently large reductions in high-canopy-cover forest are likely to negatively affect owls.

Our study, in conjunction with recent documentation of adverse impacts that large fires have had on California Spotted Owls (Jones et al. 2016a), suggests that maintaining viable Spotted Owl populations in the Sierra Nevada and reducing future wildfire risk using fuels and restoration treatments may be compatible goals, particularly if recent trends in high-severity fire continue or intensify because of climate change (Liu et al. 2013). However, we suggest that forest treatments to reduce fire risk should proceed with caution (be designed to retain some structural heterogeneity and the large trees) because we found declines in territory occupancy during our study, and other studies have reported substantial (up to 50%) declines in Spotted Owl populations in the Sierra Nevada within the past 20 yr (Conner et al. 2013, Tempel et al. 2014b). In addition, Barred Owls have not occurred in our study areas until recently, but evidence from Northern Spotted Owl studies suggest that they could pose an additional and significant threat to Spotted Owl populations in the Sierra Nevada if they continue to invade this region in future years (Yackulic et al. 2014, Dugger et al. 2016). Fuels treatments within Spotted Owl Protected Activity Centers (PACs), which contain ~ 125 ha of the best habitat around known Spotted Owl nest and roost locations, were largely excluded from treatment during our study, so we lack information on how treatments within

PACs could affect territory occupancy. However, given that PACs have been consistently used for nesting and roosting over long time periods (Berigan et al. 2012), future treatments within PACs could negatively affect Spotted Owl territory occupancy because these are centers of owl activity. Furthermore, forest restoration objectives may be achievable without implementing treatments within PACs because PACs occupy a relatively small percentage of the overall landscape in the Sierra Nevada (North et al. 2015). Nevertheless, forest treatments that reduce canopy cover within Spotted Owl territories, if judiciously implemented, could maintain Spotted Owl habitat in the short term so that any long-term benefits as a result of reductions in high-severity fire can be realized.

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Author contributions: J.J.K., R.J.G., M.Z.P., D.J.T., and J.D.W. conceived the idea, design, and experiment; J.J.K., R.J.G., M.Z.P., D.J.T., J.D.W., G.M.J., A.K., C.M.R., W.J.B., C.V.G., T.E.M., P.A.S., S.A.W., and M.Z.P. conducted the research; D.J.T., M.Z.P., R.J.G., J.J.K., A.K., J.D.W., G.M.J., S.A.W., W.J.B., C.V.G., and T.E.M. wrote the paper; D.J.T., R.J.G., A.K., C.M.R., M.Z.P., C.V.G., J.J.K., and G.M.J. developed and designed the methods; D.J.T., A.K., C.M.R., and G.M.J. analyzed the data; and R.J.G., M.Z.P., and J.J.K. contributed substantial materials, resources, and funding.

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Population decline in California spotted owls near their southern range boundary

Douglas J. Tempel¹ | H. Anu Kramer¹ | Gavin M. Jones²  |
R. J. Gutiérrez³ | Sarah C. Sawyer⁴ | Alexander Koltunov⁵ |
Michèle Slaton⁶ | Richard Tanner⁷ | Brendan K. Hobart¹ |
M. Zachariah Peery¹

¹University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA

²U.S. Forest Service Rocky Mountain Research Station, 333 Broadway Boulevard SE, Albuquerque, NM 87102, USA

³University of Minnesota-St. Paul, 2003 Upper Buford Circle, St. Paul, MN 55108, USA

⁴U.S. Forest Service Region 5, 1323 Club Drive, Vallejo, CA 94592, USA

⁵University of California-Davis, Center for Spatial Technologies and Remote Sensing (CSTARS), Davis, CA 95616, USA

⁶U.S. Forest Service Region 5, Remote Sensing Laboratory, 3237 Peacekeeper Way, Suite 201, McClellan, CA 95652, USA

⁷Tanner Environmental Services, PO Box 1254, Alameda, CA 94501, USA

Correspondence

Douglas J. Tempel, University of Wisconsin-Madison, 1630 Linden Drive, Madison, WI 53706, USA.

Email: djtempel1965@gmail.com

Present address

Brendan K. Hobart, Department of Ecology and Evolutionary Biology, University of Colorado, 1900 Pleasant Street, Boulder, CO 80309, USA.

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Abstract

Species worldwide have begun to shift their range boundaries in response to climate change and other anthropogenic causes, with population declines at the trailing edge of a species' range often foreshadowing future changes in core parts of the range. Therefore, we analyzed a 30-year (1991–2019) data set for the California spotted owl (*Strix occidentalis occidentalis*) near its southern range boundary in southern California, USA, that included the largest regional population (San Bernardino Mountains) to estimate trends in territory occupancy and reproduction. We then assessed how these demographic rates were affected by habitat, wildfire, fuel treatments, and climate. Mean occupancy declined from 0.82 to 0.39 during our study, whereas reproductive output showed no temporal trends ($\bar{x} = 0.65$ young/occupied territory). Territory extinction (extirpation) rates were relatively low in territories with more large trees (≥ 50 cm dbh), and colonization increased strongly with large tree density for low-elevation territories within the shrub-woodland ecotype but not for higher-elevation territories within mixed-conifer forest. High-severity wildfire had an adverse effect on occupancy: territory extinction rates steadily increased with the amount of high-severity fire within an owl territory during the previous 10 years, while colonization declined to nearly zero when $\geq 40\%$ of a territory burned at high-severity during the previous 10 years. The effects of high-severity fire were unlikely to be confounded with post-fire fuel treatments, which primarily consisted of the removal, burning,



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or scattering of brush and small trees and snags (<40.6 cm dbh) and affected much smaller areas than high-severity fire. Of the 40 territories that received fuel treatments within 10 years of a fire, only 3 of them had post-fire fuel treatments that affected >5% of the territory, whereas average area burned at high severity for all 40 territories was 17%. Fuel treatments intended to modify fire behavior and reduce the likelihood of large, high-severity fires led to increases in territory extinction and colonization such that their net effect on occupancy was minimal. Our simulations of occupancy dynamics indicated that high-severity fire accounted for 9.6% of the observed decline in occupancy, whereas fuel treatments effectively accounted for none of the decline. Spotted owl reproductive output was lower at territories where fuel treatments occurred, but low- to moderate-severity fire resulted in much larger, population-level reductions in reproductive output (141 fewer young) from 2006–2019 than treatments (19 fewer young). Thus, the benefits of fuel treatments that reduce fire occurrence and severity appear to outweigh potential short-term costs to spotted owls and their habitat. Because high-severity fire only explained a modest amount of the long-term occupancy decline and much of the decline occurred in the 1990s before large fires occurred, additional factors are likely adversely affecting the owl population and merit further study. Nevertheless, the large observed population decline, limited evidence of owl dispersal among mountain ranges in the southern California metapopulation, and negative effects of increasingly large and severe fire suggest that California spotted owls at their southern range boundary are vulnerable to extirpation. In an era of climate change, owls in the core part of the range will likely become increasingly susceptible to warmer temperatures and increased severe fire activity in the future. Thus, the restoration of historical, low-severity fire regimes through fuels management while maintaining large trees is important to improving owl persistence.

KEYWORDS

climate change, fuel treatment, reproduction, site occupancy, southern California, spotted owl, *Strix occidentalis occidentalis*, wildfire



Species globally have begun range shifts in response to climate change, but many species still face increased extinction risk if they cannot adjust their ranges quickly enough or respond with adaptive evolution or phenotypic plasticity (Chen et al. 2011, Vedder et al. 2013). Furthermore, risks posed by climate change are compounded by additional stressors such as habitat degradation, overexploitation, and invasive species (Brook et al. 2008, Srinivasan and Wilcove 2021). Consequently, the interaction between climate change and other anthropogenic stressors poses one of the greatest risks to species in evolutionary history. These risks may be most apparent at a species' trailing-edge range boundary (i.e., the southern edge in the northern hemisphere). Here, population fragmentation and genetic drift present unique challenges for species conservation (Hampe and Petit 2005), especially given that habitat disturbance can strongly affect remaining populations (Slaton 2015). Trailing-edge populations may also experience reduced individual fitness from physiological responses to stressful environmental conditions (Hoy et al. 2018). In addition, species adapted to montane ecosystems may be limited by a lack of suitable habitat at higher elevations because the vegetative component of their habitat does not respond rapidly enough to climate change (Anderson et al. 2009, Yandow et al. 2015).

Trailing-edge populations of long-lived organisms might respond even more slowly to environmental changes than populations in the core part of the range because of lagged extinction processes (Hampe and Petit 2005), so observations of population shifts or declines could indicate that important changes are well underway. The California spotted owl (*Strix occidentalis occidentalis*) is a long-lived raptor that is restricted to isolated mountain ranges at its southern range limit in southern California, USA, where suitable habitat is limited by microclimate and altitudinal variation (Gutiérrez et al. 2017). Owls here are threatened by hotter, drier conditions under climate change owing to their narrow thermal niche, and from habitat loss and reduced connectivity among populations because of development (Gutiérrez et al. 2017, Conlisk et al. 2021). Spotted owls are also biologically vulnerable to climate (and other environmental) change because of their low reproductive output, habitat specialization, and small population sizes (Hoffmann and Sgrò 2011, Razgour et al. 2018). For these reasons, quantifying population trends at the trailing edge of the California spotted owl range may be particularly important for predicting future responses by populations within the species' core range.

One of the most impactful broad-scale environmental trends across the range of the spotted owl is the emergence of megafires (Stephens et al. 2014; Jones et al. 2016a; Wan et al. 2018, 2019a). These large, stand-replacing wildfires can negatively affect spotted owls (Lee et al. 2013; Jones et al. 2016a, 2020; Rockweit et al. 2017) and have increased in frequency because of unnaturally high fuel loads after decades of fire suppression, increased human ignitions, and the warmer, drier conditions associated with climate change (Syphard et al. 2007, Steel et al. 2015, Abatzoglou and Williams 2016, Westerling 2016, Stevens et al. 2017). Conversely, historical fire regimes in seasonal dry forests throughout the spotted owl's range consisted of frequent fires that burned primarily at low and moderate severity with smaller patches of high-severity fire (Stephens and Collins 2004, Safford and Stevens 2017). Consequently, owls appear to be well-adapted to these regimes (Bond et al. 2002, 2009; Jones et al. 2020; Schofield et al. 2020; Kramer et al. 2021). To address the increasing threat of megafires, forest managers have implemented fuel-reduction projects that employ techniques such as tree thinning, understory removal, and prescribed fire (Collins et al. 2010, 2013). These treatments and post-fire salvage logging can potentially have negative impacts on spotted owl habitat (Lee et al. 2013, Tempel et al. 2015, Gallagher et al. 2019, Jones et al. 2020). Further investigation of the effects of wildfire and fuel treatments on owls is thus needed to resolve the uncertainty surrounding their relative impacts on owl population dynamics.

The California spotted owl is the only spotted owl subspecies not protected under the Endangered Species Act (ESA). Owl population trends in southern California have not been recently assessed, although prior research demonstrated that the largest population in southern California in the San Bernardino Mountains decreased during the 1990s (Franklin et al. 2004, LaHaye et al. 2004). Since then, temperatures in the region have risen and high-severity fire has increased in area and patch size (Nigro and Molinari 2019), which may have negatively affected these spotted owl populations at the trailing edge of their range. Therefore, we assessed owl demographic trends and the environmental factors that might be affecting these trends to help with conservation decision-making, forest management, and future ESA listing decisions.

We used a 30-year spotted owl data set in southern California to estimate trends in territory occupancy and reproduction and to understand how environmental factors and management actions, such as climate, wildfire, and fuel treatments, have shaped these demographic rates. We predicted that owl occupancy and reproduction were negatively affected by large areas of high-severity fire within their territories, and to a lesser degree, by fuel treatments. We also expected that owls fared better at high elevations than low elevations because of cooler temperatures and more extensive forest cover.

STUDY AREA

Our study area was located within the San Bernardino and Angeles national forests approximately 100–150 km northeast of Los Angeles, California, from 1991–2019. It encompassed the San Bernardino Mountains, San Jacinto Mountains, and eastern extreme of the San Gabriel Mountains (Figure 1) with a total area of approximately 9,000 km². These mountain ranges are surrounded by unsuitable landscapes for California spotted owls (e.g., desert, chaparral, urban areas) and movement of owls between the ranges has not been documented (Gutiérrez et al. 2017). Elevations ranged from approximately 500 m to 3,500 m. The climate was Mediterranean, and most precipitation occurred from December–February (winter) as rain or snow. Annual precipitation ranged from 250 mm to 1,000 mm and varied greatly with location, elevation, and topography (Minnich et al. 1995). Vegetation communities transitioned from Mojave Desert scrub and southern coastal scrub at lower elevations to alpine at the highest elevations (Minnich et al. 1995). Great horned owls (*Bubo virginianus*), northern goshawks (*Accipiter gentilis*),

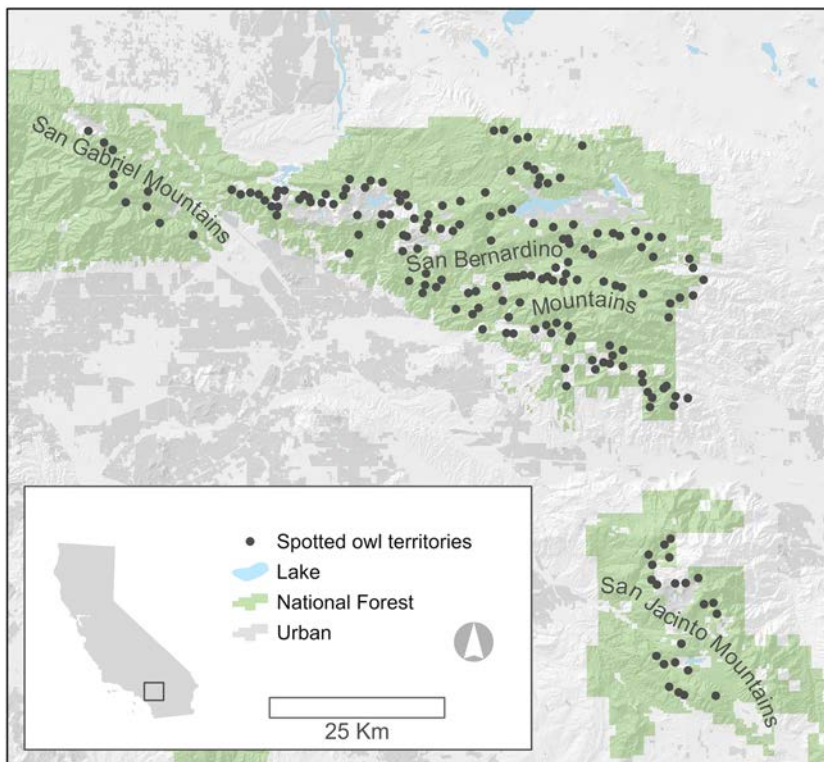


FIGURE 1 Study area in the San Bernardino and Angeles national forests in California, USA, with the locations of California spotted owl territories, 1991–2019



and red-tailed hawks (*Buteo jamaicensis*) were the main predators of spotted owls (Gutiérrez et al. 1995). The dusky-footed woodrat (*Neotoma fuscipes*), Botta's pocket gopher (*Thomomys bottae*), and northern flying squirrel (*Glaucomys sabrinus*) were the primary prey species (Smith et al. 1999). At lower elevations, owl nesting and roosting habitat was restricted to drainages that contained large big-cone Douglas-fir (*Pseudotsuga macrocarpa*) and canyon live oak (*Quercus chrysolepis*) trees and was surrounded by large expanses of shrubs. At higher elevations, mixed-conifer forests were dominated by white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), Jeffrey pine (*Pinus jeffreyi*), ponderosa pine (*P. ponderosa*), sugar pine (*P. lambertiana*), and California black oak (*Q. kelloggii*; LaHaye et al. 2004).

The historical fire regime within the mixed-conifer forest at higher elevations on our study area largely consisted of frequent, low- and moderate-intensity fires, but modern fire suppression has resulted in increased tree densities with fewer fire-resistant large trees (Minnich et al. 1995). Within the big-cone fir-live oak stands at lower elevations, historical fires occurred less frequently with a mean fire return interval of approximately 30 years (Lombardo et al. 2009). Traditional timber harvest on our study area (i.e., with the removal of larger, commercially valuable trees) ended in the early 1980s when most mills in southern California closed (I. E. Turner, U.S. Forest Service [USFS], personal communication). During our study period, forest management consisted mainly of forest restoration and fuel reduction projects to remove smaller trees (<40.6 cm dbh) and understory fuels (USFS 2005), which we collectively refer to as fuel treatments. Major disturbances during our study included the 2003 Old Fire complex, 2007 Butler and Slide fires, 2015 Lake Fire, and a pulse of tree mortality from 2002–2004 in response to drought and bark beetles (*Dendroctonus* spp.). Commercial timber harvest on private lands within our study area was rare (8 records, 140 ha; <https://gis.data.ca.gov/>, accessed 13 Jul 2020).

METHODS

Spotted owl surveys

We conducted surveys at 181 historical spotted owl territories, whose locations had been previously established during surveys by researchers, consultants, and USFS personnel. Survey effort varied each year depending on available funding, so that not all territories were surveyed every year. We surveyed owl territories from March to September 1991–2019 except for 2001, 2002, and 2014 when a lack of funding precluded any surveys. From 1991–2000, we conducted surveys within the San Bernardino Mountains for a demographic study using mark-recapture methods (LaHaye et al. 2004, Zimmerman et al. 2007). From 2003–2019, we conducted surveys in all 3 mountain ranges strictly to assess occupancy and reproduction (i.e., we did not capture or band birds). We detected owls at night by imitating owl vocalizations at call stations and along survey routes within owl territories (LaHaye et al. 2004). We then conducted diurnal walk-in surveys at territories with recent detections to assess occupancy and reproduction, and to capture and resight birds during the demographic study.

We estimated spotted owl reproduction by feeding live mice to owls and observing the owls' behavior after taking mice. We inferred non-reproduction if an owl ate or cached ≥ 4 mice or if we observed a roosting female for ≥ 45 minutes prior to 15 May. Once a pair was known to be nesting, we visited the site after 1 June to visually count fledglings (or band them during the demographic study).

Model covariates and multi-scale framework

We first identified covariates related to vegetation, disturbance, topography, and climate that could affect spotted owl site occupancy and reproduction (Table 1). When estimating covariate values, we created a circle around the territory center with a radius equal to the specified spatial scale and computed the covariate value within the

TABLE 1 Covariates along with their predicted effects and optimal spatial scale for California spotted owl territory extinction (ϵ), territory colonization (γ), and reproductive output (R) in the Angeles and San Bernardino national forests in California, USA, 1991–2019. Predicted effects of each covariate on a parameter could be positive (+), negative (–), or no specific prediction (n/a)

Covariate	Description	Type	Predicted effect			Optimal scale (m)		
			ϵ	γ	R	ϵ	γ	R
LowCC	Annual proportion of territory with canopy cover >30%	Vegetation	–	+	+	3,000	3,000	600
MedCC	Annual proportion of territory with canopy cover >50%	Vegetation	–	+	+	3,000	1,000	600
HighCC	Annual proportion of territory with canopy cover >70%	Vegetation	–	+	+	2,200	1,000	600
Tree	Annual average density of large trees ≥ 50 cm dbh (tree/ha)	Vegetation	–	+	+	3,000	2,600	2,200
Conifer	Proportion of territory containing montane conifer forest or subalpine forest ecotype	Vegetation	–	+	+	600	3,000	3,000
Hardwood	Annual proportion of hardwoods among all live trees within territory	Vegetation	–	+	+	3,000	2,200	600
Range	Mountain range (0 = San Jacinto or San Gabriel, 1 = San Bernardino, predicted effect for San Bernardino)	Topographic	–	+	+	n/a	n/a	n/a
Elevation	Average elevation (m) within territory	Topographic	–	+	+	600	600	1,800
LMU	Proportion of territory in each category: canyon or drainage, ridge, midslope NE, and midslope SW (predicted effect for canyon and midslope NE)	Topographic	–	+	+	1,800	1,000	1,000
Pnest	Average precipitation within territory during the nesting period (Mar–May)	Climate	n/a	n/a	–	n/a	n/a	1,000
Pwinter	Average winter (Dec–Feb) precipitation within territory	Climate	+	–	+	600	3,000	1,800
Tnest	Average minimum temperature within territory during the nesting period (Mar–May)	Climate	n/a	n/a	–	n/a	n/a	1,000
LSfire	Proportion of territory burned by low- or moderate-severity wildfire ^a	Disturbance	–	+	+	1,000	3,000	600
HSfire	Proportion of territory burned by high-severity wildfire ^b	Disturbance	+	–	–	600	600	600



TABLE 1 (Continued)

Covariate	Description	Type	Predicted effect			Optimal scale (m)		
			ε	γ	R	ε	γ	R
HSpatch	Maximum patch size of high-severity fire within territory ^b	Disturbance	+	-	-	1,000	600	600
WUI	Proportion of territory containing wildland-urban interface	Disturbance	+	-	-	3,000	1,400	2,200
Fuel all	Proportion of territory with possible fuel reduction treatments (all treatments in FACTS database) ^c	Disturbance	+	-	-	1,000	600	1,000
Fuel NAIP	Proportion of territory with confirmed fuel reduction treatments (using aerial photos) ^c	Disturbance	+	-	-	600	600	600
Post-fire	Proportion of territory with post-fire fuel reduction treatments ^c	Disturbance	+	-	-	1,000	1,000	1,000
Mortality	Total % tree mortality within territory from 2001–2005 that was unrelated to fuel treatments or wildfire	Disturbance	+	-	-	1,000	1,000	1,000

^aEvaluated at 2 time scales: within the previous year and previous 5 years.
^bEvaluated at 3 time scales: within the previous year, previous 5 years, and previous 10 years.
^cEvaluated at 2 time scales: within the previous year and previous 3 years.



defined area. We determined the territory center using the following hierarchy of information: the average coordinates of all nest locations, the average coordinates of all roost locations, or the centroid of the protected activity center designated by the USFS. We computed covariate values at 7 spatial scales (600–3,000 m using 400-m increments) and determined the optimal scale for each covariate independently (Statistical analyses—model selection).

Vegetation covariates

California spotted owls depend upon large trees for nest sites that are typically located in forests with high canopy cover (LaHaye et al. 1997, Roberts 2017). Blakesley et al. (2005) reported that site occupancy was positively related to the amount of forest with large trees (>61 cm dbh) and high canopy cover (>70%) in the nest area (203 ha). Other researchers reported a positive association between site occupancy in the Sierra Nevada and forests with high canopy cover that contain medium-sized (30.4–61 cm dbh) or large trees (Seamans and Gutiérrez 2007a, Tempel et al. 2014), or with forests that have medium (40–70%) or high canopy cover (Tempel et al. 2016). These studies were all conducted at a spatial scale equal to half the mean nearest neighbor distance among territories. California spotted owls also select forest stands with medium to large trees and high canopy cover for nesting (LaHaye et al. 1997, Moen and Gutiérrez 1997, Blakesley et al. 2005); therefore, reproduction may also be positively associated with larger trees and higher canopy cover. Using the same criteria for tree size and canopy cover as above, we originally defined 4 categories of owl habitat: large trees, high canopy cover; large trees, medium canopy cover; medium trees, high canopy cover; and medium trees, medium canopy cover. The resulting habitat maps showed that most owl territories on our study area contained little habitat in either large tree category, particularly with high canopy cover. This finding was likely the result of differences between southern California and the Sierra Nevada in climate, vegetation types, and growing conditions that led to sparser tree cover in southern California. These differences could also affect the optimal tree size and canopy cover for owl habitat selection in southern California. Therefore, we instead defined independent covariates for 3 categories of canopy cover (>30%, >50%, >70%) and the average density of large trees (≥ 50 cm dbh) within owl territories. The canopy cover categories were nested, which allowed us to assess the importance of specific ranges of canopy cover. For example, if a model with >50% canopy cover was a better predictor than a model with >30% canopy cover, then forests with canopy cover between 30–50% would be relatively less important than forests with canopy cover >50%.

