

Recent California Spotted Owl Foraging Studies

Blakey, R.V., R.B. Siegel, E.B. Webb, C.P. Dillingham, R.L. Bauer, M. Johnson, and D.C. Kesler. 2019. Space use, forays, and habitat selection by California spotted owls (*Strix occidentalis occidentalis*) during the breeding season: New insights from high resolution GPS tracking.

Sample Size and Methods: Tracked 8 female and 7 male spotted owls with GPS in 2015-2017 on the Mount Hough Ranger District of the Plumas National Forest.

Results: Owls selected for >70% canopy cover in areas dominated by medium and large trees for foraging and against low and very low canopy cover dominated by small trees or open areas. There was low overlap between PACs and roost locations (<50%) and foraging space (<25%), including <5% foraging and roost locations being contained within the PAC for some owls.

Notes: Good quote from discussion (p. 920) “Based on the relatively low overlap between PAC areas and roosting and foraging habitat use by the owls we studied, we hypothesize that insufficient habitat protection from stand-altering activities outside PAC areas could partially explain ongoing population declines. Most of the habitat used by owls for roosting and foraging in our study was outside of PACs and therefore available for stand-altering forestry activities. Even where PACs protect nesting stand conditions conducive to successful reproduction, stand-altering activities elsewhere in owl home ranges may reduce occupancy or reproductive success.”

Bond, M.L., D.E. Lee, R.B. Siegel, J.P. Ward. 2009. Habitat use and selection by California spotted owls in a postfire landscape. Journal of Wildlife Management DOI: 10.2193/2008-248.

Sample Size and Methods: Greenhorn Mountains and Kern Plateau. Sequoia National Forest. 2002 McNally Fire footprint. Radio telemetry of foraging habitat selection for 3 male and 4 female CSO from 4 territories during the 2006 breeding season.

Results: The vast majority of roosts were in unburned and low severity patches, but 15% of the roosts did occur in moderate and one roost may have been in high severity. “Probability that any of these 7 owls would use a site for foraging was greatest when the site was burned and was located within approximately 1 km of a nest or roost center (Fig. 1). For 5 of 7 owls, strongest selection for foraging areas was in high-severity burned forest within 1.5 km from the center of their foraging ranges. Although selection of burned forest for foraging was strong, high standard errors indicate selection was variable among owls.”

Notes: Based on maps provided by Monica, salvage did occur in the area, especially near the center of one of the territories. From an eyeball analysis, several birds appear to be foraging along the perimeters of salvaged areas.

Statistical analysis used a sample size of 7, but there are potential issues with pseudo replication, since spotted owls are central place foragers, the 3 males shared territories with the females and CSO do not forage independently.

Eyes, S.A., S.L. Roberts, and M.D. Johnson. 2017. California spotted owl (*Strix occidentalis occidentalis*) habitat use patterns in a burned landscape. The Condor DOI: 10.1650/CONDOR-16-184.1

Sample Size and Methods: Used radio telemetry to study foraging locations of 13 spotted owls with territories that overlapped burned areas in Yosemite National Park.

Results: The average area that was unburned or unchanged in all spotted owl home ranges was 53 percent, while 25 percent burned at low, 16 percent at moderate, and 4 percent at high severity. The proportion of the home range in each fire severity category declined with increasing severity, and the average size of patches used more than once by owls varied depending on fire severity, with the largest used patches burned at low to moderate severities." "The odds of owls using the high contrast edge type were 2.78 times greater than odds for the low contrast edge type and 3.5 times greater than for the no edge type."

"In our study area, nearly 75% of most owl home ranges burned in one or more fires that occurred between 1997 and 2009."

"Home range size ranged from 65 ha to 1,136 ha for male owls and 90 ha to 2,983 ha for female owls, averaging 302 ha (95% CI: 119–787 ha) and 451 ha (95% CI: 175–1,293 ha), respectively. There was no statistically significant difference in log-transformed home range size between males and females."

"Overall, the proportion of the home range in each fire severity category declined with increasing severity, and the average size of patches used more than once by owls varied depending on fire severity, with the largest used patches burned at low to moderate severities."

"Although not a focus of our analysis, it appears that owls used small patches burned at high severity, but used a much larger size range of patches burned at low and moderate severity, which implies that owls may have more flexibility in the latter burned patch types (Table 1). Further, it appears that burned patches used more than once by owls may be larger than the average available burned patch size (Table 1), suggesting that patch size could influence selection of burned habitat and warrants future investigation."

"Our study joins several others that have documented that distance to the roost or nest is important for foraging habitat selection by Spotted Owls (Glenn et al. 2004, Irwin
FIGURE 3. Modeled relative probability of California Spotted Owl habitat use as a function of distance to roost and edge type in Yosemite National Park, California, USA, 2010–2012.

et al. 2007, 2012, Wiens 2012, Bond et al. 2016). Spotted Owls have high site fidelity to nest sites and tend to roost near the eventual nest site, which is typically used for many years (Forsman et al. 1984). Furthermore, Spotted Owls are central-place foragers and often remain near the nest site in the nonbreeding season, so nest and roost locations may play a significant role in owl foraging habitat selection throughout the year (Forsman et al. 1984, Carey and Peeler 1995). Rosenberg and McKelvey (1999) argued that not including distance to the nest or roost in habitat selection models might bias selection for habitat characteristics near the central place, perhaps resulting in a false suggestion that it is the habitat type that the owls are selecting rather than merely its adjacency to the nest."

From Table 1

Unburned patch sizes were not measured because it was comprised on contiguous forest.

Patches unchanged by fire used by owls averaged 11 acres (+/-44)

Patches burned at low severity used by owls averaged 246 acres (+/-966 acres)

Patches burned at moderate severity used by owls averaged 138.8 acres (+/-392)

Patches burned at high severity used by owls average 16 acres (+/- 26 acres)

Notes: Not included in the analysis, large portions of the study area had burned in other wildfires within the past 30 years. In effect, the results are of an area that has repeatedly burned.

Gallagher, C.V., J.J. Keane, P.A. Shaklee, H. Anu Kramer, and R. Gerrard. 2019. Spotted owl foraging patterns following fuels treatments, Sierra Nevada, California. *Journal of Wildlife Management* 83(2):487-501. DOI: 10.1002/jwmg.21586.

Sample Size and Methods: Used GPS and LiDAR to study 10 spotted owls (6 females, 4 males) in the Meadow Valley project area on the Plumas National Forest from 2007 to 2008.

Results: "The top model for owl foraging locations in a post-treatment landscape included negative correlations with mechanical thin, high (>70%) canopy cover in the 32-m height strata, proportion of gaps, and distance to the owl's site center, and a marginally positive correlation with slope." "Owl foraging locations contained greater proportions of high (>70%) overall canopy cover than random locations." "probability of use for owl foraging was negatively related to the proportion of gaps (canopy height <2 m) in the ellipse, and edge was not a component in competitive models."

Notes: Gaps were defined as any area >2-m x 2-m (~36 ft²) with maximum canopy height <2 meters. Such a small gap size may not be biologically meaningful and the high number of small gaps may swamp the ability to detect selection of larger gaps.

Hobart, B.K., Kramer, H.A., Jones, G.M., Dotters, B.P., Whitmore, S.A., Keane, J.J. and Peery, M.Z. 2021. Stable isotopes reveal unexpected relationships between fire history and the diet of Spotted Owls. *Ibis* 163(1):253-259.

Sample Size and Methods: YNP, SEKI NPs- 2-year diet study with 41 owls in 31 territories, used pellets and feather isotope analyses; fire history examined in 5, 10, 20 and 33- year increments.

Results: Wildfire history is positively correlated with proportional flying squirrel consumption. Woodrats and gophers were dominant prey in study overall, but as owl territories experienced more wildfire, the proportion of woodrats and gophers in owl diets decreased. This is an unexpected result.