Territory density and nest productivity (number of young per successful nest) in the San Bernardino Mountains is greater in coniferous forests containing more oak trees (e.g., big-cone Douglas-fir–canyon live oak forest; LaHaye et al. 1997, Smith et al. 2002). Forests on our study area with a significant oak component likely support a higher density of dusky-footed woodrats than forests with fewer oaks because acorns are an important food source for the woodrats (Horton and Wright 1944, Innes et al. 2007), and woodrats in turn are the most important prey item for spotted owls on our study area (Smith et al. 1999). Owls that consume more woodrats have greater reproductive success in this area (Smith et al. 1999). Thus, we included the proportion of hardwoods within forested areas as a covariate.

Vegetation mapping

We used gradient nearest neighbor (GNN) forest maps produced by the Landscape Ecology, Modeling, Mapping & Analysis (LEMMA) research group at Oregon State University (<https://lemma.forestry.oregonstate.edu/>, accessed 14 Oct 2020) to estimate vegetation covariate values within owl territories. The GNN applied direct gradient analysis and nearest-neighbor imputation to regional field plot data, mapped environmental data, and Landsat imagery to generate predictive maps of forest structure and composition (Ohmann and Gregory 2002). The GNN



maps had a 30 × 30-m spatial resolution and were available annually for our study area. We used these maps to estimate each year the proportion of each territory containing the 3 canopy cover classes and the average large tree density within each territory. Finally, we estimated the proportion of hardwoods as the basal area of live hardwoods ≥ 2.5 cm dbh divided by the basal area of all live trees (hardwood and conifer) ≥ 2.5 cm dbh.

We also obtained Level IV ecosystem maps produced by the Environmental Protection Agency (<https://www.epa.gov/eco-research/ecoregions>, accessed 13 Jul 2020). These ecosystem maps were last updated in 2013. Four ecosystem types were present on our study area: montane conifer, subalpine-alpine, lower montane shrub-woodland, and arid montane. We combined montane conifer with subalpine-alpine and lower montane shrub-woodland with arid montane because only a few owl territory centers were located within the subalpine-alpine and arid montane zones. We were particularly interested in models that included an interaction between the proportion of montane conifer forest and hardwoods because conifer forests with more oak trees may contain more woodrats (Innes et al. 2007). Because territories containing more montane conifer forest may have been more likely to persist during our study period, we also included an interaction between montane conifer forest and a linear time trend.

Topographic and climate covariates

Higher elevations may offer refugia to owls faced with warming temperatures from climate change (Jones et al. 2016b), and reproductive success on our study area has a strong positive association with elevation (Smith et al. 1999). Because higher-elevation territories having more forest and cooler temperatures may have been more likely to retain owls over the course of our study, we also included a model with an interaction between elevation and a linear time trend. The San Bernardino Mountains harbor the largest population of spotted owls and greatest extent of suitable habitat in southern California (Gutiérrez et al. 2017), so we included a covariate for mountain range (San Bernardino vs. San Jacinto or San Gabriel). Territories located on north-facing slopes and in riparian areas may provide more favorable microclimates for spotted owls and their prey (Gutiérrez et al. 2017, Hobart et al. 2019b), so we included a covariate for land management unit (LMU; North et al. 2012). We used this covariate to classify 4 categories of topography and aspect: ridge, canyon or drainage, midslope with northeast aspect (316° to 135°), and midslope with southwest aspect (136° to 315°).

Climatic conditions (temp, precipitation) and the age of breeding females affect reproductive output in spotted owls (LaHaye et al. 2004, Seamans and Gutiérrez 2007b). We lacked information on the age and identity of territorial birds after the demographic study ended in 2000, but we obtained monthly temperature and precipitation data with a 4-km × 4-km spatial resolution from the PRISM Climate Group at Oregon State University (<https://prism.oregonstate.edu/>, accessed 18 Sep 2020). LaHaye et al. (2004) reported that reproductive output on our study area was positively associated with drier conditions during the nesting period and wetter conditions during the preceding winter. Cold weather during the nesting period can also reduce reproductive output in spotted owls (Seamans and Gutiérrez 2007b). Therefore, we estimated the annual average precipitation within spotted owl territories during the nesting period (Mar–May) and previous winter (Dec–Feb), and the annual average minimum temperature during nesting. We did not include the nesting season covariates in the occupancy models.

Disturbance covariates

We included 3 covariates that reflected wildfire history within owl territories: proportion of an owl territory that burned at low- or moderate-severity (low-moderate severity), proportion of an owl territory that burned at high-severity, and maximum patch size of high-severity fire within an owl territory. We defined high-severity fire as fire that resulted in >75% overstory mortality, then we classified all other fire as low-moderate severity. We used a



combination of 2 data sources to assess burned area and fire severity. The first was the Monitoring Trends in Burn Severity database (MTBS; <http://www.mtbs.gov/>, accessed 2 Jul 2020), which accounted for severity in all fires in our study area >405 ha in size (Eidenshink et al. 2007). We supplemented this dataset with fire perimeters for fires <405 ha in size from the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (FRAP; <https://frap.fire.ca.gov/>, accessed 22 Sep 2020), which included all wildland fires that burned >40.5 ha but did not include an assessment of severity. Because smaller fires are often of lower severity, however, we included these areas in the low-moderate severity category. If this assumption was incorrect, we expected it to have little effect on our analyses because only 6.5% of the burned area during our study was from fires <405 ha. We hypothesized that low- to moderate-severity fire would have a positive or no effect on spotted owl occupancy and reproduction (Bond et al. 2002, 2009, 2016; Schofield et al. 2020; Kramer et al. 2021) but that high-severity fire (extent and patch size) would have a negative effect (Lee et al. 2013; Jones et al. 2016a, 2020; Rockweit et al. 2017). Because fire can affect spotted owl habitat for extended time periods, we estimated these covariates at 2 temporal scales: within the previous year and within the previous 5 years. We expected the effects of high-severity fire, particularly large patches, to persist longer than low- to moderate-severity fire (Jones et al. 2021), so for high-severity fire extent and patch size we also included the amount that occurred within the previous 10 years.

To estimate the proportion of an owl territory affected by fuel treatments, we obtained fuel treatment data on our study area from the USFS Activity and Tracking System (FACTS; <https://data.fs.usda.gov/geodata/>, accessed 13 Jul 2020). When estimating fuel treatment covariates, we used all treatments in the FACTS database regardless of the activity type. Spatially explicit data were only available from 2003 onwards, so we estimated the fuel treatment covariates at a 1-year and 3-year time scale to use as much of the owl data as possible. We then conducted separate analyses of fuel treatments using a subset of the spotted owl data (2006–2019). We considered 2 spatial scales (600 m and 1,000 m) for all fuel treatment covariates. To assess the accuracy of the FACTS data, we compared the treatment boundaries to National Agriculture Imagery Program (NAIP) aerial imagery from 2002, 2005, 2009, 2010, 2012, 2014, 2016, and 2018. We specified 2 categories for treatments in the FACTS database: those that we confirmed from aerial imagery (i.e., we saw clear evidence of tree or shrub removal) and those that we could not confirm (i.e., no clear evidence from imagery). Unconfirmed treatments may have been the result of errors in the database (i.e., planned projects that were never completed) or may have been undetectable from aerial photos (i.e., understory removal obscured by overstory trees).

To reflect our uncertainty in these data, we created 2 fuel treatment covariates: one that included all treatments in the FACTS database and one that included only confirmed fuel treatments. The effect of salvage logging in the Sierra Nevada on owls has been variable (Lee et al. 2013; Jones et al. 2016a, 2020), and while there is not a direct equivalent to salvage logging in southern California, we included post-fire fuel treatments as a proxy. We defined post-fire fuel treatments as those that occurred up to 10 years after a fire and within the fire perimeter.

In addition, many treatments were performed between 2003–2010 in forests with recent tree mortality from drought and bark beetles (I. E. Turner, USFS, personal communication). Because fuel treatment effects on owls at these locations may have been confounded with prior tree mortality, we included a covariate for cumulative tree mortality unrelated to fuel treatments or wildfire that occurred from 2001–2005. We obtained tree mortality information at 30-m resolution from the Ecosystem Disturbance and Recovery Tracker (eDaRT), an image analysis system that processes historical Landsat imagery to detect disturbances as compared to a recent historical baseline (Koltunov et al. 2020; complete details available online in Supporting Information). We excluded areas with fuel treatments and wildfire during the year that these tree mortality disturbances occurred and the following year, except for high-severity fire where we excluded these areas for the following 4 years.

Finally, several communities and private developments were interspersed throughout our study area, creating areas of wildland urban interface (WUI). The WUI can negatively affect wildlife through habitat loss, fragmentation, and associated human activities such as recreation (Theobald et al. 1997, Bar-Massada et al. 2014). For public safety purposes, many fuel-reduction treatments were also located within or in proximity to the WUI. We acquired



WUI data for 1990, 2000, and 2010 from the Spatial Analysis for Conservation and Sustainability lab at the University of Wisconsin (<http://silvis.forest.wisc.edu/>, accessed 10 Sep 2020). We estimated the proportion of an owl territory containing WUI using the combined amount of the interface and intermix categories (Bar-Massada et al. 2014, Radeloff et al. 2018).

Statistical analyses

Territory occupancy

We used a dynamic occupancy model that contained parameters for initial occupancy (ψ_1), territory extinction (ϵ_t), territory colonization (γ_t), and detection probability ($p_{t,j}$; MacKenzie et al. 2003). Our primary sampling periods (t) were years, and our secondary sampling periods (j) were survey occasions within years. We used the program PRESENCE (version 12.12) to perform the analyses (Hines 2006). We initially attempted to use multi-state models (MacKenzie et al. 2009) with 3 states (unoccupied, occupied without reproduction, occupied with reproduction), but the large number of parameters in many of the multi-state models resulted in a failure to converge and precluded a robust analysis. We included only diurnal detections in our detection histories to avoid false positive responses from non-territorial floaters or birds in neighboring territories (Berigan et al. 2019). To be included in the detection histories, surveys had to be ≥ 3 days apart, and the duration of surveys with no detection had to exceed 15 minutes. Because some territories were visited up to 10 times in some years to assess reproduction or resight color bands, we truncated detection histories at 6 survey occasions per year to reduce the number of missing values in the detection data.

Reproductive output

We used mixed-model analysis of variance (PROC MIXED in SAS 9.4; Littell et al. 2006) to model covariate effects on reproductive output, which we defined as the number of young fledged at an occupied territory. We treated our covariates as fixed effects, and territory and year as random effects. We considered territory to be a random effect because reproduction within a territory may not be independent among years. We treated reproductive output as a normally distributed variable because normal regression models perform well in analyses of spotted owl reproductive data (McDonald and White 2010). We used restricted maximum likelihood estimation to assess the following variance-covariance structures for repeated observations within territories: compound symmetric, first-order autoregressive, heterogeneous first-order autoregressive, and log-linear (Littell et al. 2006). After identifying the best variance-covariance structure, we used full maximum likelihood estimation to model covariate effects on reproductive output.

Model selection

For both occupancy and reproductive output, we first determined the optimal spatial scale and functional form for each covariate by fitting univariate models (using linear and quadratic forms) at all scales and finding the univariate model with the lowest Akaike's Information Criterion (AIC) value (Burnham and Anderson 2002, Wan et al. 2019b). We centered all covariate values to improve the interpretability of regression coefficients in quadratic models (Schielzeth 2010). For occupancy, we identified a separate optimal scale and functional form for each parameter (ψ_1 , ϵ , and γ) using models with a constant value for the non-target parameters (Morin et al. 2020). For all analyses, we did not include highly correlated covariates in the same model (Spearman's rank coefficient, $r_s > 0.6$). Elevation,



for example, could not be included in models with many of the vegetation and climate covariates because of high correlations.

For the occupancy modeling, we used a multi-stage model selection strategy referred to as a secondary candidate set strategy, which can efficiently identify important covariates for models containing multiple parameters (Bromaghin et al. 2013, Morin et al. 2020). We initially determined the best structure for p , which we used in all subsequent modeling. For within-year p , we included a covariate for reproductive status (breeding vs. non-breeding owls; Tempel et al. 2014). For annual p , we used covariates for the survey objectives (1991–2000 demographic study vs. 2003–2019 occupancy surveys), a year effect, and 3 different temporal trends (linear, log-linear, and quadratic). In the first stage, we independently modeled covariate effects at their optimal scale on each parameter (ψ_1 , ϵ , and γ [i.e., a sub-model]). In addition to sub-models with covariate effects, we included a constant (i.e., null) sub-model and a sub-model with year effects for the target parameter. We again held the non-target parameters constant to allow for the investigation of more complex sub-model structures and avoid potential convergence issues (Morin et al. 2020). For each parameter, we then carried forward into the final stage all sub-models within 5 AIC units of the top-ranked sub-model that did not contain uninformative parameters; when an additional parameter was added to the top-ranked model but did not provide a net reduction in AIC, we considered the parameter to be uninformative (Arnold 2010). In the final stage, we fit all combinations of sub-models and ranked this final model set using AIC values.

To assess the effects of fuel treatments and tree mortality on occupancy and reproductive output, we conducted separate analyses using a subset of the owl survey data (2006–2019) because we lacked spatially explicit fuel treatment information prior to 2003 and calculated some covariates on a 3-year time scale. We used the top-ranked model from the 1991–2019 data analyses as a baseline model and added fuel treatment and tree mortality covariates at 2 spatial scales (600 m and 1,000 m) to this model. We used the same model selection strategies discussed above, except that we carried forward into the final stage all sub-models within 2 AIC units of the top-ranked sub-model. For initial occupancy, we ran additional models where we replaced low-severity fire (from the baseline model) with the amount of high-severity fire in the previous 10 years because major fires occurred in 2003. Initial occupancy models with the low- or moderate-severity fire covariate had lower AIC values than models with the high-severity fire covariate, so we retained the baseline model from the 1991–2019 data analyses.

Population impact analyses

We conducted territory-based simulations to assess the degree to which wildfire and fuel treatments affected occupancy and reproductive output over the study period. We simulated occupancy histories from 1991–2019 at each territory using annual colonization and extinction probabilities calculated using beta coefficients from the top-ranked model and territory-specific covariate values. We assigned each territory an initial occupancy state (0 or 1) based on its occupancy status in the first year that we surveyed it during our study, and thereafter we iteratively simulated the annual occupancy state using the following equation (MacKenzie et al. 2003):

$$\psi_t = \psi_{t-1}(1 - \epsilon_{t-1}) + (1 - \psi_{t-1})\gamma_{t-1}.$$

An occupied territory became unoccupied if a random number between 0 and 1 was less than ϵ_t , and an unoccupied territory became occupied if the random number was less than γ_t . Otherwise, the territory state remained unchanged. We also calculated turnover at each territory, which occurred when a territory changed its occupancy state from the previous year. Finally, we calculated reproductive output for each territory using coefficients from the top-ranked reproductive output model and territory-specific covariate values. If a territory was occupied during a given year, we assigned it the expected reproductive output for that year. If a territory was unoccupied during a given year, reproductive output was zero.



We ran 10,000 simulations of occupancy and reproduction dynamics under 2 scenarios: a baseline scenario that used the actual, centered covariate values from our study and a no-fire scenario that used actual covariate values except for wildfire, which was assigned zero values for all years (i.e., these values were slightly negative because we centered all covariates in our analyses). To determine the impacts of wildfire and fuel treatments from 2006–2019, we repeated these simulations under 3 scenarios: a baseline scenario that used the actual covariate values, a no-fire scenario, and a no-treatment scenario. We conducted these analyses with Microsoft Excel (Microsoft Corporation, Redmond, WA, USA) and @Risk (Palisade Software, Ithaca, NY, USA).

RESULTS

We conducted 12,965 owl surveys during our study. In years that we conducted surveys, the average number of territories surveyed was 114.0 (range = 7–179). The average number of years that a territory was surveyed was 16.3 (range = 3–25).

Occupancy

Primary analyses

Detection probability for owls was best explained by reproductive status and year with breeding owls more likely to be detected than non-breeders ($\beta = 0.95 \pm 0.07$ [SE]). With our primary analyses using data from all years, the optimal spatial scale of covariates for territory extinction and colonization was predominantly at either the smaller 2 or largest scales. Fifty percent of the covariates had an optimal scale of 600 m or 1,000 m and 33.3% had an optimal scale of 3,000 m (Table 1). We carried forward 4 sub-models for initial occupancy, 2 sub-models for colonization, and 8 sub-models for territory extinction to the final modeling stage (Tables S1–S3; available online in Supporting Information). Mountain range was a covariate in 3 of the initial occupancy sub-models, but in the final stage the beta coefficient for range could not be estimated. Thus, we removed range as a covariate from ψ_1 sub-models in the final modeling stage. In the final stage, 18 models were within 2 AIC units of the top model (Table 2), which suggested substantial uncertainty. These models contained many of the same covariates (Table 2), and the beta coefficients for territory colonization and extinction were very similar among the different models for common covariates. For example, all competing models indicated a quadratic relationship between colonization and either high-severity fire (10-yr time scale) or high-severity patch size (10-yr time scale). In addition, all models showed an effect of high-severity fire on territory extinction, either a linear relationship at the 10-year time scale or a quadratic relationship at the 5-year time scale. All models also included a quadratic relationship between large tree density and both territory colonization and extinction.

The top-ranked model contained a term for high-severity fire patch size on colonization, but the total amount of high-severity fire had a similar functional relationship with colonization and was in a closely competing model ($\Delta\text{AIC} = 0.37$; Table 2). When high-severity fire burned >40% of a territory at the 600-m scale, colonization declined to nearly zero, while extinction continued to increase with more high-severity fire (Figure 2A). Similarly, colonization declined to nearly zero when the maximum patch size of high-severity fire was >25% of a territory at the 600-m scale. The most significant fire year was 2003 when 32 territories were affected by high-severity fire at the 600-m spatial scale (Figure 3A), and the average proportion of these territories burned by high-severity fire was 0.28 (range = 0.01–0.73). Although historical fire regimes differed between low-elevation and high-elevation vegetation types, fire occurrence during our study was similar for the shrub-woodland and conifer ecotypes. Fire burned 46% of the shrub-woodland ecotype and 43% of the conifer ecotype, with nearly identical proportions of low-moderate and high-severity fire occurring in each ecotype.



TABLE 2 Top-ranked models for dynamic occupancy analysis of California spotted owl territories in the San Bernardino and Angeles national forests in California, USA, 1991–2019. Detection probability (p) varied with year and the reproductive status of territorial birds. Other model terms are initial occupancy (ψ_1), territory colonization (γ), and territory extinction (ϵ). All models with difference in Akaike's Information Criterion (ΔAIC) < 2.0 are included, K = number of parameters, and $\log\mathcal{L}$ = log likelihood. Quadratic relationships are indicated by covariate²

Sub-models ^a	ΔAIC	AIC	AIC weight	K	$-2\log\mathcal{L}$
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSpatch10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire10}, \text{WUI}^2)$	0.00	8,975.48	0.056	54	8,867.48
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSpatch10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire10}, \text{LMU}, \text{WUI}^2)$	0.08	8,975.56	0.054	57	8,861.56
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSfire10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire10}, \text{WUI}^2)$	0.37	8,975.85	0.046	54	8,867.85
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSfire10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire10}, \text{LMU}, \text{WUI}^2)$	0.65	8,976.13	0.040	57	8,862.13
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSpatch10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire5}^2, \text{LMU}, \text{WUI}^2)$	0.70	8,976.18	0.039	58	8,860.18
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSpatch10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire5}^2, \text{WUI}^2, \text{HighCC}^2)$	0.80	8,976.28	0.037	57	8,862.28
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSpatch10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire10}, \text{WUI}^2, \text{HighCC}^2)$	0.84	8,976.32	0.037	56	8,864.32
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSfire10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire5}^2, \text{WUI}^2)$	0.88	8,976.36	0.036	55	8,866.36
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSpatch10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire5}^2, \text{WUI}^2)$	0.88	8,976.36	0.036	55	8,866.36
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSfire10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire5}^2, \text{LMU}, \text{WUI}^2)$	1.01	8,976.49	0.034	58	8,860.49
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSfire10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire5}^2, \text{WUI}^2, \text{HighCC}^2)$	1.06	8,976.54	0.033	57	8,862.54
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSpatch10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire10}, \text{WUI}^2, \text{MedCC})$	1.39	8,976.87	0.028	55	8,866.87
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSfire10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire10}, \text{WUI}^2, \text{HighCC}^2)$	1.40	8,976.88	0.028	56	8,864.88
$\psi_1(\text{LMU}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSpatch10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire10}, \text{WUI}^2)$	1.48	8,976.96	0.027	53	8,870.96
$\psi_1(\text{LMU}, \text{WUI}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSpatch10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire5}^2, \text{WUI}^2, \text{MedCC})$	1.56	8,977.04	0.026	56	8,865.04
$\psi_1(\text{LMU}, \text{LSfire1}), \gamma(\text{tree}^2, \text{range}, \text{HSpatch10}^2, \text{LMU}, \text{WUI}, \text{Pwinter}), \epsilon(\text{tree}^2, \text{range}, \text{HSfire10}, \text{LMU}, \text{WUI}^2)$	1.62	8,977.10	0.025	56	8,865.10



TABLE 2 (Continued)

Sub-models ^a	ΔAIC	AIC	AIC weight	K	-2logℒ
$\psi_1(\text{LMU, WUI, LSfire1}), \gamma(\text{tree}^2, \text{range, HSfire10}^2, \text{LMU, WUI, Pwinter}), \epsilon(\text{tree}^2, \text{range, HSfire5}^2, \text{WUI}^2, \text{MedCC})$	1.80	8,977.28	0.023	56	8,865.28
$\psi_1(\text{LMU, LSfire1}), \gamma(\text{tree}^2, \text{range, HSfire10}^2, \text{LMU, WUI, Pwinter}), \epsilon(\text{tree}^2, \text{range, HSfire10, WUI}^2)$	1.82	8,977.30	0.023	53	8,871.30
$\psi_1(\text{LMU, WUI, LSfire1}), \gamma(\text{tree}^2, \text{range, HSfire10}^2, \text{LMU, WUI, Pwinter}), \epsilon(\text{tree}^2, \text{range, HSfire10, WUI}^2, \text{MedCC})$	1.92	8,977.40	0.021	55	8,867.40

^aThe covariates are defined as tree = annual average density of large trees ≥50 cm dbh (trees/ha); MedCC = annual proportion of territory with canopy cover >50%; HighCC = annual proportion of territory with canopy cover >70%; range = mountain range (0 = San Jacinto or San Gabriel, 1 = San Bernardino); Pwinter = average winter (Dec–Feb) precipitation within territory; LMU = proportion of territory in each category: canyon or drainage, ridge, midslope NE, and midslope SW; LSfire1 = proportion of territory burned by low- or moderate-severity wildfire in previous year; HSfire5 = proportion of territory burned by high-severity wildfire within previous 5 years; HSfire10 = proportion of territory burned by high-severity wildfire within previous 10 years; HSpatch10 = maximum patch size of high-severity fire within territory within previous 10 years; WUI = proportion of territory containing wildland-urban interface.

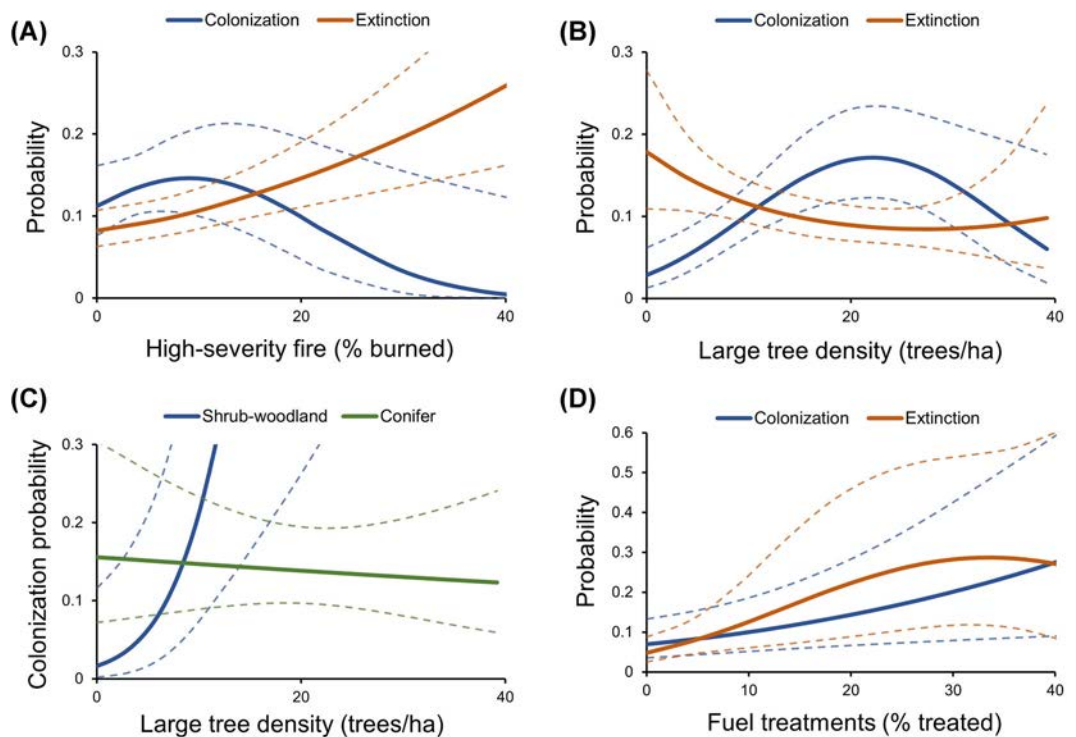


FIGURE 2 Selected covariate relationships with site colonization and extinction for California spotted owl territories in the San Bernardino and Angeles national forests in California, USA. The dashed lines indicate 95% confidence intervals. A) The effect of high-severity fire in the previous 10 years on territory colonization and extinction, 1991–2019. B) The effect of large tree density on colonization and extinction for all spotted owl territories, 1991–2019. C) The effect of large tree density on colonization for spotted owl territories within the shrub-woodland and conifer ecotypes, 1991–2019. D) The effect of fuel treatments in the previous 3 years on territory colonization and extinction, 2006–2019

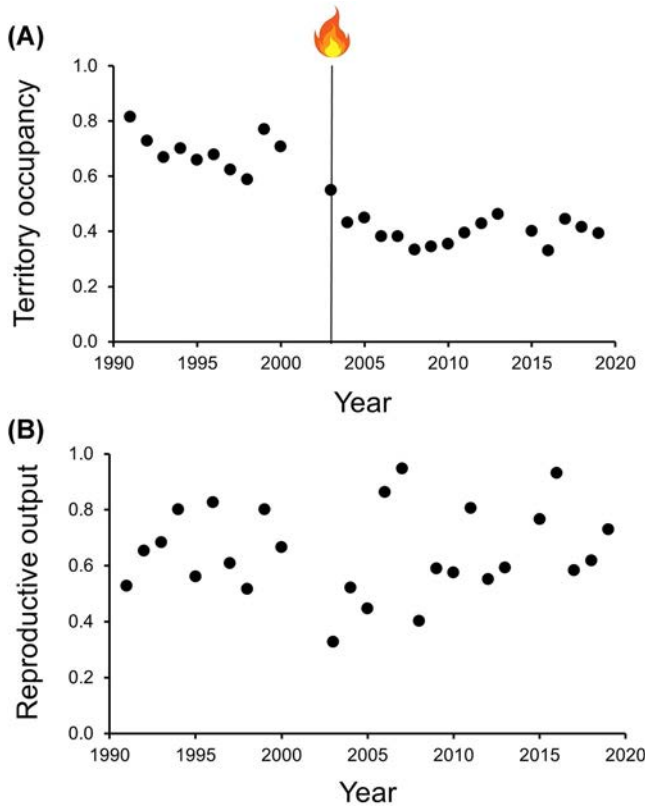


FIGURE 3 A) Mean site occupancy at California spotted owl territories ($n = 181$) in the San Bernardino and Angeles national forests in California, USA, 1991–2019. Mean occupancy was estimated from conditional occupancy probabilities at each territory provided by program PRESENCE. The 2003 fire season is indicated by the vertical bar and flame symbol. B) Mean reproductive output (number of young fledged) per occupied spotted owl territory, 1991–2019

Territory colonization increased as large tree density increased to about 20 trees/ha then declined with greater density, whereas territory extinction declined by half as tree density increased to approximately 20 trees/ha before leveling off (Figure 2B; Table 3). This quadratic relationship between large trees and colonization was apparently largely driven by the difference between lower-elevation territories in the shrub-woodland ecotype and higher-elevation territories in the conifer ecotype. Therefore, we compared parameter estimates for the linear effect of large trees on colonization from models using data from territories completely within the shrub-woodland ecotype at the 600-m scale ($n = 42$), and data from territories completely within the conifer ecotype ($n = 112$) at the 600-m scale. We observed a strong, positive relationship between colonization and large tree density for shrub-woodland territories, and a weak, negative relationship for conifer territories (Figure 2C). Furthermore, 95% of shrub-woodland territories had large tree densities <10 trees/ha, whereas 90% of conifer territories had densities >10 trees/ha. We then conducted a *post hoc* model using the full data set that contained an interaction between large tree density and the proportion of conifer forest. Although this model had $\Delta\text{AIC} = 3.89$, the beta coefficients for colonization indicated a negative interaction between large trees and conifer forest ($\beta_{\text{tree}} = 1.55 \pm 0.79$; $\beta_{\text{conifer}} = -0.25 \pm 0.59$; $\beta_{\text{tree} \times \text{conifer}} = -4.74 \pm 2.14$). This suggested that the quadratic relationship between colonization and large tree density for all territories was influenced by the dichotomy between ecotypes.

TABLE 3 Beta coefficients (SE) for covariate effects from the top-ranked models for dynamic occupancy and reproductive output (R) at California spotted owl territories in the Angeles and San Bernardino national forests in California, USA, 1991–2019. The model parameters for dynamic occupancy are initial occupancy (ψ_1), territory extinction (ϵ), and territory colonization (γ). An asterisk (*) indicates that the 95% confidence interval did not overlap zero. The beta coefficients for fuel treatment and tree mortality covariates were estimated from models using 2006–2019 data

Covariate ^a	ψ_1	ϵ	γ	R
Tree		-1.06 (0.41)*	2.15 (0.60)*	
Tree ²		1.64 (1.51)	-5.61 (1.92)*	
HighCC				0.29 (0.12)*
Range		-0.61 (0.31)*	0.56 (0.32)	
Pwinter			-2.66 (0.93)*	
Tnest				0.17 (0.11)
LMU: NE slope	-0.08 (4.83)		-4.27 (1.50)*	-0.11 (0.30)
LMU: ridge	-6.78 (8.39)		-4.22 (2.75)*	-0.92 (0.52)
LMU: SW slope	-9.86 (5.90)		-5.36 (1.72)*	-0.61 (0.35)
LSfire1	-1,269.95 (448.93)*			
LSfire5				-0.46 (0.21)*
HSfire10		3.38 (0.83)*		
HSpatch10			2.11 (4.04)	
HSpatch10 ²			-105.93 (52.46)*	
WUI	6.59 (4.08)	-2.95 (1.11)*	2.46 (0.97)*	
WUI ²		9.17 (2.67)*		
Fuel all3	-26.49 (16.91)	10.86 (4.95)*	3.93 (1.60)*	-0.87 (0.49)
Fuel all3 ²	113.12 (74.12)	-17.27 (14.05)		
Mortality	0.23 (0.06)*	-0.21 (0.05)*		
Mortality ²	-0.03 (0.01)*	0.03 (0.01)*		

^aThe covariates are defined as tree = annual average density of large trees ≥ 50 cm dbh (trees/ha); HighCC = annual proportion of territory with canopy cover $>70\%$; range = mountain range (0 = San Jacinto or San Gabriel, 1 = San Bernardino); Pwinter = average winter (Dec–Feb) precipitation within territory; Tnest = average minimum temperature within territory during the nesting period (Mar–May); LMU = proportion of territory in each category: canyon or drainage, ridge, midslope NE, and midslope SW; LSfire1 = proportion of territory burned by low- or moderate-severity wildfire in previous year; LSfire5 = proportion of territory burned by low- or moderate-severity wildfire within previous 5 years; HSfire10 = proportion of territory burned by high-severity wildfire within previous 10 years; HSpatch10 = maximum patch size of high-severity fire within territory within previous 10 years; WUI = proportion of territory containing wildland-urban interface; Fuel all3 = proportion of territory with possible fuel reduction treatments (all treatments in FACTS database) within previous 3 years; mortality = total % tree mortality within territory from 2001–2005 that was unrelated to fuel treatments or wildfire.

Other beta coefficients from the top-ranked model indicated higher colonization and lower extinction rates in the San Bernardino Mountains compared to the San Jacinto and San Gabriel Mountains, which resulted in higher occupancy rates in the San Bernardino Mountains (Table 3; Figure S1 in Supporting Information). Colonization probabilities were higher in territories that contained a greater proportion of canyon drainages relative to the other landscape types (ridges and slopes; Table 3). For example, the odds ratio indicated that a territory located entirely



on a ridge was 68 times more likely not to be colonized than a territory located entirely within a drainage (i.e., a 1-unit increase in the amount of ridge because the LMU covariates were expressed as the proportion of a territory in each category). Also, the WUI was positively related to colonization and had a quadratic relationship with extinction, which was lowest at intermediate amounts of WUI within territories (Table 3). Finally, colonization was lower in territories with more winter precipitation (Table 3). For example, the odds ratio indicated that a territory with twice the precipitation as another territory was 7.1 times more likely not to be colonized.

We used the conditional occupancy probabilities at each territory from the PRESENCE output for the top-ranked model to find the annual mean territory occupancy, and we estimated the variance of annual mean occupancy using the delta method (Powell 2007). Conditional occupancy is derived from the survey history at a territory (Hines 2006). If there is ≥ 1 detection, the territory is considered occupied with no error. If there are no detections, the occupancy probability and standard error are estimated from the number of surveys and p for each survey. The mean occupancy declined from 0.82 ± 0.01 in 1991 to 0.39 ± 0.00 in 2019, which was a proportional decline of 52.4% (Figure 3A).

Secondary analyses of fuel treatments

We confirmed that 55.8% of the fuel treatments in the FACTS database were visible in NAIP imagery. The remaining treatments may have occurred but were undetectable from the imagery (e.g., consisted of understory removal that was obscured by the tree canopy). In our initial secondary analyses using data from 2006–2019, we observed an extreme quadratic relationship between post-fire fuel treatments and territory extinction, where extinction was high at intermediate values of post-fire treated area within a territory and nearly zero for low and high values of post-fire treated area. Upon further investigation, we noted that only 40 territories received post-fire fuel treatments, and 24 of these territories had treatments that affected <0.05 of the territory. In addition, only 3 territories with >0.05 treated area were occupied prior to treatment, and thus had the potential to become locally extinct. This resulted in erratic model behavior, which dictated that we remove the post-fire fuel treatment covariate from the analyses (Appendix A). We carried forward 5 sub-models for initial occupancy, 2 sub-models for territory colonization, and 1 sub-model for territory extinction to the final modeling stage (Tables S4–S6; available online in Supporting Information). In the final stage, there were 6 models with $\Delta AIC < 2.0$ (Table S7); however, these models were similar in that the amount of all fuel treatments in the FACTS database within the previous 3 years was a covariate for both territory colonization and extinction and tree mortality from drought and bark beetles from 2001–2005 was a covariate for territory extinction.

In the top-ranked model, territory colonization increased with the amount of fuel treatments in the previous 3 years (Table 3). Fuel treatments had a quadratic relationship with territory extinction where extinction increased with the amount of fuel treatments before declining slightly at higher values (Table 3). These relationships with territory colonization and extinction offset each other, so the net effect on territory occupancy was largely neutral (Figure 2D). The amount of tree mortality caused by drought and bark beetles from 2001–2005 also had a quadratic relationship with territory extinction, which was lowest at intermediate values of tree mortality (Table 3).

Reproductive output

Our primary analyses using data from all years showed that the optimal spatial scale of covariates for reproductive output (number of young fledged at an occupied territory) was predominantly at the 2 smallest scales; 70% of the covariates had an optimal scale of 600 m or 1,000 m (Table 1). Similar to occupancy, 11



models had $\Delta AIC < 2.0$, but these models contained many of the same covariates (Table 4). In this case, the primary difference was whether the model contained a canopy cover covariate for medium or higher (>50%) or high (>70%) canopy cover within a territory with the beta coefficients for these 2 covariates always positive and of similar value.

The top-ranked model indicated that high canopy cover forest had a positive linear relationship with reproductive output (Table 3); for every 10% increase in the proportion of high canopy cover forest within a territory, reproductive output each year increased by 0.03 young fledged. In addition, territories located proportionally more within drainages or on northeast-facing slopes had greater reproductive output (Table 3). For example, a 10% increase in the proportion of drainages within a territory and a 10% decrease in the proportion of ridges resulted in 0.09 more young fledged each year. Reproduction was also positively correlated with the average minimum temperature during the nesting season (Table 3); for every 1°C increase in minimum temperature, reproductive output increased by 0.17 young fledged. Finally, reproduction was negatively correlated with the amount of low- to moderate-severity fire during the previous 5 years (Table 3); every 10% increase in the proportion of low- to moderate-severity fire within a territory resulted in 0.05 fewer young fledged each year. Mean reproductive output showed no evidence of a temporal trend over the duration of our study (Figure 3B). The average reproductive output for all years was 0.65 ± 0.16 and ranged from 0.33–0.95.

In our secondary analyses using data from 2006–2019, the top-ranked model contained a covariate for all fuel treatments in the FACTS database during the previous 3 years. A closely competing model ($\Delta AIC = 0.50$; Table S8 in Supporting Information) contained a covariate for confirmed fuel treatments in the previous 3 years. In both cases, fuel treatments were negatively correlated with reproductive output (Table 3). For example, every 10% increase in the proportion of a territory containing any fuel treatment in the FACTS database resulted in 0.09 fewer young fledged each year.

TABLE 4 Top-ranked models for reproductive output of territorial California spotted owls in the San Bernardino and Angeles national forests in California, 1991–2019. All models with difference in corrected Akaike's Information Criterion (ΔAIC_c) < 2.0 are included, K = number of parameters, and $\log \mathcal{L}$ = log likelihood

Model covariates ^a	ΔAIC_c	AIC_c	AIC_c weight	K	$-2\log \mathcal{L}$
HighCC, LMU, LSfire5, Tnest	0.00	3,207.98	0.077	10	3,187.8
HighCC, LMU, LSfire5	0.37	3,208.34	0.064	9	3,190.2
MedCC, LMU, LSfire5, Tnest	0.60	3,208.58	0.057	10	3,188.4
MedCC, LMU, LSfire5	0.97	3,208.94	0.047	9	3,190.8
HighCC, elevation, LMU, LSfire5	1.00	3,208.98	0.047	10	3,188.8
HighCC, LMU, LSfire5, Pwinter, Tnest	1.64	3,209.61	0.034	11	3,187.4
HighCC, LMU, LSfire5, Pnest, Tnest	1.74	3,209.71	0.032	11	3,187.5
MedCC, LMU	1.74	3,209.72	0.032	8	3,193.6
HighCC, LMU, LSfire5, Pnest, Tnest	1.84	3,209.81	0.031	11	3,187.6
HighCC, LMU, LSfire5, Pwinter	2.00	3,209.98	0.028	10	3,189.8
MedCC, elevation, LMU, LSfire5	2.00	3,209.98	0.028	10	3,189.8

^aThe covariates are defined as MedCC = annual proportion of territory with canopy cover >50%; HighCC = annual proportion of territory with canopy cover >70%; elevation = average elevation (m) within territory; Pnest = average precipitation within territory during the nesting period (Mar–May); Pwinter = average winter (Dec–Feb) precipitation within territory; Tnest = average minimum temperature within territory during the nesting period (Mar–May); LMU = proportion of territory in each category: canyon or drainage, ridge, midslope NE, and midslope SW; LSfire5 = proportion of territory burned by low- or moderate-severity wildfire within previous 5 years.

Population impact analyses

Territory occupancy declined from 75.0% in 1991 to 42.7% in 2019 under the baseline scenario, which was similar to our empirical analyses (Table 5). In the no-fire scenario, the mean territory occupancy in 2019 was 45.8%. Thus, high-severity fire accounted for 9.6% (3.1/32.3) of the overall decline in occupancy during our study period. This translates to about 6 territories that became unoccupied as the result of high-severity fire (0.031×181). Mean turnover at territories (i.e., change in occupancy status from the previous year) was 10.5% under both scenarios (Table 5). Total reproductive output was higher under the no-fire scenario than the baseline scenario (1,531 vs. 1,423; Table 5).

Territory occupancy increased slightly from 36.8% in 2006 to 37.9% in 2019 under the baseline scenario and 38.2% under the no-treatment scenario (Table 5). In contrast, territory occupancy in 2019 was 44.3% for the no-fire scenario, which translates to about 12 territories that became unoccupied as the result of high-severity fire (0.064×181). There was an even greater effect of high-severity fire on occupancy for the 2006–2019 simulations because most of the high-severity fire on our study area occurred from 2003 onwards. Compared to high-severity fire, fuel treatments had relatively little effect on occupancy. Mean turnover at territories was slightly lower for the no-treatment scenario (7.2%) than for the baseline (7.8%) and no-fire (8.1%) scenarios (Table 5). Total reproductive output was higher for the no-fire scenario (840) than the no-treatment (718) and baseline scenarios (699; Table 5).

DISCUSSION

California spotted owl territory occupancy on our study area in southern California declined by 52.4% from 1991 to 2019, which predicts actual changes in population size (Tempel and Gutiérrez 2013). This population decline near the subspecies' southern range boundary is even more precipitous than in the core part of its range in the Sierra Nevada, where occupancy declined by 15–30% on 3 study areas outside of national parks between 1993–2011 (Tempel et al. 2016). Within our study area, the San Bernardino Mountains had higher occupancy rates than the San Jacinto and San Gabriel Mountains. Owls in other mountain ranges in southern California may also have experienced greater population

TABLE 5 Results of population impact analyses for territorial California spotted owls in the San Bernardino and Angeles national forests in California, USA, 1991–2019. We ran 10,000 simulations of occupancy dynamics and reproductive output at each territory under the following scenarios: baseline where we used actual covariate values at each territory, and no fire where we assigned zero values for all fire covariates. Because we lacked fuel treatment data for part of the study period, we repeated the simulations from 2006–2019 for the following scenarios: baseline, no fire, and no treatments where we assigned zero values for all fuel treatment covariates. We provide mean values and SD for occupancy rate in 2019, turnover rate, and total reproductive output

Scenario	Occupancy 2019 (%)		Turnover (%)		Total reproduction	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
1991–2019:						
Baseline	42.7	3.5	10.5	0.5	1,423	50
No fire	45.8	3.5	10.5	0.5	1,531	53
2006–2019:						
Baseline	37.9	3.2	7.8	0.5	699	36
No fire	44.3	3.3	8.1	0.6	840	40
No treatments	38.2	3.2	7.2	0.5	718	37



declines than the San Bernardino Mountains. Naïve occupancy rates (i.e., not accounting for imperfect detection) within the Cleveland National Forest have declined from 0.52 in 1991 to 0.11 in 2020, and fires in 2003 and 2007 may have contributed to this decline (K. J. Winter, Cleveland National Forest, unpublished data). In general, smaller populations in the region appear to be at risk of local extirpation owing to small population size, population isolation, and limited dispersal among populations (Gutiérrez et al. 2017). Combined with the potential loss of suitable habitat to climate change in coming decades (Conlisk et al. 2021), these results suggest that California spotted owl populations near the species' southern range boundary may be vulnerable to local extinction. This steep population decline near their trailing-edge range boundary may also indicate that owls in the core part of the range in the Sierra Nevada will become increasingly susceptible to warming temperatures and changing fire regimes. As with our study area, stand-replacing patches of fire in the Sierra Nevada from 1984–2015 became larger and more regularly shaped (Stevens et al. 2017). In addition, future increases in burned area within this subspecies' range are projected to be similar for southern California and the Sierra Nevada (Wan et al. 2019a).

High-severity fire contributed to the decline in our study population, but its deleterious effects on occupancy occurred at higher values of high-severity patch size and total area burned within the territory. These effects were also independent of post-fire fuel treatments because most territories that burned were not treated and post-fire fuel treatments were small relative to the amount of burned area. Our results corroborate several previous studies from the Sierra Nevada and southern California that revealed negative effects on owl occupancy (Lee et al. 2013; Jones et al. 2016a, 2021) and habitat use (Eyes et al. 2017, Jones et al. 2020, Schofield et al. 2020, Kramer et al. 2021) when high-severity fire occurred in larger patches or burned a higher proportion of a spotted owl territory. We specifically observed that colonization approached zero when approximately 40% of a territory burned at high-severity, which suggested that it may take decades for these areas to become suitable owl habitat. Our simulations suggested that high-severity fire accounted for 9.6% of the long-term decline in occupancy. This effect size can be significant for an already declining population, even though much of the decline occurred during the 1990s before high-severity fire had affected much of our study area. Therefore, additional research will be required to assess other potential causes for the decline, such as changes in forest structure during the decades prior to our study (Minnich et al. 1995) or long-term shifts in owl diet owing to land use and management (Hobart et al. 2019a).