Notes: Several mechanisms for an increase in flying squirrel consumption following wildfire are discussed including greater availability of flying squirrel food (hypogeous fungi), a reduction in woodrat and gopher hiding and nesting habitats, and influx of flying squirrels from adjacent severely burnt forest. CSO with flying squirrel diets are associated with fire suppression regimes, decreased fitness and decreased demographic benefits in other studies on USFS lands. Authors wonder if fire heterogeneity in this study may increase biomass of prey overall, thus increasing fitness. Fire history on NPS lands is closer to NRV than USFS lands.

Irwin, L.L., D.F. Rock, S.C. Rock, C. Loehle and P. Van Deusen. 2015. Forest ecosystem restoration: initial response of spotted owls to partial harvesting. *Forest Ecology and Management* 354:232-242.

Sample Size and Methods: Used radio telemetry to study foraging habitat selection of 16 northern and 3 California spotted owls 2 years before and 2 years after logging (primarily seed-tree and shelterwood harvest methods) on 5 study sites in the Klamath in western Oregon and California and the southern Cascades in Oregon and California. Study sites were a mixture of federal, private, and state lands, with the only California spotted owl study site having been composed almost entirely of private timberlands.

Results: Radio-tagged owls selected against stands scheduled for harvest and selected recently harvested stands in proportion to availability. Nearly 50% of the harvested units were not found to be used before or after harvest. They also found weak evidence for a positive effect of retained basal area of trees over 26 inches dbh and strong evidence for a quadratic effect of basal area of mid-story conifers. The authors did not observe site abandonment during the study.

Notes: The authors did not include any variables associated with the forest structure of stands scheduled for treatment in their models.

Jones, G.M., Stanley, C.K., Peery, M.Z., Maxwell, C. and Wilson, K.N., 2024. Accelerated forest restoration may benefit spotted owls through landscape complementation. *Animal Conservation*.

https://nwfirescience.org/sites/default/files/publications/rmrs_2024_jones_g002.pdf

Sample Size and Methods: Landscape complementation was defined as the presence of multiple, spatially segregated cover types to satisfy an animals ecological needs. Models for the Tahoe-Central Sierra Initiative (TCSI) simulated CSO nesting /roosting habitat (definition included CWHR 5P, which is not considered CSO habitat by most researchers), foraging habitat and co-occurrence (landscape complementation) through midcentury as a function of fuel reduction, fire and climate change. The two management scenarios were 1) minimal management: WUI and private lands treatments only, 2) accelerated management: TZ, DZ, private, roadless and general forest treatments. Vegetation classification used CWHR forest types. Targets for ideal territory management were based on Jones 2018¹ ie. territory extinction rates decline substantially when about 20% of territory contains large old trees (p.5).

**Jones et al. 2018 showed that CSO territory extinction rates were 4 times lower in SKC than in ENF, LNF and SIE and that these SKC territories were also characterized by 33% of territory in large trees (QMD>24 inches) and 19% in high canopy (>70%) and large trees.

There are many assumptions in the models discussed in Notes section, below.

Results: Accelerated management treatment model increased area treated and decreased area burned, but only under 5,000 feet elevation and only under some climate scenarios. Models showed no difference between two management intensities on the area (amount) of CSO habitat (including 5P) remaining until at least 2040. The models did not show a difference between accelerated vs. minimal management scenarios influence on area (amount) of high severity fire and instead showed “prediction uncertainty”.

Notes: (from D not authors) 5P included in model of CSO nesting/roosting habitat despite lack of evidence that owls use this forest type (Table 3 p.5). Assumes that CSO foraging habitat is synonymous with woodrat habitat and CSO foraging habitat includes open habitat as well as brushy, however other research doesn't support this (ie. Kuntze 2023: CSO don't forage in open habitat, just young forest). Spatial juxtaposition concept is applied to species where thermal refugia is important ie. manatees, lizards and frogs. With CSO it is tricky and shouldn't lead to habitat fragmentation or loss.

¹ Jones et al. 2018 showed that CSO territory extinction rates were 4 times lower in a National Park (SKC) than in National Forests (ENF, LNF and SIE) and that these SKC territories were also characterized by 33% of territory in large trees (QMD>24 inches) and 19% in high canopy (>70%) and large trees.

Jones, G.M. and Tingley, M.W. 2021. Pyrodiversity and biodiversity: a history, synthesis, and outlook. Diversity and Distributions March 2021.

Sample Size and Methods: Literature review of pyrodiversity and biodiversity: 33 studies with discussion of CSO and BBWP.

Results: A total of 18 (44%) studies presented evidence that pyrodiversity increases biodiversity, 23 studies (56%) did not find a relationship. Influencing factors were mechanism (investigating 1 fire vs. fire history across landscape), evolutionary history (ie. tropical temperate or boreal forests) and scale (geographic and temporal). CSO were expected to avoid pyrodiversity because of their association with old forest, but CSO were instead found to forage in severe fire if patches were small relative to their territory (Jones et al. 2020 and Kramer et al. 2021). Surprisingly, these two studies describe opposite CSO responses to pyrodiversity.

"Relative importance of pyrodiversity in creating owl foraging habitat may depend on the existing degree of surrounding landscape heterogeneity in forest structure." (p.10).

BBWP were also expected to avoid pyrodiversity because of their affinity to recent severely burned forest; yet, BBWP were not found in several recent megafires as expected. Rather they nested in areas with higher heterogeneity in burn severity perhaps because, as other studies have shown, juvenile survival is low (due to predation) in large high severity burns without nearby cover in green forest.

Notes: Authors identify six research gaps and suggest forest pyrodiversity brings a "boon of resources" adjacent to areas with more protection and cover, thus facilitating patch diversity and intermediate disturbance regimes that are hypothesized to support greater biodiversity.

Kramer, A., Jones, G.M., Whitmore, S.A., Keane, J.J., Atuo, F.A., Dotters, B.P., Sawyer, S.C., Stock, S.L., Gutiérrez, R.J. and Peery, M.Z. 2021a. California spotted owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes. Forest Ecology and Management (479):118576.

Sample Size and Methods: YNP (13 owls), SEKI NPs (9 owls), foraging habitat selection of 22 GPS tagged spotted owls (18 male, 4 female) during 2018 breeding season. Recent fires occurred 2002-2017.

Results: Spotted owls avoided foraging in larger patches of severely burned forest. Median size of severe fire burn in this study was relatively small at 18 ha. Largest severe fire patch was 225 ha. (in comparison King Fire severe burn patches were sometimes 8,000 ha). Nevertheless, odds of CSO selection for severe fire decreased by 20% with every 10 ha increase in severe fire patch size. Maximum permeation distance into severe fire patches was 169 m. Selection for lower-severity recent fires increased as this type of burned area became more abundant within home ranges (indicating a functional response to habitat availability); although owls showed neutral

selection for lower severity burns overall without considering availability of this habitat in individual home ranges. Owls showed weakly negative selection against pyrodiversity as they slightly select against areas that were only composed of low severity or unburned areas. This result is the opposite of the King Fire and Jones et al. (2020) who found a stronger selection against pyrodiversity was explained by an avoidance of large areas of severe fire. Owls showed no preference for areas that burned between 1953-2002. Owls selected for forests dominated by large and medium trees (>40% cc and QMD >25 cm) and avoided areas with small trees (<40% cc and QMD <25 cm).

Notes: Authors conclude that owls are resilient and likely adapted to a patchwork of fire effects that characterize frequent-fire regimes on NPS lands (primarily low- and moderate-severity intermixed with small-high severity patches). These three National Parks have been managed for use-fire for approximately the past 50 years and are closer to NRV compared to USFS lands managed with fire-suppression.