Low- to moderate-severity fire had a negative impact on the initial probability of occupancy and on reproductive output. These results were opposite of our predictions because previous research has not found a negative effect of low- or moderate-severity fire on spotted owl habitat selection or demographic traits (Bond et al. 2009, 2016; Jones et al. 2020; Schofield et al. 2020; Kramer et al. 2021). With respect to initial occupancy, a *post hoc* examination showed that only 6 territories experienced any low- to moderate-severity fire in the year prior to being surveyed for the first time, and 5 of these sites were initially unoccupied. Thus, the relationship between initial occupancy and low- to moderate-severity fire was derived from a small sample size. With respect to reproduction, we hypothesize that adverse effects of low- to moderate-severity fire would be mediated by changes in prey abundance or access. In the Sierra Nevada, for example, spotted owl diet has been strongly affected by fire history, in terms of extent and frequency (Hobart et al. 2021). In addition, prey may show functional responses in our study area that are different from prey populations in spotted owl ranges where previous owl-fire studies have occurred. Low- to moderate-severity fire could affect small-mammal populations if it reduces important habitat elements such as shrub cover, grass cover, or coarse woody debris (Lee and Tietje 2005, Innes et al. 2007), but impacts of fire on small-mammal abundance can vary by species and location. Some researchers reported an increase in rodent biomass after fire in Mexican spotted owl (*S. o. lucida*) habitat (Converse et al. 2006, Ganey et al. 2014). In contrast, abundance was lower for several species, including the desert woodrat (*N. lepida*), in burned areas within southern California chaparral and woodlands (Brehme et al. 2011).

Fuel-reduction treatments can reduce the future risk of high-severity fire, but these treatments may have short-term negative effects on spotted owls (Lee et al. 2013, Tempel et al. 2015, Gallagher et al. 2019, Jones et al. 2022). Fuel treatments, though not expressly intended to reduce the risk of drought-induced insect mortality, have also been reported to reduce drought effects by reducing water competition among surviving trees (Knapp et al. 2021,



Steel et al. 2021). Tree mortality in California caused by drought and insect outbreaks has increased in recent decades and is forecast to accelerate because of climate change (Preisler et al. 2017, Fettig et al. 2019, Madakumbura et al. 2020). Thus, more extensive tree mortality could necessitate continued fuel treatments, both to mitigate mortality and to reduce the risk of megafires. Fuel treatments were correlated with increased territory extinction and reduced reproductive output, but treatments increased the probability of colonization. In this case, fuel treatment effects on territory colonization and extinction offset so that occupancy was largely unaffected. Our population impact analyses indicated that fuel treatments may have caused small declines in occupancy and total reproductive output, but these effects were minor compared to the effects of fire on occupancy and reproduction. The adverse effects of fire on total reproductive output resulted from a reduction in the number of occupied territories and from the impact of low- to moderate-severity fire on reproduction. Higher extinction and higher colonization rates following treatments suggested greater turnover (change in occupancy status) at treated territories, but the population impact analyses revealed that mean turnover rates between the baseline and no-treatment scenarios were similar.

Several other factors appeared to affect occupancy dynamics during our study. First, large trees were the most important habitat element, which has been a consistent finding among spotted owl habitat studies (Roberts 2017). Territory extinction declined as large tree density increased, which has also been reported previously for 4 study areas in the Sierra Nevada (Jones et al. 2018). We observed a quadratic relationship between large tree density and colonization where colonization was highest at intermediate densities. Although this could indicate that some level of habitat heterogeneity within a territory is optimal for owls (Franklin et al. 2000), our *post hoc* analysis suggested that differences between low-elevation, shrub-woodland territories and high-elevation, conifer forest territories were important in accounting for this relationship. Most territories in the shrub-woodland ecotype had few large trees, and a strong positive relationship with large tree density existed at these sites. Second, territories located predominantly within drainages were more likely to be colonized, less likely to go locally extinct, and had higher reproductive output. Sites in drainages may provide a favorable microclimate for spotted owls that are prone to heat stress (Barrows 1981). Finally, we observed an unexpected positive association between occupancy and the proportion of WUI within a territory, even though many fuel reduction treatments were located within or near WUIs. We speculate that WUIs may support a greater abundance of rodents than the surrounding wildlands, although we found no evidence in the literature to support this conjecture. Alternatively, WUIs on our study area simply may have been associated with other unknown factors that supported spotted owl territories.

The optimal spatial scales for our covariates were predominantly 600 m, 1,000 m, or 3,000 m. Ecological processes have been recognized to operate in a scale-dependent manner (Wiens 1989, Mayor et al. 2009), so studies that incorporate multiple scales should provide a more accurate assessment of how environmental factors affect wildlife populations. Most previous spotted owl studies have defined the territory using a single spatial scale based on nearest-neighbor distances or typical home-range sizes and may have missed important ecological relationships at a different spatial scale (Jackson and Fahrig 2015, Moraga et al. 2019). Previous spotted owl researchers that did incorporate multiple spatial scales have also reported that optimal scales can vary widely among covariates (Timm et al. 2016, Wan et al. 2019b). Our 1,000-m scale roughly corresponds to home-range size estimates from our study area (Zimmerman et al. 2001), but the importance of other scales in our analyses suggests that future studies should consider the use of multiple spatial scales and attempt to evaluate the underlying ecological mechanisms at optimal spatial scales. In addition, we encourage future research on the connectivity and demographic status of other local populations in southern California to address current information gaps.

MANAGEMENT IMPLICATIONS

Active forest management that includes fuel treatments with the concomitant retention and recruitment of large trees is likely to provide long-term benefits that outweigh any short-term costs for spotted owls. The retention of large trees is likely to be particularly important at low-elevation sites in southern California, which have fewer large



trees than sites at higher elevations and where owl presence is strongly linked to greater large tree densities. When planning fuel treatments, managers could reduce potential impacts to owls by retaining relatively higher canopy cover in drainages while implementing more intensive treatments on ridges and drier sites, thereby still achieving desired fuel-reduction goals across the landscape. Our estimates of population trends and characterization of environmental factors that influence these trends will provide an improved scientific basis for future evaluations of the spotted owls' protected status in southern California.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

ETHICS STATEMENT

We ensured proper care and handling of all animals by following procedures that were part of a study plan approved by the University of Minnesota Institutional Animal Care and Use Committee (protocol number 0003A4261).

ORCID

Gavin M. Jones  <http://orcid.org/0000-0002-5102-1229>

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SUPPORTING INFORMATION

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APPENDIX A: POST-FIRE FUEL TREATMENTS

In our initial analyses of data from 2006–2019 where we assessed the effects of fuel and post-fire fuel treatments on California spotted owl territory occupancy dynamics, we found an extreme quadratic relationship between post-fire fuel treatments and extinction probability (Figure A1A). Territory extinction probability approached 0.8 when 10% of a territory was subject to post-fire fuel treatment in the previous 3 years, but territory extinction was nearly zero at lower (<1%) and higher (>20%) values of post-fire treated area. In addition, colonization probability was nearly zero after about 3% of a territory received post-fire fuel treatments. These relationships were not biologically realistic, so we investigated the results further. We found 3 factors that affected the relationships between post-fire fuel treatments and both territory colonization and extinction:

1. Post-fire fuel treatments were less common and less spatially extensive than other fuel treatments (i.e., those that did not occur after fire) and high-severity fire. Forty territories received post-fire fuel treatments, but 24 of these territories had <5% of the territory area affected by the treatments (Figure A1A). In contrast, other fuel treatments and high-severity fire affected more territories and affected proportionally more area within territories (Figure A1B).

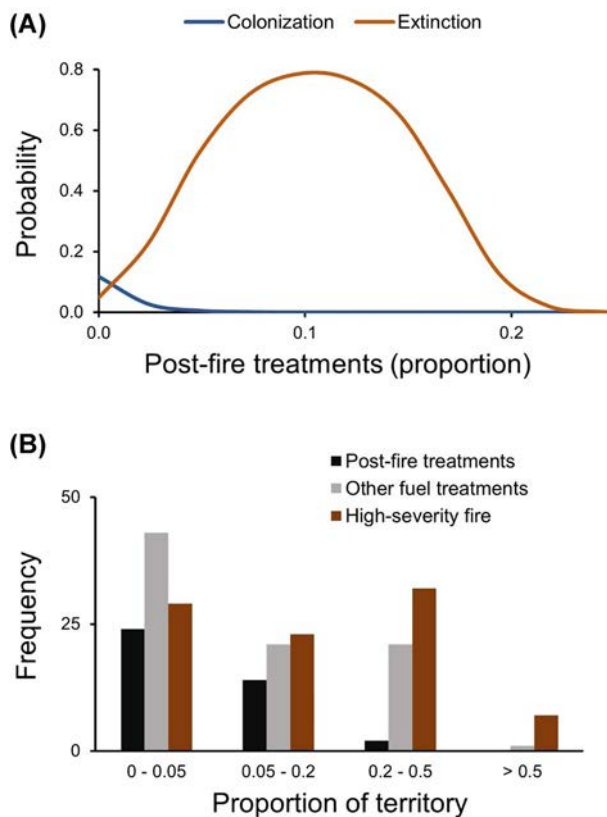


FIGURE A1 A) The effect of post-fire fuel treatments in the previous 3 years on the probabilities of colonization and extinction at California spotted owl territories in the San Bernardino and Angeles national forests in California, USA, 2006–2019. The territory spatial scale is 1,000 m. B) The number of spotted owl territories affected by post-fire fuel treatments, other fuel treatments, and high-severity fire within categories based on the proportion of the territory affected at the 1,000-m spatial scale



2. Only 3 of the territories with post-fire treated area >5% were occupied prior to the post-fire fuel treatment, and thus had the opportunity to go locally extinct. Two territories went extinct in the year following the treatment, and the third remained occupied for 2 years before going extinct. Thus, most of the curve for territory extinction probability (Figure A1A) was based on a sample size of 5 total extinction opportunities. Furthermore, the post-fire fuel treatments occurred the year after the fire at 2 of these territories, and 5 years after the fire at the third territory. So, the territory extinction events at these sites may have been a delayed response to the fire itself, particularly since spotted owls display high site fidelity.
3. Thirty-two of the 40 territories with post-fire fuel treatments were also affected by high-severity fire, including 13 of 16 territories with >5% post-fire treated area. For the 3 territories above with post-fire treated area >5% that were occupied prior to the post-fire fuel treatment, high-severity fire burned 8%, 21%, and 40% of the territories, respectively. For all 40 territories with post-fire fuel treatments, the proportion of high-severity fire within the territory (0.17) was greater than the proportion of post-fire treated area (0.06; one-tailed *t*-test, $P \leq 0.001$). Thus, the effects of post-fire fuel treatments were confounded with the effects of high-severity fire, and this may have affected the relationships between post-fire fuel treatments and both territory colonization and extinction.

These findings suggested that the inclusion of post-fire fuel treatments in our analyses led to erratic model behavior due to extremely low sample size (territory extinction opportunities) and extended or delayed effects of fire. In addition, the significantly greater amount of high-severity burned area compared to treated area within post-fire fuel treatment territories makes it likely that fire effects obscured any potential relationships between occupancy and post-fire fuel treatments. As a result, we removed the post-fire fuel treatment covariate from our analyses.

Tall, heterogeneous forests improve prey capture, delivery to nestlings, and reproductive success for Spotted Owls in southern California

Zachary A. Wilkinson,¹ H. Anu Kramer,¹ Gavin M. Jones,^{2,3} Ceeanna J. Zulla,¹ Kate McGinn,¹ Josh M. Barry,¹ Sarah C. Sawyer,⁴ Richard Tanner,⁵ R. J. Gutiérrez,⁶ John J. Keane,⁷ and M. Zachariah Peery^{1,*}

¹Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, Wisconsin, USA

²U.S.D.A. Forest Service, Rocky Mountain Research Station, Albuquerque, New Mexico, USA

³Biology Department, University of New Mexico, Albuquerque, New Mexico, USA

⁴U.S.D.A. Forest Service – Region 5, Sacramento, California, USA

⁵Tanner Environmental Services, Alameda, California, USA

⁶Department of Fisheries, Wildlife, and Conservation Biology, University of Minnesota, St. Paul, Minnesota, USA

⁷U.S. Forest Service, Pacific Southwest Research Station, Davis, California, USA

*Corresponding author: mpeery@wisc.edu

ABSTRACT

Predator–prey interactions can be profoundly influenced by vegetation conditions, particularly when predator and prey prefer different habitats. Although such interactions have proven challenging to study for small and cryptic predators, recent methodological advances substantially improve opportunities for understanding how vegetation influences prey acquisition and strengthen conservation planning for this group. The California Spotted Owl (*Strix occidentalis occidentalis*) is well known as an old-forest species of conservation concern, but whose primary prey in many regions—woodrats (*Neotoma* spp.)—occurs in a broad range of vegetation conditions. Here, we used high-resolution GPS tracking coupled with nest video monitoring to test the hypothesis that prey capture rates vary as a function of vegetation structure and heterogeneity, with emergent, reproductive consequences for Spotted Owls in Southern California. Foraging owls were more successful capturing prey, including woodrats, in taller multilayered forests, in areas with higher heterogeneity in vegetation types, and near forest-chaparral edges. Consistent with these findings, Spotted Owls delivered prey items more frequently to nests in territories with greater heterogeneity in vegetation types and delivered prey biomass at a higher rate in territories with more forest-chaparral edge. Spotted Owls had higher reproductive success in territories with higher mean canopy cover, taller trees, and more shrubby vegetation. Collectively, our results provide additional and compelling evidence that a mosaic of large tree forest with complex canopy and shrubby vegetation increases access to prey with potential reproductive benefits to Spotted Owls in landscapes where woodrats are a primary prey item. We suggest that forest management activities that enhance forest structure and vegetation heterogeneity could help curb declining Spotted Owl populations while promoting resilient ecosystems in some regions.

Keywords: chaparral, habitat selection, prey capture, reproduction, *Strix occidentalis*, southern California, woodrat

How to Cite

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LAY SUMMARY

- Identifying where prey is captured can help understand high-quality hunting habitat for predators but is very difficult to do for small cryptic predators.
- We combined high-resolution GPS and camera technology to examine how vegetation conditions influence prey capture, delivery rate, and reproductive success for a small nocturnal predator, the Spotted Owl (*Strix occidentalis occidentalis*).
- Spotted Owl prey captures increased with heterogeneous vegetation, larger trees, complex multilayered canopies, and more forest-chaparral edge. Prey delivery increased with more cover type heterogeneity and forest-chaparral edge.
- Spotted Owl reproductive success was higher in territories having taller canopies, greater canopy cover, and more shrubby vegetation.
- Forest management activities that increase the number of large trees, promote multilayered canopies, and enhance vegetative heterogeneity are likely to benefit Spotted Owls.

Los bosques altos y heterogéneos mejoran la captura de presas, la entrega a los polluelos y el éxito reproductivo de *Strix occidentalis* en el sur de California

RESUMEN

Las interacciones depredador-presa pueden verse profundamente influenciadas por las condiciones de la vegetación, particularmente cuando el depredador y la presa prefieren diferentes hábitats. Aunque tales interacciones han demostrado ser difíciles de estudiar para depredadores pequeños y crípticos, los avances metodológicos recientes mejoran sustancialmente las oportunidades para comprender cómo la vegetación influye en la adquisición de presas y para fortalecer la planificación de la conservación de este grupo. *Strix occidentalis occidentalis* es bien conocida como una especie de bosque maduro de interés para la conservación, pero cuya presa principal en muchas regiones, la rata de bosque (*Neotoma* spp.), se presenta en una amplia gama de condiciones de vegetación. Aquí, utilizamos el seguimiento por GPS de alta resolución junto con el monitoreo por video de nidos para evaluar la hipótesis de que las tasas de captura de presas varían en función de la estructura y heterogeneidad de la vegetación, con consecuencias reproductivas emergentes para *S. o. occidentalis* en el sur de California. Los búhos que forrajearon tuvieron más éxito en la captura de presas, incluidas las ratas de bosque, en los bosques más altos con varios estratos, en áreas con mayor heterogeneidad en los tipos de vegetación y cerca de los bordes de bosque y chaparral. De acuerdo con estos hallazgos, *S. o. occidentalis* entregó presas a los nidos con mayor frecuencia en territorios con mayor heterogeneidad en los tipos de vegetación y entregó biomasa de presas a una tasa más alta en territorios con más borde de bosque y chaparral. *S. o. occidentalis* tuvo un mayor éxito reproductivo en territorios con mayor cobertura media del dosel, árboles más altos y vegetación más arbustiva. Colectivamente, nuestros resultados proporcionan evidencia adicional y convincente de que un mosaico de bosques con grandes árboles con un dosel complejo y vegetación arbustiva aumenta el acceso a las presas con beneficios reproductivos potenciales para *S. o. occidentalis* en paisajes donde las ratas de bosque son una presa principal. Sugerimos que las actividades de gestión forestal que mejoran la estructura forestal y la heterogeneidad de la vegetación podrían ayudar a frenar la disminución de las poblaciones de *S. o. occidentalis* y, al mismo tiempo, promover ecosistemas resilientes en algunas regiones.

Palabras clave: captura de presas, chaparral, rata de bosque, reproducción, selección de hábitat, *Strix occidentalis*, sur de California

INTRODUCTION

Predator–prey interactions are shaped by the ability of predator and prey to detect and respond to each other (Sih 1984, Lima and Dill 1990). Vegetation conditions can have profound effects on these interactions if they favor either predator or prey (Gorini *et al.* 2012). Vertical structure in vegetation can benefit either predators when it provides ambush cover (Preston 1990, Gorini *et al.* 2012) or prey when it provides escape cover (Boinski *et al.* 2003, Gorini *et al.* 2012). Horizontal heterogeneity in vegetation conditions (e.g., vegetation types or heights; hereafter “heterogeneity”) can create spatial refuges for prey populations, such that predators preferentially hunt in areas having lower prey density without prey refuges (Hopcraft *et al.* 2005, Horinouchi *et al.* 2009). However, prey refuges constraining hunting success can benefit predators by acting as source populations for prey that disperse into habitats more favorable to hunting success (Kauffman *et al.* 2007, DeMars and Boutin 2018, Smith *et al.* 2019). Thus, understanding how vegetation influences predator–prey interactions can strengthen conservation plans, particularly for rare predators threatened by habitat change (Katzner *et al.* 2005, Cattray *et al.* 2013, Hobart *et al.* 2019a, Smith *et al.* 2020).

Most studies about how vegetation conditions shape hunting success have focused on large mammalian carnivores, for which both predator and prey are easily observed (Gorini *et al.* 2012). Yet, the majority of predators—such as birds of prey—are small and cryptic, leaving little, if any, prey remains at a predation site, instead concentrating remains in pellets or scat (Andrews and Cook 1990). Studies of foraging habitat selection in small, cryptic predators typically rely on telemetry approaches that yield locational data agnostic to the activity of the predator and include unrelated behaviors like territory defense, general location change, courtship, and resting (Marsh *et al.* 2014a). Consequently, such approaches could produce misleading representations of high-quality foraging habitat, potentially compromising conservation plans (Marsh *et al.* 2014a). However, the pairing of small, accurate GPS telemetry units (Tomkiewicz *et al.* 2010) to follow predator movement and video camera technology to identify prey delivered to nests have recently—and substantially—facilitated the identification of prey capture locations for small and cryptic predators during the critical

nesting or denning periods (Marsh *et al.* 2014a, 2014b, Sanjose *et al.* 2020, Wood *et al.* 2021).

The Spotted Owl (*Strix occidentalis*) is a small, nocturnal predator closely associated with commercially valuable older forests (i.e., large trees, high canopy cover) and has substantial influence on conservation decisions and forest management across its range (Verner *et al.* 1992, Marcot and Thomas 1997, Gutiérrez *et al.* 2017). Although it is among the most well-studied birds in the world and its diet and nocturnal habitat use are well documented (Gutiérrez *et al.* 1995, Lohmus 2004), vegetation conditions conferring successful hunting are generally unknown, owing to its small body size and cryptic hunting methods (but see Zulla *et al.* 2022). While Spotted Owls frequently use older forests during nocturnal activities, woodrats (*Neotoma* spp.) are a primary prey across the majority of their range and occur in a wide variety of environments including younger forests and shrub-dominated communities (Sakai and Noon 1993, Innes *et al.* 2007, Kelt *et al.* 2013). It has been presumed that owls do not typically forage in some environments harboring high densities of woodrats because of lack of perches, difficulty in capturing prey, or an increased risk of their own predation (Call *et al.* 1992, Sakai and Noon 1993, Franklin *et al.* 2000). However, woodrats cross ecotones along which owls are known to forage (Zabel *et al.* 1995, Sakai and Noon 1997, Parmenter *et al.* 2003, Kramer *et al.* 2021b). Thus, early seral stage forests, oak woodlands, and shrub communities may serve as source populations of woodrats for foraging Spotted Owls—particularly when they occur adjacent to older forest with suitable perching structures (Ward *et al.* 1998, Franklin *et al.* 2000, Hobart *et al.* 2019b). Abundant sources of woodrats could benefit nesting Spotted Owls as woodrat consumption by owls appears to increase reproductive success (Ward *et al.* 1998, Smith *et al.* 1999). Thus, Spotted Owl hunting success, and ultimately fitness and population status, may benefit from a mosaic of vegetation conditions including forests with vertical structure and heterogeneity in vegetation types.

Here, we paired recent advances in GPS telemetry with nest video monitoring to understand how vegetation structure and heterogeneity influenced Spotted Owl hunting success and nest provisioning. Spotted Owls in southern California provide a unique opportunity to understand how vegetation structure and heterogeneity shape prey capture

success given: (1) that woodrats constitute the dominant prey species (composing 74% of diet by biomass; [Smith et al. 1999](#)), and (2) the broad range of vegetation conditions that occur in this region (see study area below). We hypothesized that both vertical structure and heterogeneity in vegetation conditions influence the ability of Spotted Owls to acquire prey, with emergent effects on reproductive success. Under this hypothesis, we predicted that Spotted Owls would capture woodrats and potentially other prey species in areas having greater vertical structure, more spatial heterogeneity in vegetation composition, and more edge between forest and shrubby areas. We also predicted that Spotted Owls would deliver more prey to nest sites when their territories contained greater amounts of the vegetation conditions that facilitated prey captures (identified in the first analysis). Finally, we predicted that Spotted Owls would have higher reproductive success when their territories contained more of the vegetation conditions that facilitated prey captures and deliveries to nests (identified in the first and second analyses). Our study population occurs near the southern range boundary of California Spotted Owls and has experienced substantial declines, in part due to interactions among vegetation change (e.g., loss of large trees), climate change, and severe wildfire ([Tempel et al. 2022](#)). Thus, an improved understanding of the vegetation conditions that promote successful prey acquisition, nest provisioning, and reproductive success could strengthen conservation planning for owls in this region.

METHODS

Study Area

We studied Spotted Owls in the San Bernardino and San Jacinto Mountains of southern California ([Figure 1](#)), which have been almost continuously monitored for over 3 decades. Elevations ranged from ~800 to 2,600 m. Vegetation community types included mixed conifer, bigcone Douglas fir/live oak woodlands, hardwood forests/riparian areas, and chaparral. Mixed-conifer forests primarily occur at higher elevations and consisted of a mixture of pines and other conifer species as well as scattered hardwoods. Woodlands occurring at intermediate elevations, were dominated by bigcone Douglas fir (*Pseudotsuga macrocarpa*) and canyon live oak (*Quercus chrysolepis*). Chaparral vegetation was often found interspersed with bigcone Douglas fir/canyon live oak woodlands. Hardwood forests/riparian areas dominated the canyon bottoms and were primarily comprised of canyon live oak, California sycamore (*Platanus racemosa*), cottonwood (*Populus spp.*), and white alder (*Alnus rhombifolia*). For our analyses, we reduced these community types to the dominant vegetation types of conifer, hardwood, or chaparral ([Figure 1](#)).