Kramer, H.A., Jones, G.M., Kane, V.R., Bartl-Geller, B., Kane, J.T., Whitmore, S.A., Berigan, W.J., Dotters, B.P., Roberts, K.N., Sawyer, S.C. and Keane, J.J. 2021b. Elevational gradients strongly mediate habitat selection patterns in a nocturnal predator. *Ecosphere* 12(5):e03500.

Sample Size and Methods: TNF and interspersed private lands, foraging study with 16-18 GPS tagged CSO at between 500 m to 1800 m elevation. LiDAR-derived tree metrics taken with deciduous leaves still on trees was later corrected for.

Results: Owls at lower elevations were more likely to forage in areas with 10% more short stand area (young trees, LiDAR tallest trees 2 to 20 m). Owls at lower elevations selected for homogeneous stands with shorter trees, near ridges, and southwest aspect. Owls at higher elevation were more likely to select interior areas of forest stands with medium and tall trees (older trees, LiDAR tallest trees 20 to >32m). Owls at higher elevation selected stands with higher seral stage diversity overall, further away from hard edges, with less ridge and less southwest aspect.

Notes: Differences in foraging habitat selection were strongly associated with elevation and likely correspond to CSO prey availability. Flying squirrels occur in higher elevation closed canopy forests, and woodrats in lower elevation forests with masting black oak.

Kuntze, C.C., Pauli, J.N., Zulla, C.J., Keane, J.J., Roberts, K.N., Dotters, B.P., Sawyer, S.C. and Peery, M.Z., 2023. Landscape heterogeneity provides co-benefits to predator and

prey. *Ecological Applications*, 33(8), p.e2908.

<https://esajournals.onlinelibrary.wiley.com/doi/10.1002/eap.2908>

Sample Size and Methods: Woodrat abundance and survival in different forest cover types was measured by mark-recapture trapping; woodrats were radio collared to measure individual survival and cause of mortality; video cameras at California spotted owl nests recorded prey type and quantity. Woodrat trapping took place between 3,200 to 4,921 feet elevation, while EDSA encompasses 1,200-7,404 feet elevation.

Forest cover was categorized into three types: 1) mature forest >40% canopy cover of dominant trees >12" dbh; 2) young forest >40% canopy cover of saplings or dominant trees <12 inches dbh; 3) open habitat <40% canopy cover. A total of 28 CSO home ranges on Eldorado NF were divided into two categories 1) heterogeneous (averaged 78% mature, 10% young, 11% open) and 2) homogeneous (averaged 58% mature, 28% young, 12% open). Prey biomass was estimated using pellets collected during previous sample years in the Eldorado demography study area (EDSA).

Results: Spotted owl predation occurred exclusively in mature forest types (CSO are not foraging in young forest or open habitat; young forests may serve as a refuge and/or source for woodrat). CSO prey delivery frequency for flying squirrels and for all prey besides woodrat were the same between heterogeneous and homogenous territories. CSO consumed 2.5 times greater woodrat biomass in territories categorized as heterogeneous at the landscape scale. Owls in homogeneous territories consumed greater biomass of other prey species such as flying squirrel, nevertheless overall biomass of prey was 30% higher in heterogeneous territories because woodrat (big chunky animal) was primary prey item. The additional prey biomass delivered in heterogeneous territories was estimated by authors to be enough to raise three young compared to two young in homogenous territories (Fig.5, p.13). Predation events were only observed in mature forest (p.12) so the balance of evidence indicates that young forests, to a degree, act as woodrat refuges from spotted owl predation. The vegetation configuration results (heterogeneous vs. homogeneous vegetation) are only applicable in parts of CSO range where woodrat is a primary prey species (p.13).

Authors are stretching the differences between territories categorized as heterogeneous and homogeneous forest cover a little. First, woodrat consumption rates in territories with heterogeneous forest cover were somewhat greater than homogeneous territories (Fig.4 p.9-10) *however this trend was only significant at the 0.1 but not 0.05 level*. Second, average woodrat density did not differ between heterogeneous and homogenous territories in the

mark-recapture study (Fig.3 p.8) as confidence intervals overlapped considerably between the two forest cover categories.