GPS Tagging and Video Monitoring

We used standard call-based survey methods to locate breeding pairs of Spotted Owls in 2021 ([Franklin et al. 1996](#)), from which we selected 10 owl pairs for GPS tagging and video camera monitoring of prey deliveries to nest sites between late April and early June. Sites with nesting owls were selected to include a wide range of elevations (~1,200–2,300 m), contain the 3 dominant vegetation cover types (conifer, hardwood, and chaparral), and not

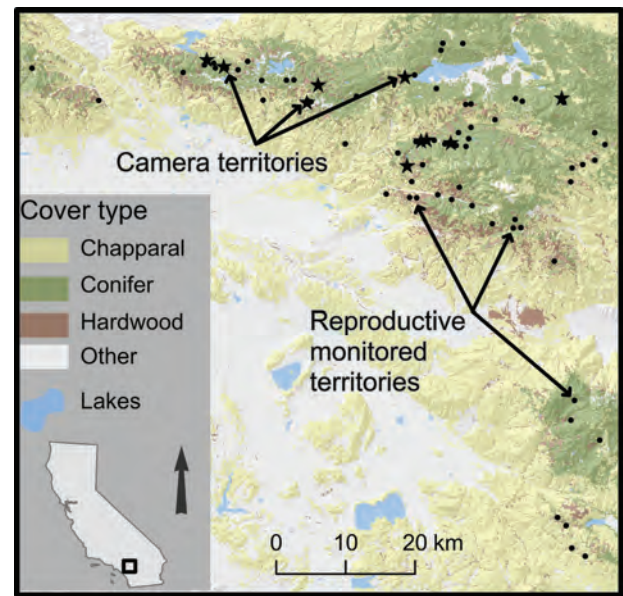


FIGURE 1. Map depicting 10 nest video camera locations for California Spotted Owl (*Strix occidentalis occidentalis*) hunting success and delivery rate analyses (black stars) as well as the 71 territories used in the reproductive success analysis (black circles) overlaid over dominant vegetation types. Elevations in the study area ranged from ~800 to 2,600 m with camera territories sampled between ~1,200 and 2,300 m. Inset map shows broader location in southern California, USA.

have been exposed to widespread (>10% of the territory) high severity wildfire. Additionally, while first ensuring a range of elevations and cover type abundances, we prioritized sites closer to roads and trails, with males that could be captured, and accessible nests. At each site, we captured male Spotted Owls using noose poles and “hand capture” techniques ([Wood et al. 2021](#)) and attached GPS tags (Alle-300, Ecotone, Poland) via tail mounts ([Kramer et al. 2021b](#)). Males are responsible for the vast majority of foraging by Spotted Owls during incubation and brooding, such that focusing on males should provide reasonable insights into foraging patterns during nesting for this species ([Delaney et al. 1999](#)). We programmed GPS tags to record a location every 2 min, for 10 hr each night (2000–0600 PDT) over the life of the tag ($\bar{x} = 6$ nights). Median positional error was 45 m (individual tag median range: 15–74 m; S.A. Whitmore and H.A. Kramer, personal communication) and GPS filtering to improve accuracy was not possible with the details associated with each GPS location (i.e., dilution of precision or other similar metrics were not reported by the tags).

We installed infrared cameras (AXIS Q1786 – LE, 4 megapixel) in a tree adjacent to each nest tree to monitor nests during the same 10-hr period that the GPS tags were collecting locations, plus an additional 30 min each morning (2000–0630 PDT). Owing to the effort required to install and remove cameras, we frequently acquired extra nights of video data ($\bar{x} = 8.9$ nights, $\bar{x} = 93.5$ hr). Cameras were placed at least 10 m from the nest tree to minimize disturbance to nesting activities. To install video cameras, we climbed trees using single rope technique, which avoids climbing spurs and thus does much less damage to trees and increases the safety and efficiency of climbers ([Anderson et al. 2015](#)).

Identifying Successful Hunting Locations

To identify successful hunting locations, we first reviewed all video data and identified the time of prey delivery and the species delivered (when possible). We then examined GPS data for clusters of GPS points recorded just before a relatively straight movement path back to the nest (Marsh *et al.* 2014a, Wood *et al.* 2021). Following Zulla *et al.* (2022) we defined clusters as containing up to 10 GPS locations before the male's return to the nest, where all points in the cluster occurred over a span of 20 min or less and with no more than 250 m between the farthest points (Figure 2). After we linked prey deliveries observed in video recordings to a GPS point cluster, we calculated a minimum convex polygon around those points, then enlarged the perimeter of ("buffered") that polygon by 50 m (hereafter "capture polygon") to better account for GPS positional error, the potential effects of surrounding habitat on prey acquisition, and to maintain consistency with a similar study completed in the Sierra Nevada (Zulla *et al.* 2022). To compare vegetation conditions in these polygons to the overall composition of the owl's territory (see statistical analysis for more details), we generated 10 available polygons that matched the shape and size of each capture polygon within Spotted Owl home ranges. We placed each of these available polygons at a random location within the owl's home range and rotated each to a random orientation.

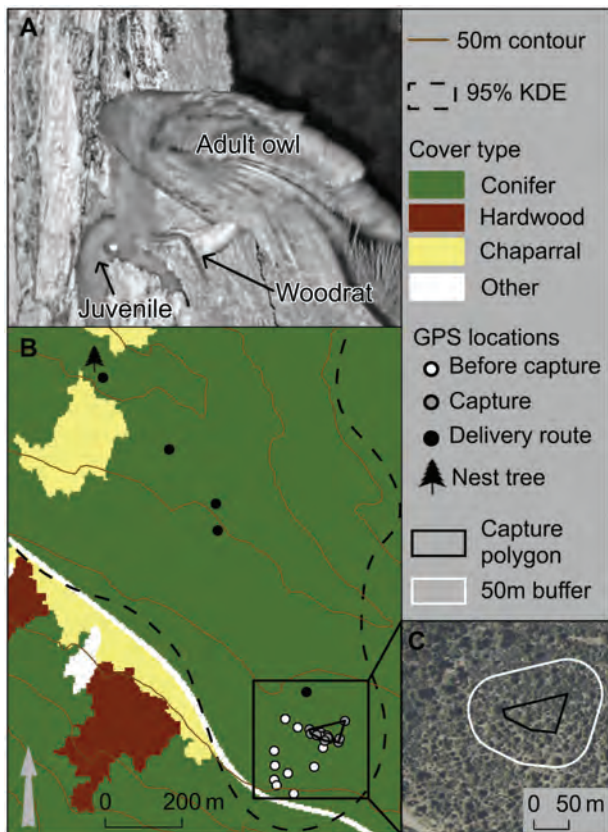


FIGURE 2. (A) Male delivering a woodrat to a juvenile on video camera. (B) Map of GPS points before (white), during (grey), and after (black) a successful hunt by a Spotted Owl as it returns to the nest with the prey, within the owl's 95% kernel density estimate (KDE). Note that the grey points in (B) are used to create the capture polygon shown in a map (C) over NAIP imagery, including both the capture polygon (black) and buffered capture polygon (white).

tation. We defined approximate home ranges using a 95% kernel density estimate (KDE) of each tagged owl, estimated using fixed kernel width using the *adehabitat* package in R ($\bar{x}$ = 142.57 ha, range: 86.50–238.55 ha; Seaman and Powell 1996, Calenge 2006).

Estimating Prey Delivery Rates

To estimate prey delivery rate, we recorded the number of prey deliveries captured on video per hour. To further investigate the relationship between vegetative conditions and prey delivery rate to nest, we analyzed how prey biomass (i.e., estimated mass in grams of prey items delivered to nests) was related to vegetative conditions in a home range. For prey identified to the species level, we assigned body mass (g). For woodrats and flying squirrels (*Glaucomys sabrinus*), we estimated an average body mass of individuals captured by owls by relating measurements of bones collected from regurgitated pellets to bones of museum specimens of known body mass following Zulla (2021). Briefly, this approach involved developing allometric relationships between body mass and skeletal measurements using museum specimens and then using these relationships to predict the average body mass of woodrats and flying squirrels in owl pellets based on skeletal measurements in those pellets (Zulla 2021). We then assumed that the average body mass of these two prey species was equivalent between pellets and the prey we observed delivered to nests in this study. For other identified species, we obtained an average mass for delivered individuals of each prey species by averaging masses of museum specimens from the southern California region (latitude: 32.3 to 34.6°N, longitude: -117.9 to -115.9°W) using the ARCTOS collections database (<https://arctos.database.museum/search.cfm>; specimens from collections MVZ, UWB, MSB, and DMNS). In cases that we could not identify to the species level ("unknown"), we assigned prey to 1–4 size classes (tiny, small, medium, and large) based on the prey's size relative to the owl delivering it and other, known prey items delivered to the nest. To calibrate the size ranges in each category, we assigned identified prey species into size classes (e.g., deer mice [*Peromyscus* spp.] were small, whereas woodrats were large). We then used the average mass of all identified species within each size class to assign a mass to that size class, and thus assigned that mass to each unknown prey in that size class.

Characterizing Vegetation Conditions

We characterized vegetation conditions within both used and available polygons to test for selection of vegetation that was associated with capture sites (Table 1). We also characterized vegetation conditions within home ranges to understand how vegetation conditions are related to prey delivery rates and reproductive success (Table 1). We estimated vegetation structure using remotely sensed data from the California Forest Observatory (CFO) which uses deep learning models to link available airborne LiDAR with satellite imagery using pattern recognition to predict vegetation structure across the state of California at a spatial scale of 100 m² on an annual basis (CFO 2020). We used CFO data from 2020 to estimate average canopy cover (%), canopy height (m), canopy layer count (0–3), and ladder fuel density (%). For clarity we renamed ladder fuel density "shrubby

vegetation density,” henceforth, since the term “ladder fuel” is often associated with vegetation under overstory vegetation, yet this metric is simply an estimate of the density of vegetation between 1 and 4 m, agnostic to overstory. We used vegetation type data from the Classification and Assessment with Landsat of Visible Ecological Groupings (CALVEG) vegetation classification system, specifically the Anderson land use/land cover level two classification system (Anderson *et al.* 1976), a mid-level vegetation mapping product that classifies existing dominant vegetation with a rough minimum polygon size of 2 ha (Brewer *et al.* 2015). We used the CALVEG dataset, last updated in 2018, to estimate percentage of conifer, hardwood, and chaparral dominated vegetation types within polygons. To minimize the temporal mismatch between the timing of vegetation metric and foraging data collection, we avoided collecting GPS and camera data in areas with large impacts from recent fires or other vegetation altering events.

We then used a combination of the CFO and CALVEG data to estimate 2 measures of relative edge and two measures of vegetation heterogeneity within capture polygons, available polygons, and home ranges (Table 1, Supplementary Material Figure 1). We defined “primary edge” as any boundary between chaparral and a forest type (conifer or hardwood). We defined “secondary edge” as any boundary between vegetation types and between short (<10 m canopy height) or tall (>10 m canopy height) vegetation of the same or different type. We normalized primary and secondary edge measures in polygons and home ranges by dividing the sum of edge length by the area of each polygon so that they represented a measure of the “density” of edge. We estimated

coarse heterogeneity within capture polygons using the Shannon Diversity Index of the proportions of each of the 3 main vegetation classes (conifer, hardwood, chaparral) and a class representing any other (“other”) vegetation. We estimated “fine heterogeneity” similarly to coarse heterogeneity, but we split conifer and hardwood forest classes into 3 classes each, short forests (canopy height <10 m), tall forests sparse canopy (canopy height >10 m, canopy cover <70%), and tall forests dense canopy (canopy height >10 m, canopy cover >70%).

Assessing Reproductive Success

To examine the relationship between vegetation conditions and reproductive success, we used a broader set of reproductive outcomes for Spotted Owl territories in both the San Bernardino and San Jacinto Mountains collected between 2006 and 2020 (Tempel *et al.* 2022). These historical reproductive outcomes were estimated by assuming that a pair of owls was not nesting if (1) when offered mice by researchers, one member ate or cached four or more mice; or (2) a female was observed roosting for more than 45 min before 15 May (Tempel *et al.* 2022). For nesting owls, the number of young fledged was counted during follow-up visits following fledging young. Reproductive data collected before 2006 was not considered because southern California experienced widespread drought related tree mortality between 2002 and 2005 (Preisler *et al.* 2017) and the remotely sensed vegetation data we used (see characterizing vegetation conditions above) were collected after this period. Hence, the vegetation conditions during the study were different before 2006.

TABLE 1. Vegetation covariates used to investigate Spotted Owl hunting success, prey delivery rate, and reproductive success. California forest observatory (“CFO”) and Classification and Assessment with Landsat of Visible Ecological Groupings (“CALVEG”).

Variable	Description	Data source
Canopy cover	Mean percent canopy cover	CFO
Canopy height	Mean canopy height	CFO
Shrubby vegetation density	Mean “ladder fuels density” (estimated vegetation density 1–4 m above ground divided by estimated vegetation 0–4 m)	CFO
Canopy layers	Mean count of canopy layers	CFO
Percent hardwood	Percent of vegetation considered hardwood within a polygon	CALVEG
Percent chaparral	Percent vegetation considered chaparral within a polygon	CALVEG
Percent conifer	Percent vegetation considered conifer/mixed conifer within a polygon	CALVEG
Primary edge density	Boundaries between Chaparral and any conifer or hardwood	Smoothed CALVEG layer
Secondary edge density ^a	Boundaries between Chaparral, small conifer, small hardwood, large conifer and large hardwood stands	Merged smooth CALVEG layer and smoothed canopy height layer >10 m
Coarse heterogeneity	Shannon diversity index of chaparral, conifer, hardwood, and other vegetation	CALVEG
Fine heterogeneity ^{a,b}	Shannon diversity index of 8 classes 3 Conifer (small trees, large trees sparse canopy, large trees dense canopy) 3 Hardwood (small trees, large trees sparse canopy, large trees dense canopy) Chaparral and other vegetation	Merged CALVEG with CFO canopy height and canopy cover layers

^aSmall: canopy height <10 m; large: canopy height >10 m.

^bSparse canopy: canopy cover <70%; dense canopy: canopy cover >70%.

Statistical Analyses

To test for vegetation conditions correlated with hunting success, we compared used and available polygons in a resource selection framework. We conducted 2 separate analyses, one where we considered all prey and one for only woodrats, given the importance of this species for Spotted Owls in the region (e.g. [Smith et al. 1999](#)). We used binomial generalized linear mixed models (GLMMs), with capture polygons coded as 1 and available polygons coded as 0, while treating all vegetation covariates as fixed effects. Following [Duchesne et al. \(2010\)](#), we allowed for individual random intercepts to relax the assumption of homogenous selection among individuals. We weighted available polygons ($W = 1,000$) to enable convergence to an inhomogeneous Poisson process, where “ W ” refers to the weight given to available polygons in the GLMMs ([Muff et al. 2020](#)). We included the fixed effects of polygon area and distance to nest to account for different polygon sizes between prey types and to control for Spotted Owls central place foraging tendency, respectively ([Rosenberg and McKelvey 1999](#)).

To determine how vegetation affected prey deliveries to nests, we used 2 sets of linear regression analyses: the first treating prey delivery rate (prey items prey hour) as the response variable, and the second treating prey biomass delivery (grams per hour) as the response variable. We treated vegetation metrics within Spotted Owl 95% KDE approximate home ranges as explanatory variables but limited potential covariates to those deemed informative from our first analysis because of smaller sample sizes ($n = 10$).

To determine if vegetation features that influence foraging also influence reproductive success, we evaluated how the same eleven vegetation covariates from our first analysis ([Table 1](#)) related to historical reproductive success (0–3 young fledged) using GLMMs. To account for lack of independence for reproductive success within sites and between years and to account for Spotted Owl reproductive cycling unrelated to vegetation conditions, we included both site and year as random effects. We delineated hypothetical home ranges as circles centered on the geometric mean of nest trees found within a territory with a radius of 1,000 m. Thus, each “home range” area was 314 ha, which approximates owl home range areas in the San Bernardino Mountains, which range between about 220 and 650 ha ([Zimmerman et al. 2001](#)). We excluded samples for sites which were either not occupied by pairs or occupied by pairs that did not attempt to nest because our first two analyses were fundamentally limited to nesting pairs. Further, events besides foraging success can influence an owl pair’s decision to nest each year (e.g., winter/spring weather; [North et al. 2000](#)). We also removed any home ranges where over 10% of their area burned in high severity wildfire since 2006 to avoid mismatch between the measured vegetation (based on CALVEG [2018] and [CFO \[2020\]](#) data) and vegetation when owls attempted reproduction. Previous research showed owl territories that did not experience major events like wildfire or timber harvest showed minimal changes in vegetation over an 18-yr period ([Tempel et al. 2016](#)). As our study area has no substantive timber harvests, we assumed that any other differences in vegetation type or structure were minimal over the period for which nesting data was analyzed (2006–2020). After removing sites and samples because of fire impacts or lack of nesting pairs, we retained 71 sites and 268 samples for an average of 3.7 years of reproductive data per site.

Our objective in these analyses was to identify the suite of vegetation conditions potentially, but meaningfully, influencing the location of prey captures, prey delivery rates, and reproductive success rather than identifying a “top model” per se. Therefore, we performed an all-subsets model selection procedure for each of the 3 analyses using Akaike’s Information Criterion with a correction for small sample sizes (AIC_c) and considered all models within 2 AIC_c of the most supported model to be competitive ([Burnham and Anderson 2002](#)). We did not allow highly correlated ($r \geq 0.7$) variables to be included in the same model. We z -standardized all covariates (mean = 0, SD = 1) to aid in interpreting the relative importance of covariates with different units ([Schielzeth 2010](#)). Owing to considerable model selection uncertainty with multiple competitive models in the hunting success and reproductive success analyses, we averaged model predictions of covariate relationships to make inferences. For the hunting success and reproductive success analyses we report model averaged coefficients to aid in contextualizing the results (using the structure β , [confidence interval]), and adopted 85% confidence intervals as recommended by [Arnold \(2010\)](#). We avoided using model averaged coefficients to make inferences directly, because multicollinearity among covariates increases uncertainty and can cloud the interpretation of model-averaged coefficients ([Cade 2015](#)). Thus, note that some confidence intervals for model-averaged coefficients may overlap zero due to uncertainty introduced from the model averaging procedure. We also did not make inferences about uninformative parameters ([Arnold 2010](#)) or parameters that appeared in only one competitive model, which we assumed could be spurious effects. We did not perform corrections for multiple comparisons because such corrections decrease the probability of detecting relationships as more statistical tests are performed ([Moran 2003](#)). We conducted all analyses in program R 4.0.2 ([R core team 2021](#)). We fit GLMMs using package *glmmTMB* ([Bolker 2021](#)) and performed model selection using package *MuMIn* ([Barton 2020](#)).

RESULTS

Characteristics of Successful Hunting Locations

We identified 120 putatively successful hunting locations and the prey caught in those locations by combining the GPS clusters we defined as capture polygons with the subsequent prey delivery to the nest recorded by the cameras at the 10 nest sites. These capture polygons were an average of 0.80 ha in size (range: 0.47–2.76 ha), while capture polygons with a 50-m buffer averaged 3.94 ha in size (range: 1.46–6.91). Woodrats were the most common prey item captured within the 120 capture polygons, accounting for 42 (35%) of all prey items. The next most common prey were deer mice (24%), followed by pocket gophers (*Thomomys bottae*; 12%), and flying squirrels (3%); 22% of captured prey could not be identified.

Spotted Owls generally captured prey (“all-prey” analysis) in areas with higher canopy height (model-averaged coefficient 0.33, model-averaged 85% CI [0.17, 0.49]), more canopy layers (0.34, [0.16, 0.53]), greater fine heterogeneity (0.14, [−0.03, 0.31]), and increased primary edge (0.15, [−0.02, 0.32]) and secondary edge densities (0.22, [0.06, 0.38]) than expected based on available polygons. Model averaged predictions of these relationships are provided in

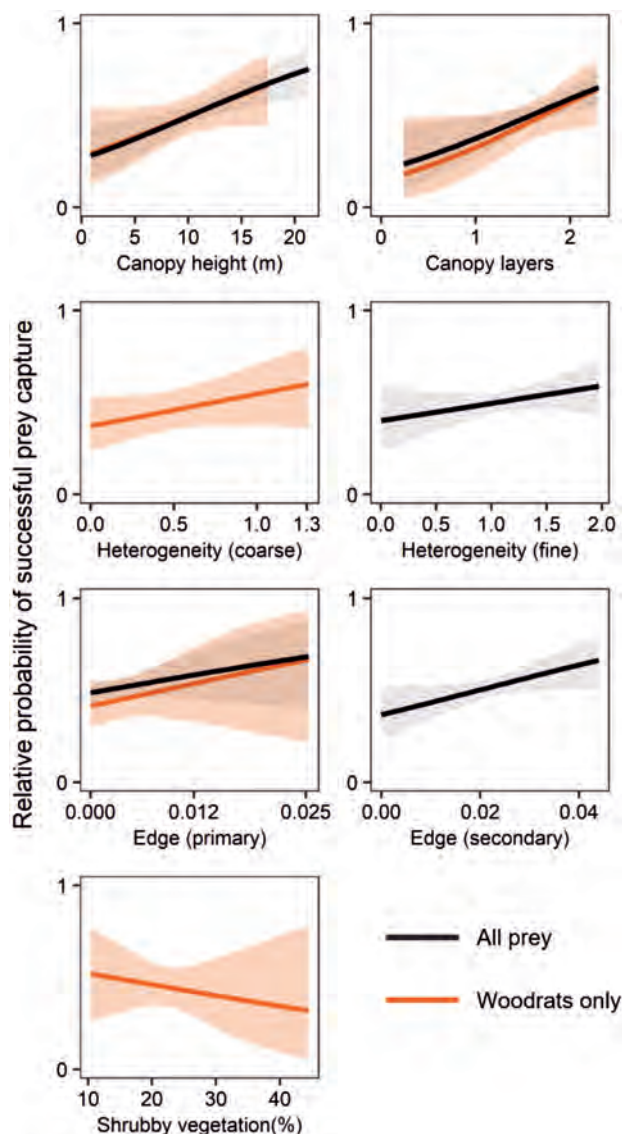


FIGURE 3. Averaged model predictions for relative probability of hunting success for all prey and woodrats only plotted against vegetation conditions for foraging Spotted Owls, with 95% confidence intervals shown as shaded areas. Heterogeneity metrics calculated as Shannon diversity of vegetation types within polygons and edge is calculated as the edge density within polygons (see Characterizing vegetation conditions).

Figure 3. Spotted Owls were more likely to capture woodrats (“woodrat only” analysis) in areas with higher canopy height (0.31, [0.06, 0.57]), more canopy layers (0.4, [0.11, 0.70]), greater coarse heterogeneity (0.24, [−0.02, 0.50]) and more primary edge density (0.19, [−0.11, 0.48]) and were less likely to capture woodrats in areas of higher shrubby vegetation density (−0.12, [−0.45, 0.20]) compared to available polygons (Figure 3). A considerable degree of model selection uncertainty occurred in both the “all-prey” and “woodrat only” analyses because there were 13 and 12 competitive models, respectively (<2 Δ AIC; Supplementary Material Tables 1 and 2). Nevertheless, canopy height and secondary edge density occurred in 8 and 10 of the 13 top models, respectively, in the all-prey analysis. In contrast, canopy layers occurred in 11 of the 12 woodrat models. The null model in the all-

prey analysis had a Δ AIC of 9.30 ($w_i < 0.001$) whereas Δ AIC for the null model was 2.94 ($w_i = 0.01$) in the woodrat-only analysis.

Prey Delivery Rates

We observed 289 prey deliveries at the 10 nests, with individual males delivering between 15 and 46 prey items ($\bar{x} = 28.9$). Among these deliveries were 91 woodrats (31% count, 62% biomass), 72 deer mice (24% count, 4% biomass), 28 pocket gophers (10% count, 9% biomass), 10 flying squirrels (3.0% count, 4% biomass), 2 grey squirrels (*Sciurus griseus*), 2 passerine birds, 2 chipmunks (*Tamias* spp.), 1 Townsend’s mole (*Scapanus townsendii*), 1 vole (*Microtus* spp.), and 80 unknown prey items (28% count, 18% biomass). Unknown prey items included 11 large, 25 medium, 32 small, and 12 tiny deliveries. Delivery rates ranged from 0.22 to 0.45 prey items per hour ($\bar{x} = 0.30$ items hr^{−1}) while biomass delivery rates ranged from 17.74 to 51.05 grams per hour ($\bar{x} = 29.22$ g hr^{−1}).

Spotted Owls delivered prey at a higher rate in home ranges with higher coarse heterogeneity (0.06, [0.04, 0.09]; Figure 4A), and the null model was not competitive (Δ AIC = 5.74, $w_i = 0.04$; Supplementary Material Table 3). Spotted Owls delivered biomass to nests at higher rates in home ranges with more primary edge density (7.20, [4.49, 9.90]; Figure 4B), and the null model was not competitive (Δ AIC = 6.15, $w_i = 0.03$; Supplementary Material Table 4). The positive association between prey biomass delivered and primary edge density was sensitive to a single influential male which occurred in a territory with a high value for primary edge, without which the association was not supported (i.e., the null model was more supported). However, the association between coarse heterogeneity and prey delivery rates remained important even when this “outlier” territory with the highest heterogeneity value was removed (i.e., the top model based on AIC remained the same and no other models became competitive).

Reproductive Success

Spotted Owl reproductive success was most strongly related to canopy cover, canopy height, and shrubby vegetation (Figure 5). Of the 5 top models 2 contained uninformative parameters, which we did not report (see Arnold 2010). Thus, we retained 3 top models: (1) canopy cover only, (2) canopy height and shrubby vegetation density, and (3) canopy height only (Supplementary Material Table 5). Spotted Owl reproductive success increased with greater canopy cover (model averaged coefficient 0.12, model averaged 85% CI [0.04, 0.20]) and taller canopy height in a home range (0.10, [0.02, 0.18]). Spotted Owls reproduced more successfully in areas with on average more shrubby vegetation, (0.08, [0.003, 0.13]). The null model was not competitive (Δ AIC = 2.60, $w_i = 0.04$; Supplementary Material Table 5).

DISCUSSION

Consistent with our predictions, Spotted Owls more frequently captured prey in areas with greater vertical structure in vegetation (canopy layers and height), spatial heterogeneity in vegetation types or structures (coarse and fine heterogeneity), and along edges of different vegetation types or structures

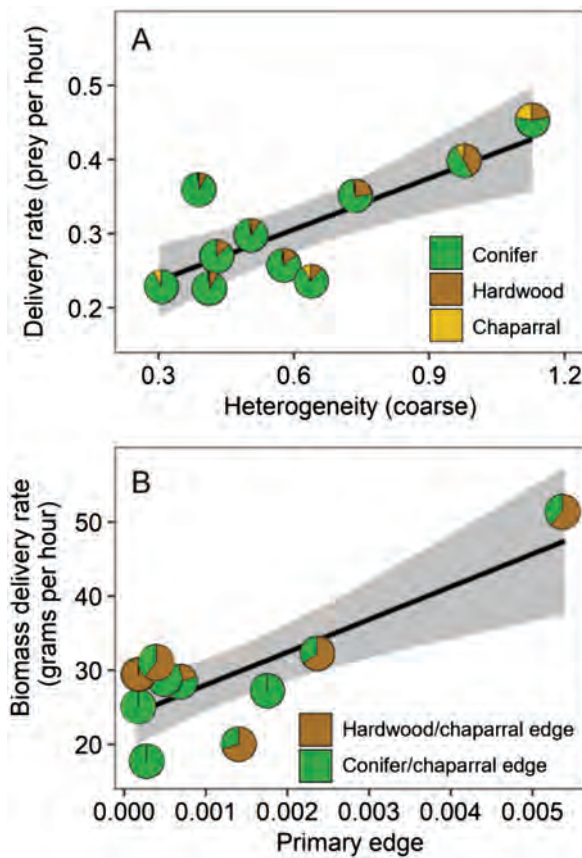


FIGURE 4. Prey delivery rate per hour (A) and prey biomass delivery rate (B) as functions of coarse vegetative heterogeneity (Shannon diversity of vegetation types) and primary edge (edge density of chaparral-forest edge), respectively. Each point represents an owl territory, with points in (A) displayed as pie charts of the proportion of the three main vegetation types (conifer forest in green, hardwood forest in brown, and chaparral in yellow) in the territory and points in (B) displayed as the proportion of the two primary edge types in the territory: conifer-chaparral edge (green) or hardwood-chaparral edge (brown).

(primary and secondary edge density). Our results support results from a similar study in the Sierra Nevada (Zulla *et al.* 2022), which also found Spotted Owls tended to capture prey, and particularly woodrats, in areas with more large trees, heterogeneity in vegetation conditions, and edge. Relationships between prey acquisition and canopy layers and height supported numerous previous studies demonstrating that VHF- and GPS-marked individuals preferentially use forests with larger trees and vertically complex structure during nocturnal activities, but indicates that owls do so, in part, because they promote successful foraging (Atuo *et al.* 2019, Blakey *et al.* 2019, Kramer *et al.* 2021b, Zulla *et al.* 2022). However, our findings also indicate that foraging owls likely benefits from a mosaic of large tree forest with complex canopy and other vegetation types given that woodrats, the primary Spotted Owl prey species in the southern California region, were more likely to be captured in areas with (1) high heterogeneity in vegetation types (conifer forest, hardwood forest, chaparral) and (2) along forest-chaparral edges. Indeed, associations between woodrat capture locations and both heterogeneity and edge density provide compelling support for previous suggestions that areas with low-lying vegetation serve as sources of woodrat prey for owls foraging in adjacent older forests (Zabel *et al.* 1995, Sakai and Noon 1997, Kramer *et al.* 2021b, Zulla *et al.* 2022). While shrubby vegetation appeared to provide habitat for woodrats and provide foraging opportunities for Spotted Owls along forest-chaparral edges, owls were less likely to capture woodrats in areas with more shrubby vegetation, which included both pure chaparral vegetation and shrubby understories of forested areas. Without adjacent forests, larger areas of chaparral may not offer suitable perching for owls to hunt for and capture woodrats, whereas dense shrubby areas within forests may provide woodrats with sufficient cover to avoid predation. Associations between all prey captured and both secondary edge density and fine heterogeneity suggest that fine-scale variation in heterogeneity and vertical structure also improve overall hunting success. These features could provide foraging owls, as ambush predators,

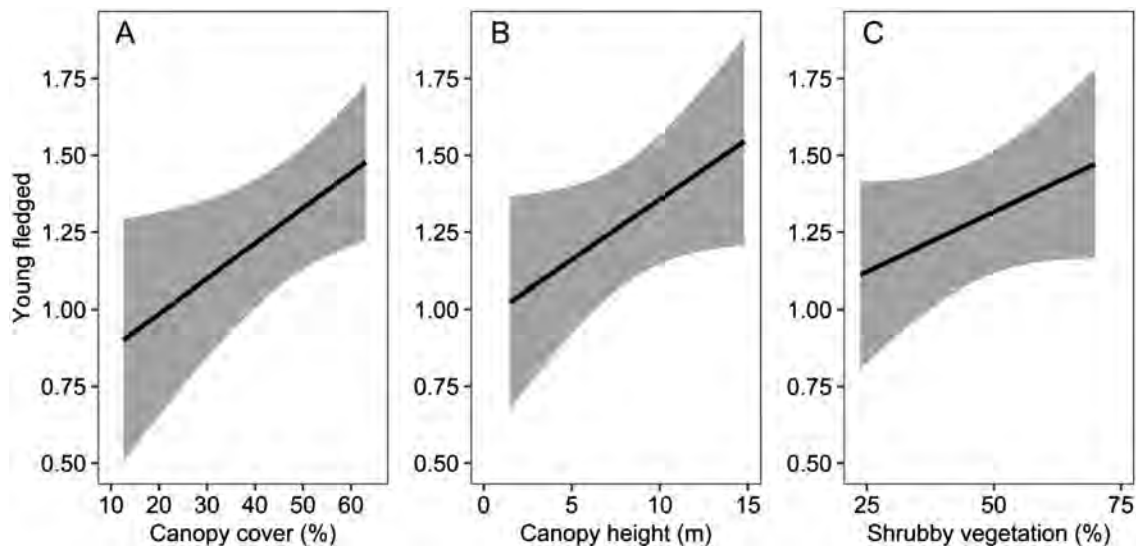


FIGURE 5. Averaged model predictions of number of young fledged plotted against (A) mean percent canopy cover, (B) mean canopy height, and (C) mean shrubby vegetation density within the territory, with shaded 95% confidence intervals.

with more perches to locate and approach prey. Higher variation in vegetation types and forest structure could also provide a greater diversity of niches for prey, such that owls encounter more species of prey in forests with these features.

Prey delivery rates by Spotted Owls to nests were greater when territories contained more of some of the vegetation conditions (coarse heterogeneity and primary edge density) that promoted successful prey acquisition. Higher prey delivery rates in territories with more coarse heterogeneity suggest that a diversity of vegetation types increase either prey abundance or accessibility to prey by Spotted Owls or both. In comparison, the delivery of prey biomass to nests was greatest in owl territories containing more forest chaparral edge (i.e., “primary edge density”), with woodrats likely driving this relationship as the most frequent and one of the largest species of prey delivered to nests. The biomass delivery-edge density relationship was sensitive to a single influential data point with high forest chaparral edge density. While additional studies involving larger sample sizes are merited, a clear ecological basis exists for believing the relationship is real. Indeed, in conjunction with the prey capture analysis, these two results provide further evidence that although Spotted Owls’ primary prey species (woodrats) may be more abundant in vegetation cover types like chaparral, they become increasingly vulnerable to predation by owls when they occur near ecotones with older forests, where owls tend to forage (Zabel *et al.* 1995, Sakai and Noon 1997, Ward *et al.* 1998). Hence, there appears to be a direct link between vegetation conditions that promote successful foraging and the energy, in the form of prey biomass, provided by adult owls to nestlings.

Spotted Owl reproductive success was greater when owls occurred in territories that contained some of the vegetation conditions (e.g., taller forest) that apparently benefited prey captures, yet reproductive success was also higher under conditions: (1) unrelated to prey captures (denser canopy cover); (2) associated with fewer captures (more shrubby cover); and (3) unrelated to higher prey delivery rates to nests (denser canopy cover). Canopy height and cover had a positive influence on reproductive success, likely because older forest also serves as nesting habitat that provides a suitably cool microclimate and concealment from nest predators (LaHaye *et al.* 1997, North *et al.* 2000, Weathers *et al.* 2001). However, taller forests (with larger trees) may also provide Spotted Owls with better hunting perches or ambush cover, given the positive association we observed between the probability of prey capture and taller forests (see Figure 2A; Atuo *et al.* 2019, Blakey *et al.* 2019, Kramer *et al.* 2021a), which could have contributed to higher reproductive success. The apparent contradiction between higher reproductive success, yet lower prey capture, in areas with more shrubby cover is likely a matter of scale. At the fine scale at which we assessed foraging habitat (mean polygon size = 3.6 ha), owls may encounter fewer prey—or be less successful capturing prey—in dense shrubby areas because of the concealment or refuge it provides. But at a larger, territory scale (314 ha), areas of dense shrubby vegetation such as chaparral or shrubby areas within forested patches may serve as sources for small mammal prey (particularly woodrats) for Spotted Owls (Zabel *et al.* 1995, Sakai and Noon 1997, Parmenter *et al.* 2003). Thus, even though heterogeneity or edge density, strictly speaking, were not associated with higher reproductive success, we suggest that the juxtaposition of the taller, closed canopy forest and shrubby

conditions (both in forest understories and as chaparral vegetation) constitutes forms of vertical structure and spatial heterogeneity that were indeed positively associated with Spotted Owl reproductive success—presumably because they improved prey acquisition. Broadly, these results supported our predictions that some of the vegetation conditions that facilitated prey captures by Spotted Owls would also increase reproductive success, but also suggested that other processes affect successful reproduction.

Environmental features such as vegetation conditions can strongly influence encounter and kill rates of prey by predators, and thus likely predator fitness and population status. The vast majority of predator–prey studies in the wild have focused on large carnivores, which typically leave noticeable kill sites (Gorini *et al.* 2012). We capitalized on new GPS tagging and nest video monitoring techniques (Marsh *et al.* 2014a, Wood *et al.* 2021) to better understand how vegetation conditions, including forest structure and heterogeneity, affect these processes in a small-bodied, nocturnal predator at the center of forest management in western North America. In doing so, we provide a more mechanistic understanding of previous observations suggesting that a mosaic of large-treed forests with complex canopies and shrubby vegetation increases prey availability and provides fitness-level benefits to Spotted Owls in landscapes where woodrats are a primary prey (Ward *et al.* 1998, Hobart *et al.* 2019a, Kramer *et al.* 2021b). Future studies involving concurrent woodrat trapping to estimate densities in owl foraging areas and habitats could provide additional mechanistic insights into predator–prey interactions between the two species. Additionally, this study was limited to actively nesting owls—albeit a critical stage for population dynamics—and further research would be required to determine if observed patterns change when breeding owls are no longer constrained to feeding juveniles. However, our work in conjunction with similar research in the Sierra Nevada (Zulla *et al.* 2022), suggests that continued development and implementation of forest management practices intended to promote vegetation heterogeneity (North and Manley 2012) could also benefit declining Spotted Owl populations (Peery *et al.* 2017).

Conservation Implications

Characterizing vegetation conditions constituting high-quality foraging habitat and how those conditions translate to fitness components such as reproductive success can strengthen conservation planning for threatened predators (Katzner *et al.* 2005, Catry *et al.* 2013, Hobart *et al.* 2019a, Smith *et al.* 2020). Spotted Owl populations in southern California have declined upwards of 40% in occupancy over the past 30 years and appear vulnerable to extirpation, likely due to complex interactions between vegetation conditions, climate change, and large severe wildfires (Tempel *et al.* 2022). The exclusion of historically frequent wildfires from southern California forests over the past century has promoted denser, more homogenous stands of trees and denser stands of chaparral (Minnich *et al.* 1995), driving a transition from frequent low- and moderate-severity wildfires to large high-severity wildfires that (1) can eliminate extensive areas of habitat (Jones *et al.* 2016), and (2) reduce foraging opportunities (this study) for Spotted Owls. Our study indicates that increasing forest heterogeneity, and particularly taller, vertically complex forests with higher canopy that are interspersed with chaparral

could benefit owl foraging and reproduction. Specifically, restoration of more frequent low- to moderate- severity fire regimes to these forests could both increase forest heterogeneity and resilience to severe wildfire and other disturbances (Stephens *et al.* 2008, Collins *et al.* 2009), and ultimately improve Spotted Owl viability in the region. Integral to such efforts is consideration of temporal scales and the importance of conserving and restoring large trees which can take decades to centuries to grow, with the dynamics of chapparral and shrub types adapted to disturbance and replacement over much shorter time scales.

Importantly, fire management with purely fuels-reduction objectives may not increase vegetation heterogeneity in a way that will improve foraging success, because such practices typically remove understory vegetation and can simplify vertical forest structure (Tempel *et al.* 2015). Rather, fire and vegetation management that creates a mosaic of fuel and vegetation condition, including juxtaposed areas of higher resistance (e.g., taller forests with minimal ladder fuels) and potential lower resistance (e.g., areas of shrub cover both independent of and under overstory trees) is more likely to improve owl fitness. While such juxtaposition may also put forest edges at higher risk of severe fire, a diverse vegetation mosaic should result in self-limiting fire behavior at the landscape scale (Lydersen *et al.* 2013), perpetuating heterogeneous conditions—potentially helping recover declining owl populations. A future study investigating thresholds in the beneficial effects of chapparral or shrubby vegetation, as well as the influence of patch size, could provide insights into the potential costs of too much heterogeneity. Nevertheless, we suspect that many smaller patches may benefit owls by providing more edge habitat with a lower risk of large severe fire that is associated with large, dense stands of chapparral. Similarly, the judicious application of mechanical vegetation management practices or variable retention harvesting that increases tree sizes and fine-scale variation in vegetative conditions (Kuehne *et al.* 2015), by creating canopy openings that promote shrub cover and edges in foraging areas, could also benefit Spotted Owls in this region. Forest management in nest stands, however, should avoid simplifying forest structure or creating gaps that reduce survival by increasing predation risk or thermoregulatory costs (Franklin *et al.* 2000, Weathers *et al.* 2001, Ma *et al.* 2010). In conclusion, this study adds to the growing body of literature indicating that forest management activities intended to promote forest heterogeneity could benefit the conservation of Spotted Owls (e.g., Tempel *et al.* 2015, Jones *et al.* 2021, Kramer *et al.* 2021a, Zulla *et al.* 2022).

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

Data collection was performed under USGS Bird banding lab permit #23685 and California department of fish and wildlife scientific collection permit S-193180001-19324-001). Handling of all animals was performed in accordance with the University of Wisconsin -Madison IACUC (Institutional animal care and use committee) protocol #A005367-R02.

Author contributions

MZP, SCS, JJK, RJG Conceived the idea, design, or experiment (supervised research, formulated questions or hypotheses). ZAW Performed the experiments (collected data, conducted the research) with support from CJZ, KM, JMB, RT, RJG. ZAW, HAK, GMJ, RJG, MZP wrote the paper (or substantially edited the paper). ZAW, HAK, GMJ, MZP, CJZ developed or designed methods. ZAW, HAK, GMJ, MZP analyzed the data and RT contributed substantial materials, resources, or funding.

Data deposits

Analyses reported in this article can be reproduced using the data provided by Wilkinson *et al.* (2022).

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RESEARCH ARTICLE

Optimizing landscape-scale monitoring programmes to detect the effects of megafires

Connor M. Wood 

Center for Conservation Bioacoustics,
Cornell Lab of Ornithology, Cornell
University, Ithaca, NY, USA

Correspondence

Connor M. Wood, Center for Conservation
Bioacoustics, Cornell Lab of Ornithology,
Cornell University, Ithaca, NY, USA.
Email: cmw289@cornell.edu

Editor: Morgan Tingley

Abstract

Aim: By virtue of their spatial extent, landscape-scale monitoring programmes may be well-suited to support before-after/control-impact (BACI) studies of major disturbances such as megafires, but they may only have a few affected sites, reducing statistical power. I tested whether a variety of hypothetical but logistically plausible survey designs could provide statistically powerful assessments of hypothetical but empirically based population responses to megafire.

Location: Simulation focused on fire-prone forests.

Methods: I varied the number of affected sites, detection probability, baseline occupancy and species' responses to fire to create 72 monitoring scenarios. I then simulated 10 years of site occupancy data in which a megafire or other disturbance occurred between years 5 and 6 ($n = 500$ iterations).

Results: Statistical power to correctly reject the null hypothesis of no population response to megafire was high (mean across all scenarios = 0.78), but power to identify the correct population response (e.g. post-fire occupancy declined and then recovered) was low (mean = 0.29). Statistical power to not underestimate the effect of a megafire on site occupancy was fairly high (mean = 0.66), but power to accurately estimate site occupancy was low (mean = 0.25). Statistical power increased with the number of affected sites (i.e., sample size) and with the intensity of the focal species' response to megafire. Case study simulations based on an existing acoustic monitoring programme in the Sierra Nevada, USA, indicate that it is likely to identify Spotted Owl and Black-backed Woodpecker population responses to megafires. Researchers can use the included simulation tutorial to implement their own power analyses.

Main conclusions: Landscape-scale monitoring programmes can identify population changes following megafires, but cannot reliably produce nuanced results, especially with only five years of post-fire data. Smaller-bodied species, which could be studied at more sites, are likely to be better focal species for megafire BACI studies. Aggregating landscape-scale studies' sampling coverage across many fire footprints to study the overall effects of megafires—rather than the effects of individual fires—may be a more informative approach.

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acoustic survey, autonomous recording unit, bioacoustics, camera trap, non-invasive sampling, power analysis, simulation, statistical power

1 | INTRODUCTION

From climate change to species range shifts, ecological processes are occurring at increasingly extensive spatial scales. The occurrence of megafires—atypically large and severe fires—is one such process, and a combination of climate change and both historical and contemporary land use is making them more common in dry forests in North America (Miller et al., 2009; Stevens et al., 2017; Westerling, 2016), eastern Australia (Boer et al., 2020) and the Amazon (Fidelis et al., 2018). These changing fire regimes increase the risk of lasting forest conversion reinforced by positive feedback loops (Coop et al., 2020). In regions where vast swaths of land are managed by single entities, management decisions made in response to the growing risk of megafires can also have sweeping ecological ramifications (Wood & Jones, 2019). However, the direct effects of megafires on wildlife populations can be difficult to discern because most studies to date have been conducted opportunistically after fires have occurred.

By virtue of their spatial extent, landscape-scale monitoring programmes should be well-suited to provide survey coverage within the footprints of future megafires, potentially allowing for before-after/control-impact (BACI) studies. Data from camera traps, hair snares and autonomous recording units (ARUs) collected at landscape scales can support statistically powerful multispecies occupancy and mark-recapture analyses to assess population trends (Banner et al., 2018; Ellis et al., 2014; Magoun et al., 2011; Steenweg et al., 2016; Wood et al., 2021; Wood et al., 2019). However, the statistical power of these types of non-invasive monitoring programmes has primarily been evaluated in the context of population trends affecting many or all sites, rather than the effects of localized disturbances (e.g., Banner et al., 2019; Ellis et al., 2014; Steenweg et al., 2016; Wood et al., 2019).

Ironically, compelling demonstrations of the effects of megafires on threatened species have actually come from small- to moderate-scale studies. In the Sierra Nevada, USA, the 2014 King Fire burned 30 of 45 Spotted Owl (*Strix occidentalis*) territories in a ~ 350-km² study area in which marked individuals had been censused annually, enabling an elegant BACI study with which researchers showed conclusively that large, severe fires drastically reduce Spotted Owl territory occupancy and increase territory extinction (Jones et al., 2016). The 2013 Rim Fire also in the Sierra Nevada had a contrasting effect on an unmarked population of Great Gray Owls (*S. nebulosa*) that had been surveyed for 10 years before the fire, with territory occupancy remaining high for three years post-fire (Siegel et al., 2019). In south-eastern Australia, three years of pre-fire data and four years of post-fire data revealed that the 2009 Black Saturday fire complex (720 km²) caused 12 of 13 bird species to decline in response to the amount of severely burned forest on the landscape (Lindenmayer

et al., 2014). The overlap of megafires with longer-term, smaller-scale studies circumvented a fundamental trade-off monitoring programmes face between survey intensity and spatial extent, but such events are unlikely.