Almost 1/3 of all prey deliveries were flying squirrel and 1/3 were woodrats (a total of 93 woodrats, 90 flying squirrels, 63 unidentified, 30 mice, 4 voles, 2 gophers, 2 moles, 1 bird, 1 bat). Authors found no effect of landscape forest composition on delivery frequency of flying squirrels or all alternative (non-woodrat, non-flying squirrel) prey combined (p.11). Radio collared woodrat mortality was recorded in 12 woodrats: 3 avian predation, 3 mammalian predation, 6 non-predation events.

Notes:

Authors point out sample size was low for a woodrat abundance study (this explains why the confidence intervals were so large). Wondering if this study is at the correct scale, i.e. is owl hunting success influenced by forest type at the landscape scale or smaller vegetation patch sizes? A total of 26 large-bodied prey items were not identified by the nest cameras. Response variables in “old growth” forest not examined independently of mature forest type, therefore impact of forest age and structural complexity on owl prey densities, hunting success and survival were not included in this study. Incredibly biased statement: *“reduction in mature forest spotted owl habitat in heterogeneous landscapes did not come at a cost to, but rather benefited, spotted owl prey acquisition.”*

Lee, D.E., 2020. Spotted owls and forest fire: Reply. Ecosphere 11(12):e03310.

Sample Size and Methods: Reply to critique of Lee et al. 2018 meta-analysis of fire effects on spotted owl in Jones et al. 2020.

Results: Lee re-analyzed part of his 2018 meta-analysis in response to critiques from Jones et al. 2020 including: 1) statistical threshold for significance ($p=0.05$ vs. $p<0.05$), 2) post-fire logging compounding severe fire effects, 3) data duplication, and 4) separation of results by subspecies (CSO vs. MSO). His second analysis per these suggestions did not lead to different results than Lee et al. 2018. Both Lee et al. 2018 and Jones et al. 2020 agree spotted owl responses to recent mixed severity fires are variable and that severe fire can pose negative consequences for CSO; There is disagreement between these authors about how to characterize recent megafires and magnitude of consequences megafires pose for CSO populations.

Notes:

Lee suggests that land managers emphasize fire management in human communities rather than owl communities because of limited resources for fuel reduction treatments.

Reid, D.S., Wood, C.M., Whitmore, S.A., Berigan, W.J., Keane, J.J., Sawyer, S.C., Shaklee, P.A., Kramer, H.A., Kelly, K.G., Reiss, A. and Kryshak, N. 2021. Noisy neighbors and reticent

residents: Distinguishing resident from non-resident individuals to improve passive acoustic monitoring. *Global Ecology and Conservation* (28):e01710.

Sample Size and Methods: Testing spotted owl acoustic monitoring programs in the Lassen demographic study area where occupancy is well known. Comparing passive acoustic monitoring (PAM) during 2018-2019 and GPS-tagged/acoustic monitoring from 2019-2020 with known results from the mark-recapture demographic study. Acoustic/GPS monitoring collected acoustic and location data from 17 owls for < one week. PAM arrays recorded sounds for four months.

Results: PAM was effective in detecting all known resident owls, and the array was able to avoid double counting the same owls; yet, false positive error rates were high (false positive error rate of 0.39). PAM over estimated the number of resident owls, whereas active nighttime CSO surveys identified floater individuals at six sites during that same time period. This suggests the overestimate by PAM was not from double counting but from the inability to distinguish between resident and floaters. An experienced CSO survey crew could make this distinction.

Notes: Adjusting diurnal and seasonal timing of PAM may help with false positive errors.