Resource and logistical constraints dictate that landscape-scale monitoring programmes survey only a fraction of the landscape; consequently, the number of survey sites within the footprint of any given megafire may be low. For example, a landscape-scale acoustic monitoring programme designed for Spotted Owls in the Sierra Nevada initiated after the King Fire (Wood et al., 2019) would have included just 8–10 owl territory-sized sites within the footprint of the King Fire, as opposed to the 30 owl territories that were surveyed by Jones et al., (2016). Precision and statistical power improve with the number of survey sites (Ellis et al., 2014; Steenweg et al., 2016; Wood et al., 2019), so if a megafire were to overlap the footprint of such a monitoring programme, its ability to deliver critical information—such as whether endangered species' populations suffered as a result of the fire—could be limited.

Landscape-scale monitoring is incipient or ongoing for a variety of species in fire-prone regions. The Spotted Owl, which is negatively affected by megafires (Jones et al., 2016; Rockweit et al., 2017), is the focal species of passive acoustic surveys across the Sierra Nevada and Pacific north-west (Duchac et al., 2020; Wood et al., 2019). Bats, which may also be negatively affected by megafires (Jung, 2020), are subject to acoustic monitoring across the Pacific Northwest (Rodhouse et al., 2019). Carnivores such as fisher (*Pekania pennanti*) and marten (*Martes americana*) are monitored in the Sierra Nevada (Zielinski et al., 2013), and wolverines (*Gulo gulo*) and grizzly bears (*Ursus arctos*) are monitored in the northern Rocky Mountains (Ellis et al., 2014; Steenweg et al., 2016). Camera traps are used extensively to assess invasive carnivore removals across Australia, and such data could also be leveraged to conduct megafire-related monitoring (Comer et al., 2020; Robley et al., 2014). Importantly, the legal protections and public prominence of some species already subject to landscape-scale monitoring confer to them considerable influence on forest management policy. Therefore, accurately measuring the effects of megafires on such species—like the Spotted Owl—will have direct bearing on forest restoration, the provisioning of ecosystem services, and human health and safety across fire-prone landscapes (Wood & Jones, 2019).

I hypothesized that the ability of landscape-scale monitoring efforts to provide insight into wildlife responses to megafires depended on the number of survey sites affected and focal species' seasonal detection probability, baseline prevalence and responses to disturbance (Ellis et al., 2014; Southwell et al., 2019; Steenweg et al., 2016; Wood et al., 2019). I simulated logistically plausible survey designs and ecologically realistic responses to large, severe fires to determine whether hypothetical landscape-scale monitoring

programmes may be capable of detecting population changes caused by megafires or other large-scale disturbances that affect focal species' habitat suitability. I predicted that statistical power would increase with the number of affected sites and that power would be higher for more pronounced changes (e.g., a severe decline in a common species or a rapid increase in a rare species). No aspect of the simulation was taxa- or ecosystem-specific; the results are applicable to any case in which the detection probability, baseline occupancy and response to disturbance are similar to the values used here. Moreover, the simulation tutorial is freely available so that researchers can conduct customized power analyses based on their needs (Supporting information). Wildfires with atypically large and homogeneous patches of severely burned areas are increasingly common (Miller et al., 2009; Stevens et al., 2017; Wintle et al., 2020), so understanding whether landscape-scale monitoring programmes are capable of identifying subsequent population changes is increasingly important for conservation.

2 | METHODS

2.1 | Hypothetical monitoring designs and population baselines

I simulated 10 years of site occupancy data for eight hypothetical survey designs in which a high-severity fire or other disturbance occurred between years 5 (t_5) and 6 (t_6).

Either seven, 15, 30 or 60 monitoring sites were affected, which reflects a range of possibilities that depend on the size of the disturbance and the density of survey sites on the landscape, which itself may vary within a study (e.g. ARUs may be co-deployed and their results pooled for species with large home ranges, such as Spotted Owls, but analysed independently for other species, like most passerines). Simulating seasonal detection probability (p^* ; the probability of detecting a species over the course of the sampling season) simplified the simulation by reducing two dimensions, detection probability (p) and the number of secondary sampling periods (n) into a single number ($p^* = 1 - (1 - p)^n$), though both can be modified in the code. Limiting the occurrence of the fire to between years 5 and 6 had two important benefits. First, it made pre-fire occupancy less sensitive to stochastic changes, which was particularly important when sample size was low. Second, it reflected the importance of timely information when implementing adaptive management. While ten or more years of post-fire data would yield higher statistical power (Banner et al., 2019), it would also delay management responses in an era when ecosystem change is unfolding very rapidly. The included power analysis tutorial explains how users can extend (or decrease) the post-fire period to as many years as desired.

For each of the eight hypothetical study designs, I considered nine types of populations in which a hypothetical species had a realistic prevalence on the landscape and a plausible response to a megafire. Initial site occupancy (ψ) could be 0.25, 0.5 or 0.75, which encompasses occupancy rates reported for most Sierra Nevada

TABLE 1 Simulation parameters and the number of levels in each parameter. Baseline extinction and colonization probabilities were conditional on starting occupancy and were calibrated to yield a stable control population

Survey design		Levels
Number of affected sites	7, 15, 30, 60	4
Seasonal detection probability	0.75 or 0.95	2
Population attributes		
Initial occupancy (ψ)	25%, 50%, or 75% of sites	3
Baseline pr(extinction)	0.13 ($\psi = 0.25$) / 0.08 ($\psi = 0.25$) / 0.05 ($\psi = 0.25$)	NA
Baseline pr(colonization)	0.05 ($\psi = 0.25$) / 0.08 ($\psi = 0.25$) / 0.13 ($\psi = 0.25$)	
Post-fire extinction	Dynamic (-), dynamic (+), permanent (+)	3
Post-fire colonization	Dynamic (+), dynamic (-), permanent (-)	

passerines for which point counts have been a viable survey technique (Table S2 of Tingley et al., 2009) and two species of bat in the Pacific Northwest (Rodhouse et al., 2019). It is also consistent with species relevant to the management of fire-prone forests: Spotted Owl site occupancy in the northern Sierra Nevada is approximately 0.53 (Wood et al., 2020), fisher site occupancy in the southern Sierra Nevada is 0.26–0.058 depending on the subregion (Zielinski et al., 2013), and Black-backed Woodpecker (*Picoides arcticus*) site occupancy in the Sierra Nevada can span that entire range of values depending on the time since fire (Tingley et al., 2018). Baseline site extinction (ϵ_B) and site colonization (γ_B) ranged from 0.05 to 0.13 depending on initial site occupancy such that the control population was stable for the duration of the simulation (Table 1).

2.2 | Hypothetical megafire responses

The three simulated disturbance responses were necessarily general, but resembled the published responses of focal species in fire-prone forests to large, severe fire (Jones et al., 2016; Latif et al., 2016; Tingley et al., 2018). Response 1 was an ephemeral increase in site quality (ϵ dropped to 0.0 in t_6 and increased linearly to $2^*\epsilon_B$ by t_{10} ; γ increased to 0.8 in t_6 and decreased linearly back to γ_B by t_{10}), which represented a post-fire specialist like the Black-backed Woodpecker or Flame Robin (*Petroica phoenicea*) (Lindenmayer et al., 2014; Tingley et al., 2018). Response 2 was an ephemeral reduction in site quality (ϵ increased to $4^*\epsilon_B$ in t_6 and decreased linearly back to ϵ_B by t_{10} ; γ decreased to $0.25^*\gamma_B$ in t_6 and increased linearly to $2^*\gamma_B$ by t_{10}), which represented a species like the Brown Thornbill (*Acanthiza pusilla*), which can recover from fires more quickly than most sympatric bird species (Lindenmayer et al., 2014). Response 3 was a permanent,

severe reduction in site quality (for t_{6-10} , ε increased to 0.9; γ decreased to 0.03), which represented a hypothetical old-forest specialist like the Spotted Owl for which some configurations and intensities of fire represent quasi-permanent losses of habitat (Jones et al., 2016). Importantly, these are generalized, hypothetical responses: even “post-fire specialists” like Black-backed Woodpeckers can be negatively affected by fires when patches are extremely large and burn at uniformly high severity (White et al., 2019).

2.3 | Simulation

2.3.1 | General simulations

The eight survey designs and nine population types yielded 72 possible scenarios, each of which I simulated 500 times using Program R 4.0.2 (R Core Development Team, 2020). Each scenario included the impacted sites (i.e., seven, 15, 30 or 60) and four times as many unaffected control sites because increasing the number of control sites increases statistical power in BACI designs (Popescu et al., 2012) and reflects an ideal scenario in which many more unburned sites would be available to serve as a baseline for comparison to the impacted sites. A BACI design would not be possible following a catastrophic event in which most or all sites are burned (e.g. Wintle et al., 2020), and an alternative modelling approach would be necessary.

Occupancy at t_1 at all sites was a Bernoulli trial based on the given probability of initial occupancy; site occupancy at unaffected sites in subsequent time steps (i.e., t_{2-10}) was a Bernoulli trial based on the given baseline probabilities of extinction (if the site was occupied at t_{t-1}) or colonization (if the site was vacant at t_{t-1}). Site occupancy in impacted sites before the fire was determined in the same manner; after the fire (t_{6-10}), site extinction and colonization probabilities were determined by the response type in that scenario rather than the baseline. This process yielded the true site occupancy for all sites (control and impacted) for all 10 years. Next, I simulated the effect of detection probability: over three secondary sampling periods, detections at occupied sites were Bernoulli trials based on a detection probability (0.37 or 0.54) that yielded the appropriate seasonal detection probability (0.75 or 0.90).

I then formatted the simulated encounter histories for package *RMark* (Laake, 2013) and implemented three dynamic occupancy models with the ψ - ε formulation. Extinction (ε) and detection (p) were held constant in all models; the simulated variation in extinction (and colonization) would still be represented as changes in occupancy with the ψ - ε formulation. This simplified the modelling process and allowed me to present direct estimates of the more commonly used state variable (ψ , rather than ε or γ), rather than derive them from models using the γ - ε formulation. I compared three models: a null model (three parameters; ψ is constant across sites and years), a BACI-static model (four parameters; $\psi_{\text{Burn-stat}}$ allowed post-fire occupancy to differ between burned and control sites) and a BACI-ephemeral model (four parameters; $\psi_{\text{Burn-eph}}$ allowed post-fire occupancy at burned sites to change linearly with time). I

recorded each model's Akaike information criterion with a correction for small sample size (AICc), occupancy estimates (intercept and β_{burned} , if applicable) and associated standard errors.

2.3.2 | Case study: Sierra Nevada focal species simulations

I conducted another set of simulations using parameters that matched the existing Sierra Nevada acoustic monitoring programme to serve as a case study. I fixed the number of burned sites at 4 and 12, which reflects the survey site density of that programme and its hierarchical design. The landscape is divided into 4 km² hexagonal grid cells, 20% of which are surveyed with two or three ARUs deployed ≥ 500 m apart (Wood et al., 2019 for further detail). Thus, this scenario represents a 100 km² patch of uniformly high-severity fire. I defined the population attribute parameters to reflect two prominent fire-affected species, Spotted Owls and Black-backed Woodpeckers.

Spotted Owl site occupancy, which would be assessed at four grid cells, and seasonal detection probability under this monitoring programme are 0.43–0.53 and 0.88–0.84, respectively (Wood et al., 2019, 2020), and megafires result in quasi-permanent habitat loss (response 3) (Jones et al., 2016). Black-backed Woodpecker baseline occupancy in the Sierra Nevada region is 0.20 and seasonal detection probability is 0.90–0.93 when vocal lure surveys are used (Tingley et al., 2018). Site occupancy of species would be assessed at the 12 ARUs because their spacing corresponds with comparable surveys (Tingley et al., 2014), and it preferentially colonizes recently burned forests (response 1) (Tingley et al., 2018).

2.4 | Computing statistical power

I measured statistical power in four ways: two based on model selection and two based on occupancy estimates. For the model selection approach, I first tested whether the null model was correctly rejected ($\Delta\text{AICc}_{\text{Null}} > 0$) and then I tested whether the correct model had been identified. In scenarios with responses 1 and 2 (ephemeral increase or decrease in habitat quality), the BACI-ephemeral occupancy model should have the most support ($\Delta\text{AICc}_{\text{Burn-eph}} = 0$); in scenarios with response 3 (a permanent reduction in site quality), the BACI-static model should have the most support ($\Delta\text{AICc}_{\text{Burn-stat}} = 0$).

For the occupancy estimation approach, I compared true occupancy in burned sites to the 85% confidence interval of occupancy at burned sites as estimated by the top model of site occupancy (Arnold, 2010). First, I tested whether the top model underestimated the effect of a megafire on site occupancy. Underestimating the effects of a fire—whether or positive or negative—could lead to insufficient policies that could jeopardize focal species populations, while correctly estimating or overestimating the effects would at worst lead to unnecessarily strict conservation measures that would be unlikely jeopardize a species. In this context, I expressed power

as 1—the underestimation rate. When the population increased in response to fire (response 1), I calculated the overall average number of post-fire years ($n = 5$ years across $n = 500$ simulations) in which true occupancy at burned sites was greater than the lower 85% confidence interval of estimated occupancy. When the population decreased in response to fire (responses 2 and 3), I calculated the average number of post-fire years in which true occupancy at burned sites was lower than the upper 85% confidence interval of estimated occupancy. Second, I tested whether occupancy had been estimated accurately by calculating the overall average number of post-fire years in which true occupancy at burned sites was within the 85% confidence interval of estimated occupancy.

Finally, I used package *betareg* (Zeileis et al., 2020) to implement four sets of univariate generalized linear models with beta distributions in which the dependent variable was the rate at which (i) any megafire response was detected via model selection, (ii) the correct megafire response was detected via model selection, (iii) the effect of a megafire on site occupancy was not underestimated, or (iv) occupancy was correctly estimated. The number of affected sites, detection probability, baseline occupancy and megafire response type were independent variables. I then compared Efron's pseudo- R^2 of all models to quantify which aspect of the simulation had the most influence on each of the four metrics of statistical power.

2.5 | Assumptions and scope of inference

The most fundamental assumption of these power analyses was that the megafire, or, more generically, spatially extensive disturbance, had a uniform effect on focal species habitat suitability in all affected sites. The size and shape of a wildfire, variation in burn severity, post-fire management practices (e.g., salvage logging) and other factors can influence post-fire habitat suitability in complex and interacting ways. A systematic examination of these factors was beyond the scope of this study, but stochasticity of extinction and colonization probabilities among years and sites allowed for some variation. Moreover, large fires that burn at uniformly high severity are increasingly common (Miller et al., 2009; Stevens et al., 2017; Westerling, 2016; Wintle et al., 2020). Thus, it is both important to understand such fires and not unlikely that real fires would generate several or even many sites that are affected very similarly. By November 2020, three separate fires in the Sierra Nevada had burned >650 km², and, under the existing Sierra Nevada acoustic monitoring programme (coverage of 20% in a 4 km² grid, see 2.3.2), just 14% of such a fire would need to burn at high severity to yield seven affected sites, the fewest considered in these simulations. Alternatively, multiple fires could give rise to the cumulative number of affected sites considered in this study. Thus, the fire considered in these simulations could represent a single high-severity fire or patches of high-severity burns within a larger fire complex.

Detection (p) remained constant throughout the simulation, indicating the hypothetical focal species' behaviour (e.g. vocalization rates) and survey device efficacy did not differ between burned and

unburned forest, or that monitoring protocols were modified such that more (or less) effort was expended to achieve the same season detection probability (p^*).

This approach focuses on the effect of a particular megafire (or patch of high-severity fire, or other spatially extensive disturbance) on a subset of the focal species' population rather than on the effects of megafires generally on the entire population. The simulated "population response" reflects a localized fluctuation in an otherwise stable population, and ongoing population trends and high interannual variation would challenge the detection of a megafire-driven population decline. However, by improving our understanding of the effects of individual high-severity fires (or patches), such studies improve our capacity to make informed ecosystem management decisions in contexts where such fires are likely to become increasingly common (e.g., Jones et al., 2016).

Finally, the simulations assume that site occupancy is an appropriate method of measuring population change. For territorial resident species such as Spotted Owls, territory occupancy is a reliable proxy for abundance (Tempel & Gutiérrez, 2013); with some data modification, site occupancy may reflect territory occupancy (Wood et al., 2020), but the relationship warrants further exploration. For non-territorial or migratory species, site occupancy may not be the most informative metric of population change because abundance could vary substantially among occupied sites. Fortunately, bioacoustics affords managers some flexibility in changing their state variable (e.g., from occupancy to density Pérez-Granados et al., 2019). For these analyses, however, I focused solely on site occupancy.

3 | RESULTS

3.1 | General simulation results

Statistical power to detect any population response to a megafire via model selection (i.e. $\Delta AIC_{Null} > 0$) was generally high (mean = 0.78, range: 0.42–1.00), but power to identify the correct population response was low (mean = 0.29, range: 0.00–0.61; Table 2). Similarly, statistical power to not underestimate the effect of a megafire on site occupancy was fairly high overall (mean = 0.66, range: 0.46–0.96), but power to correctly estimate site occupancy was low (mean = 0.25, range: 0.05–0.44; Table 2). However, there was substantial variation among scenarios, and results for all 72 scenarios are listed in Table 2, so researchers can identify the scenario most relevant to their study.

Baseline occupancy and seasonal detection probability did not substantially affect statistical power (Table 3). Statistical power to detect a population response was very high (>0.9) when 15 or more sites were affected and when species displayed ephemeral positive or lasting negative responses to megafires (i.e., responses one and three) (Figure 1a; Figure 2a,b; Table 2). The number of affected sites explained 9.6% of the variation in statistical power, and response type explained 52% of the variation (pseudo- $R^2 = .096$ and

TABLE 2 Complete list of monitoring scenarios with four metrics of statistical power based on 500 iterations of the simulation. Researchers can cross-reference these scenarios with their own projects to estimate their potential statistical power; if none of these scenarios are a sufficient match to a relevant monitoring programme and focal species, a simulation tutorial (Supporting information) can be used to create fully customized power analyses

Survey design choices		Population attributes		Model selection		Occupancy estimates	
Affected sites	p^*	ψ_1	Response	Null rejected	Correct response	Not underestimated	Within 85% CI
7	.37	0.25	1	0.998	0.002	0.692	0.385
7	.37	0.25	2	0.410	0.230	0.533	0.277
7	.37	0.25	3	0.584	0.532	0.668	0.084
7	.37	0.50	1	0.902	0.098	0.590	0.234
7	.37	0.50	2	0.386	0.242	0.449	0.394
7	.37	0.50	3	0.892	0.630	0.700	0.104
7	.37	0.75	1	0.726	0.274	0.371	0.174
7	.37	0.75	2	0.378	0.204	0.357	0.394
7	.37	0.75	3	0.980	0.732	0.742	0.078
7	.54	0.25	1	0.986	0.014	0.656	0.368
7	.54	0.25	2	0.354	0.202	0.568	0.278
7	.54	0.25	3	0.544	0.446	0.728	0.086
7	.54	0.50	1	0.914	0.086	0.590	0.269
7	.54	0.50	2	0.412	0.268	0.479	0.388
7	.54	0.50	3	0.860	0.526	0.766	0.116
7	.54	0.75	1	0.746	0.254	0.387	0.196
7	.54	0.75	2	0.432	0.256	0.400	0.405
7	.54	0.75	3	0.952	0.610	0.800	0.105
15	.37	0.25	1	0.996	0.004	0.687	0.409
15	.37	0.25	2	0.454	0.344	0.531	0.381
15	.37	0.25	3	0.660	0.358	0.684	0.168
15	.37	0.50	1	0.946	0.054	0.777	0.200
15	.37	0.50	2	0.436	0.336	0.532	0.379
15	.37	0.50	3	0.966	0.524	0.703	0.150
15	.37	0.75	1	0.896	0.104	0.608	0.286
15	.37	0.75	2	0.416	0.308	0.466	0.395
15	.37	0.75	3	1.000	0.606	0.659	0.135
15	.54	0.25	1	0.990	0.010	0.628	0.355
15	.54	0.25	2	0.484	0.358	0.536	0.398
15	.54	0.25	3	0.696	0.276	0.727	0.179
15	.54	0.50	1	0.942	0.058	0.702	0.248
15	.54	0.50	2	0.572	0.440	0.503	0.437
15	.54	0.50	3	0.954	0.352	0.742	0.189
15	.54	0.75	1	0.914	0.086	0.602	0.324
15	.54	0.75	2	0.468	0.356	0.467	0.419
15	.54	0.75	3	1.000	0.382	0.694	0.202
30	.37	0.25	1	1.000	0.000	0.593	0.317
30	.37	0.25	2	0.480	0.342	0.629	0.315
30	.37	0.25	3	0.786	0.296	0.760	0.185
30	.37	0.50	1	0.980	0.020	0.906	0.159
30	.37	0.50	2	0.510	0.434	0.583	0.342

(Continues)

TABLE 2 continued

Survey design choices		Population attributes		Model selection		Occupancy estimates	
Affected sites	p^*	ψ_1	Response	Null rejected	Correct response	Not underestimated	Within 85% CI
30	.37	0.50	3	0.998	0.450	0.802	0.131
30	.37	0.75	1	0.988	0.012	0.710	0.339
30	.37	0.75	2	0.474	0.400	0.551	0.359
30	.37	0.75	3	1.000	0.398	0.703	0.199
30	.54	0.25	1	1.000	0.000	0.556	0.287
30	.54	0.25	2	0.578	0.412	0.591	0.356
30	.54	0.25	3	0.702	0.198	0.825	0.162
30	.54	0.50	1	0.926	0.074	0.731	0.174
30	.54	0.50	2	0.600	0.486	0.554	0.394
30	.54	0.50	3	0.994	0.354	0.784	0.185
30	.54	0.75	1	0.992	0.008	0.632	0.363
30	.54	0.75	2	0.534	0.438	0.536	0.396
30	.54	0.75	3	1.000	0.290	0.731	0.209
60	.37	0.25	1	1.000	0.000	0.502	0.202
60	.37	0.25	2	0.538	0.374	0.736	0.210
60	.37	0.25	3	0.924	0.526	0.941	0.053
60	.37	0.50	1	0.994	0.006	0.934	0.146
60	.37	0.50	2	0.556	0.470	0.752	0.205
60	.37	0.50	3	1.000	0.508	0.934	0.055
60	.37	0.75	1	0.998	0.002	0.646	0.328
60	.37	0.75	2	0.508	0.458	0.702	0.238
60	.37	0.75	3	1.000	0.456	0.825	0.144
60	.54	0.25	1	1.000	0.000	0.456	0.179
60	.54	0.25	2	0.642	0.426	0.677	0.272
60	.54	0.25	3	0.846	0.482	0.955	0.045
60	.54	0.50	1	0.944	0.056	0.774	0.099
60	.54	0.50	2	0.616	0.458	0.684	0.270
60	.54	0.50	3	1.000	0.580	0.939	0.058
60	.54	0.75	1	0.998	0.002	0.564	0.278
60	.54	0.75	2	0.574	0.492	0.635	0.306
60	.54	0.75	3	1.000	0.378	0.891	0.103

TABLE 3 Amount of variation in statistical power explained by each simulation parameter (pseudo- R^2)

Parameters (Table 1)	Model selection		Occupancy estimates	
	Null rejected	Correct response	Not underestimated	Within 85% CI
Study design choices				
Affected sampling sites	0.017	0.096	0.233	0.089
Detection probability (p^*)	0.000	0.001	0.002	0.003
Population attributes				
Initial occupancy (ψ_1)	0.015	0.039	0.019	0.007
Response type	0.515	0.704	0.363	0.607

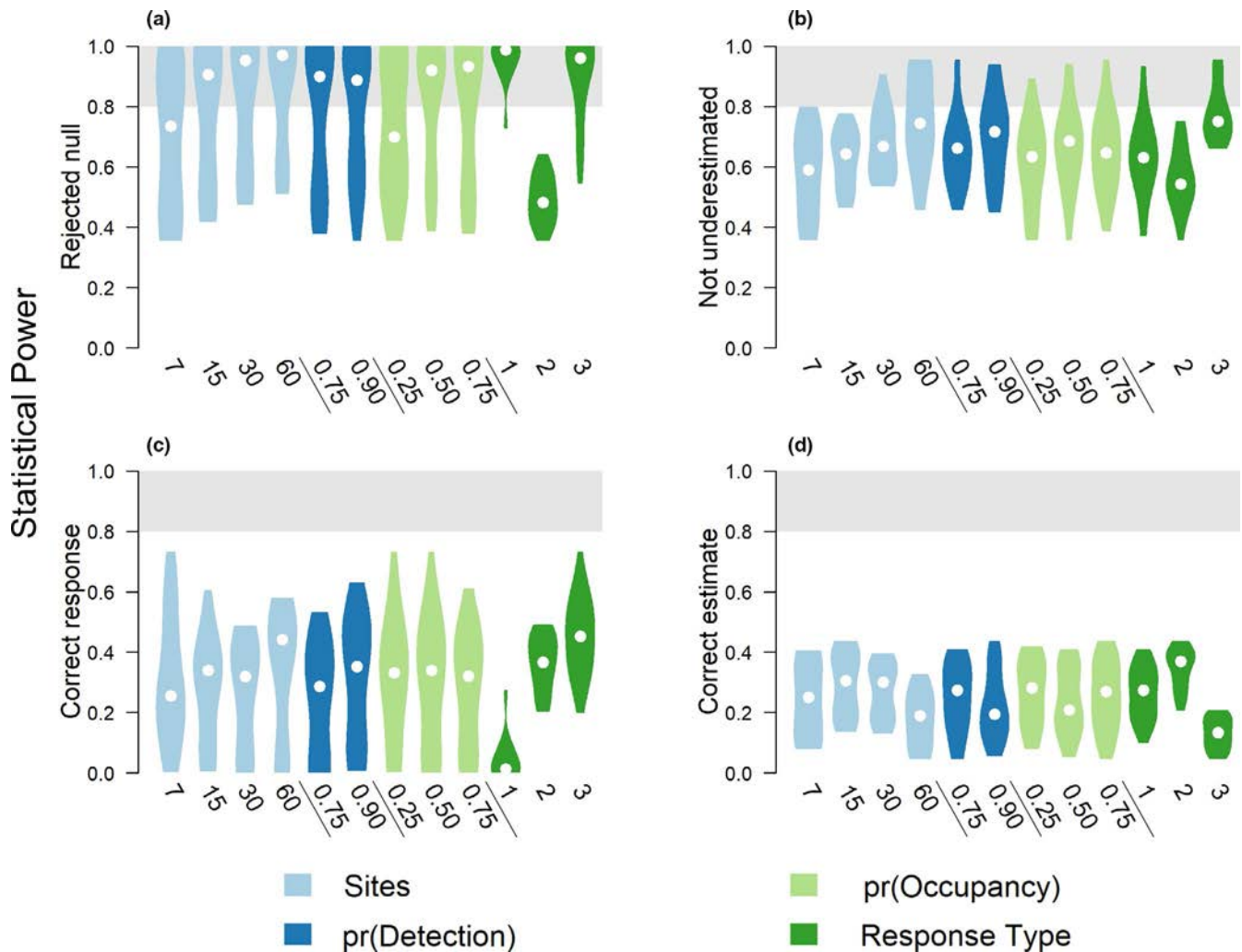


FIGURE 1 Statistical power to detect a population response by rejecting the null hypothesis of no population change (a) and to identify the correct population response (i.e. static or ephemeral post-fire differences in occupancy; (c) via model selection, and statistical power to not underestimate the effect of a megafire on site occupancy (b) and to correctly estimate site occupancy at burned sites (d). Median values indicated with white circles; grey polygons highlight regions of the plots in which statistical power ≥ 0.8 ; Table 1 for study design choices and population attributes

.515, respectively; Table 3); when the two were included in a *post hoc* bivariate generalized linear model, the two explained 60% of the variation, suggesting that the methodological and ecological aspects of a scenario were accounting for separate and largely additive processes affecting variation in statistical power. Statistical power to not underestimate the effect of a megafire on site occupancy rates increased with the number of affected sites but was generally <0.8 ; power was highest for response 3 but again was generally <0.8 (Figure 1b; Figure 2a; Table 2). The number of affected sites was more important, explaining 23% of the variation in statistical power to not underestimate the effect of a megafire on site occupancy, while response type explained 36% of the variation; together, they explained 60% of the variation (Table 3).

Under most scenarios, monitoring programmes performed slightly worse than chance (<0.5) when choosing between the BACI-static and BACI-ephemeral dynamic occupancy models, and almost never correctly identified ephemeral, positive responses to megafires

(i.e., response 1) (Figure 1c; Figure 2c,d). Response type explained most of the variation in statistical power (pseudo- $R^2 = .704$) and was the only aspect of a monitoring scenario that explained $>4\%$ of the variation in statistical power (Table 3). Statistical power to accurately estimate occupancy (i.e., the 85% confidence intervals of the top occupancy model overlap true occupancy at burned sites) was uniformly very low (Figure 1d). Statistical power to correctly estimate occupancy was lowest for the species most negatively affected by fire (response 3), but monitoring programmes were best able to correctly identify that population response (Figure 2a). Response type again explained the most variation in statistical power (pseudo- $R^2 = .607$), though the number of affected sites explained 9% of the variation (Table 3).

As noted above, the simulation tutorial is freely available (Supporting information) and explains how each parameter can be changed to suit user's needs (including creating "after-only" or "impact-only" versions of the BACI design). Thus, if a relevant

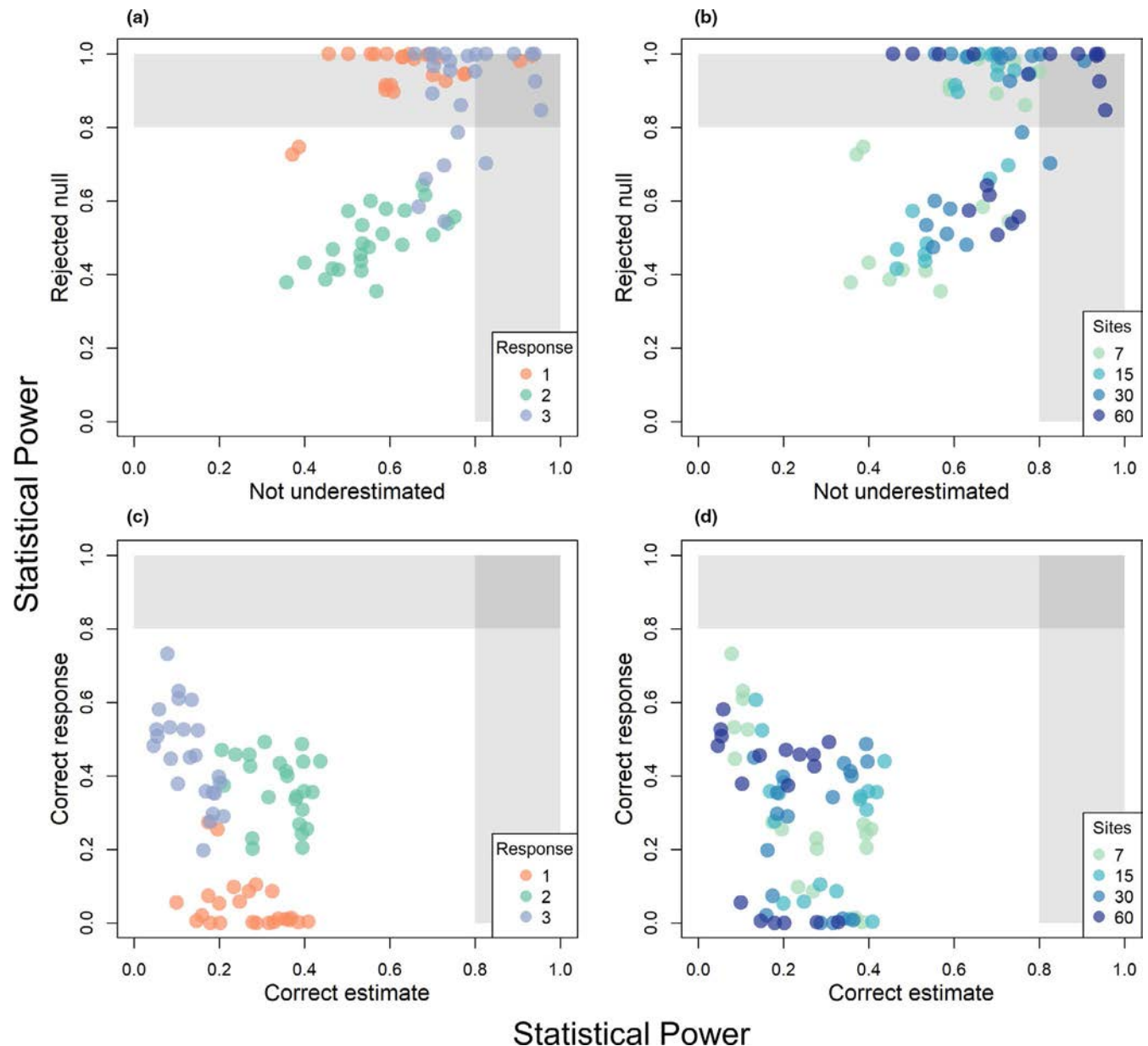


FIGURE 2 Statistical power to detect a population response by rejecting the null hypothesis of no population change (a and b, vertical axis) and to identify the correct population response (i.e. static or ephemeral post-fire differences in occupancy; c and d, vertical axis) to megafires via model selection, and statistical power to not underestimate the effect of a megafire on site occupancy (a and b, horizontal axis) and to correctly estimate site occupancy at burned sites (true occupancy is within the 85% confidence interval of estimates derived from the top model of site occupancy; c and d, horizontal axis). Grey polygons highlight regions of the plots in which statistical power ≥ 0.8

scenario is missing from Table 2 (i.e. was not considered in these analyses), it can be created.

3.2 | Sierra Nevada case study results

The results of the Sierra Nevada case study simulations followed the same patterns as the generalized simulations reported above. Statistical power to identify any Spotted Owl response to megafire (via model selection) was 0.62–0.88, with lower detection probability leading to greater power (Table 4). Yet, increased detection

probability led to increased statistical power to detect the minimum effect of a megafire on site occupancy (0.86 versus 0.77). Statistical power to identify the correct megafire response (via model selection) or the correct occupancy rates (via estimated occupancy) was low (Figure 3).

Statistical power to identify any Black-backed Woodpecker response to megafire was 1.0 regardless of detection probability, and power to detect the minimum effect of a megafire on site occupancy was 0.70–0.66, with power decreasing with increasing detection probability (Table 4; Figure 3). Similarly, statistical power to estimate site occupancy correctly was greater when detection was lower

TABLE 4 Statistical power to detect Spotted Owl and Black-backed Woodpecker responses to megafires in the existing Sierra Nevada acoustic monitoring program

Species	Sites	p^a	Initial occupancy	Response	Model selection		Occupancy estimates	
					Null rejected	Correct response	Not underestimated	Within 85% CI
Spotted Owl	4	.75	0.5	3	0.878	0.600	0.769	0.040
		.90			0.622	0.108	0.859	0.038
Black-backed Woodpecker	12	.75	0.25	1	0.998	0.002	0.697	0.386
		.90			1.000	0.000	0.659	0.352

^aseasonal detection probability.

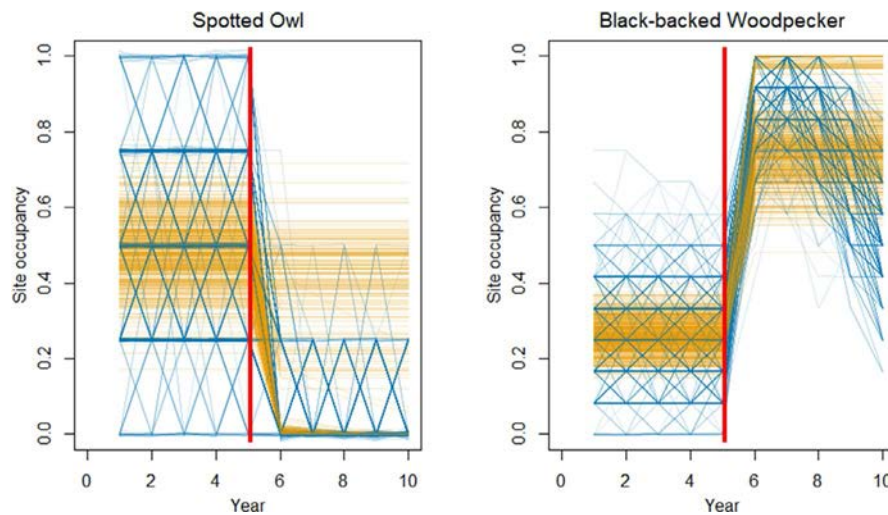


FIGURE 3 Simulated site occupancy (blue lines) of sites affected by 100 km² of severe fire occurring between years 5 and 6 (red line) in the Sierra Nevada acoustic monitoring programme and estimated occupancy (orange lines) derived from the most supported occupancy model in each of 500 iterations of the simulation. Spotted Owls populations (left) are assessed in 4 km² grid cells, which yields four affected sites, and have initial occupancy and seasonal detection probabilities of 0.5 and 0.9, respectively. Black-backed Woodpecker populations (right) are assessed at individual recording units, of which there are two or three in each grid cell, which yields 12 affected sites, and have estimated pre-fire occupancy and seasonal detection probabilities of 0.25 and 0.75, respectively. A slight vertical jitter was applied to the true occupancy (blue lines) values, which have a tessellated pattern because the scarcity of sites yielded relatively few possible occupancy values

(0.39) than when it was high (0.35). The monitoring programme was unable to identify the correct population response via model selection (i.e. the BACI-ephemeral dynamic occupancy model) (statistical power <0.08). Importantly, the occupancy and detection estimates reported in the literature were derived using species-specific vocal lure surveys, not passive acoustic surveys, so those values (particularly seasonal detection probability) could differ substantially under a different sampling approach.

4 | DISCUSSION

Biodiversity conservation in the face of the looming, but uncertain threat posed by megafires is complicated by species-specific responses to fire. Species of management concern may not be suitable umbrella species for their entire communities (e.g., Burnett &

Roberts, 2015), and sometimes large, severe fires may have opposing implications for focal species (e.g., the Spotted Owl and Black-backed Woodpecker [Jones et al., 2016; Tingley et al., 2018], or the Flame Robin compared to 12 other birds in south-eastern Australia [Lindenmayer et al., 2014]). Implementing holistic ecosystem management plans will require understanding varying and sometimes conflicting trade-offs, both among species and among objectives such as biodiversity conservation and ecosystem restoration (Wood & Jones, 2019). Forest management is further complicated by the temporal trade-offs managers may face in balancing the short-term costs of fuel reduction treatments to sensitive species against the desired long-term benefits (Wood et al., 2018). In short, understanding species' responses to megafires is a difficult but urgent task. These simulations suggest that in most cases landscape-scale monitoring programmes can provide high statistical power to determine whether wildlife populations have changed in response

to large patches of high-severity fire, an increasingly common attribute of megafires (Stevens et al., 2017), or other spatially extensive and relatively homogeneous disturbance. However, the results are likely to lack nuance: reliably identifying ephemeral responses and accurately estimating site occupancy may not be possible, especially with only five years of post-fire data as considered here (Banner et al., 2019).

The most important population attribute affecting statistical power was the species response to fire: more pronounced responses—positive or negative—to fire were more likely to be identified than a moderate, ephemeral negative response. Landscape-scale monitoring programmes may therefore be unsuitable for rapidly identifying subtle responses to fire, so the absence of evidence for such responses should only with caution be construed as evidence of absence. Identifying changes in local survival is more challenging when local survival varies among sites (Popescu et al., 2012), so control sites should be as ecologically and demographically similar to burn sites as possible—ideally, pre-fire habitat and site extinction/colonization in control and impact sites would be indistinguishable. In these simulations, using four times as many control sites as burned sites balanced swamping the effects of the fire with unaffected sites and having low precision because of small sample size (Popescu et al., 2012).

The number of affected sites was the most important determinant of statistical power from a study design perspective. While researchers cannot determine how much of their study area may burn at high severity (or be subject to some other spatially extensive disturbance), there are at least three ways to influence potential sample size, each of which entails trade-offs between resource availability and desired statistical power and are informed by the probability of a megafire occurring. First, increasing sampling density (e.g., from 15% to 25% of the landscape) will ensure that more area within any given disturbance is surveyed. Second, stratifying sampling to increase survey density in areas that are more likely to experience fire could lead to more affected sites, though this would complicate population trend assessments. Third, implementing a hierarchical design such that co-deployed detectors (e.g., ARUs or camera traps) jointly provide data about some species and yield independent data about others would yield higher sample sizes for the latter group of species. The paradoxical finding that lower seasonal detection probability led to higher power in several cases is likely driven by the fact that lower detection probability leads to lower precision and thus a greater chance of the 85% confidence intervals containing the true occupancy value.

The results of the Sierra Nevada case study suggest that the acoustic monitoring programme in that region will likely be adequate to provide rudimentary information on two prominent fire-affected birds, the Spotted Owl and Black-backed Woodpecker, five years post-fire. Whether a given megafire affected the population of either species is likely to be reliably measured (power to reject the null hypothesis = 0.622–1.00), but further details, such as ephemeral responses to post-fire conditions or even accurate site occupancy estimates, may not be attainable. It is therefore unlikely

that Sierra Nevada acoustic monitoring programme's current design will be capable of replicating the type of BACI experiments that a long-term mark-recapture study provided in the aftermath of the 2014 King Fire (Jones et al., 2016). However, landscape-scale studies are not designed to provide detailed fine-scale information. Data from the acoustic monitoring programme can support inferences that even networks of fine-scale mark-recapture studies cannot: landscape-scale insights arising from a randomized design (Wood et al., 2019).

The biggest strength of landscape-scale monitoring projects may lie not in their ability to detect the effects of one fire, but to measure the effects of many fires. If multiple megafires occur in a single season, affected monitoring sites from multiple fires could be pooled (within reasonable context-dependent limitations) to effectively increase sample size and move beyond a single-fire focus. Alternatively, comparing site occupancy to fire history for all sites in a monitoring programme could allow researchers to infer colonization rates based on the duration of post-fire vacancy, which, in turn, could be used to develop mechanistic understandings of focal species and even whole communities' responses to megafires (Wood et al., 2021). The proliferation of landscape-scale monitoring programmes, especially in the western United States, represents a further opportunity to increase sample sizes: if acoustic, camera or other data from multiple monitoring programmes can be pooled and analysed in a unified framework, regional-scale understandings of species' responses to fire and other disturbances may be attainable (Rich et al., 2019). Moreover, such an approach would be better able to reflect the nuanced responses to fire that many species exhibit—and which are minimized in simulations such as these. For example, pyrodiversity supports age-dependent Black-backed Woodpecker foraging (Stillman et al., 2019) and influences Spotted Owl foraging habitat selection (Jones et al., 2020), and increasing sample size by including many burned sites could support the inclusion of variables such as distance to unburned habitat and patch shape complexity.

Large patches of high-severity fire, as considered in these simulations, may result in substantial displacement of individuals of large-bodied and/or volant species, rather than outright mortality. A possible outcome of such movements, either by resident or migratory species, is increased population density adjacent to the fire. Acoustic surveys of small-bodied species may be capable of detecting these changes because the vocal activity rate—as opposed to detection/nondetection data, as considered in this simulation—can be used to estimate population density (Pérez-Granados et al., 2019). Within-site changes would be difficult to measure for territorial species whose home ranges are larger than the detection radius of the survey device, but visual or acoustic differentiation of individuals could facilitate such analyses (Wood et al., 2020).

In the context of identifying the effects of individual megafires, small-bodied species with relatively limited spatial requirements may be the optimal umbrella species, a reversal of conventional approaches in which large-bodied species are often treated as umbrella species because of their relatively vast spatial requirements.

For example, Hermit Warblers (*Setophaga occidentalis*) are strongly associated with Spotted Owl habitat in the Sierra Nevada (Burnett & Roberts, 2015) but are just ~2% the weight of Spotted Owls and are therefore likely to maintain much smaller territories (Haskell et al., 2002). Under the hierarchical design used in the existing Sierra Nevada acoustic monitoring programme, co-deployed ARUs 500–1660 m apart constituting a single Spotted Owl survey site could serve as independent Hermit Warbler sites (putatively independent point counts are as close as 250 m). This instantly doubles or triples the number of affected survey sites, thus increasing statistical power. To the extent that similar habitat requirements lead to similar responses to disturbance, the responses of smaller-bodied species to large, severe fires and other spatially extensive disturbances could be statistically powerful proxies for the lower-power estimates of larger-bodied species' responses. Of course, the validity of linking habitat associations and disturbance responses would need to be examined carefully.

Charismatic species with existing or potential legal protection are likely to continue to impel funding for landscape-scale monitoring efforts. Although prominent species such as the Spotted Owl may not represent the diverse ecological needs of entire communities (Burnett & Roberts, 2015; Latif et al., 2016; Lindenmayer et al., 2014), the monitoring programmes those species justify can still provide community-wide benefits if such programmes yield community-level data (Rodhouse et al., 2019; Wood et al., 2021). These simulations and other power analyses (e.g., Banner et al., 2019; Southwell et al., 2019; Steenweg et al., 2016; Wood et al., 2019) demonstrate that passive acoustic monitoring and other non-invasive sampling techniques can support research on multiple species' populations a unified framework. By helping to justify such programmes, charismatic habitat specialists such as the Spotted Owl may indirectly provide ecosystem-wide conservation benefits and thus provide a far broader protective umbrella than ever before.

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DATA AVAILABILITY STATEMENT

The R code used for these simulations is available in html and pdf formats as an RMarkdown tutorial at <https://doi.org/10.5281/zenodo.4741174>.

ORCID

Connor M. Wood  <https://orcid.org/0000-0002-0235-5214>

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BIOSKETCH

Connor M. Wood is an Edward Rose Postdoctoral Fellow at the Cornell Lab of Ornithology's Center for Conservation Bioacoustics, where his research focuses on conservation biology, community ecology and developing tools for landscape-scale monitoring programmes. Website: connormwood.com.

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