Steel, Z.L., Jones, G.M., Collins, B.M., Green, R., Koltunov, A., Purcell, K.L., Sawyer, S.C., Slaton, M.R., Stephens, S.L., Stine, P. and Thompson, C., 2023. Mega-disturbances cause rapid decline of mature conifer forest habitat in California. *Ecological Applications*, 33(2), p.e2763. <https://nature.berkeley.edu/stephenslab/wp-content/uploads/2024/07/Steel-et-al-Mega%E2%80%90disturbances-Eco-Apps-121-22.pdf>

Sample Size and Methods: Conifer forest cover and density from F³ data (using FIA plots and other data from 2011) for the southern Sierra Nevada (including ENF to SQF + private lands) between 2011-2020. Non-forest cover is defined as conifer canopy cover < 25%. Moderate density forest was defined as 40-60% conifer cover, and high density forest was 60-100% conifer canopy cover of trees that were 90' or taller.

Results: Between 2011-2020, canopy cover across 30% of conifer forests were converted to non-forest (ie. 40% canopy or better going to below 25% canopy cover resulting in either sparse woodland/savanna or in many cases a transition to nontree-dominated vegetation). Canopy cover across 50% of moderate or high density mature forest also declined below 40% canopy cover, constituting a decline to a lower density forest. Moderate density forests experienced little canopy cover decline during this decade. Within the mature forest classification, higher density areas experienced more extensive declines with 85% of this forest class falling below 60% canopy cover. Canopy cover decline in CSO PACs was greater than non-PAC areas (49% vs. 42%). Tree mortality from drought contributed the greatest (51%) total area of conifer forest transition to non-forest. Wildfires were attributed to 45% of the area converted to non-forest,

and mechanical treatments contributed to 4%. Cumulatively, 'drought + beetle' was worse (produced a greater area of mortality) than 'drought + fire' in converting conifer forest to non-forest. The moderate and dense mature forest classes were also affected by these disturbances in the same way, with 85% of dense mature habitat declining in a decade either by transitioning to lower density forest or through complete conversion to non-forest.

Notes: Authors emphasize that all 3 natural disturbances caused greater canopy cover decline than mechanical treatments. Authors also note that the forests that survive these natural disturbances represent "...*opportunity for improved resilience to future disturbances...*" Wouldn't expected canopy cover decline be greater in PACs b/c it's greater in those areas to begin with? Interestingly: "*Oaks, especially California black oaks, are relatively resilient to both wildfire and drought, and are utilized by species such as the spotted owl and fisher (Aubry et al. 2013; Green et al. 2019; North et al. 2000).*" Authors urge managers to use North 2011 and not to eliminate protected reserves, but rather to employ managed fire as 'pyrosilviculture'.

Wilkinson, Z.A., Kramer, H.A., Jones, G.M., Zulla, C.J., McGinn, K., Barry, J.M., Sawyer, S.C., Tanner, R., Gutiérrez, R.J., Keane, J.J. and Peery, M.Z., 2023. Tall, heterogeneous forests improve prey capture, delivery to nestlings, and reproductive success for Spotted Owls in southern California. *Ornithological Applications*, 125(1), p.duac048.

Sample Size and Methods: San Bernadino and San Jacinto Mountains, southern California. 10 breeding male owls tagged with GPS and nest-site video monitoring to document location of prey capture and type of prey delivered to nest. Study took place over 8.9 nights. Elevation 2,600-8,500 feet. Vegetation was divided into 3 different classes using California Forest Observatory and LiDAR data from 2020: 1) short forests (canopy height <10 m), 2) tall forest sparse canopy (canopy height >10m canopy cover <70%), and 3) tall forest dense canopy (canopy height >10m canopy cover >70%).

The 2 edge classifications include: 1) primary edge boundary between chaparral and forest type (conifer or hardwood), 2) secondary edge boundary between vegetation types and short or tall vegetation in the same or different type. Heterogeneity was categorized as 1) coarse heterogeneity (proportion of 3 vegetation classes compared to 'other' vegetation class) or 2) fine heterogeneity measured using proportion of the same 3 vegetation classes compared between conifer vs. hardwood forests. Home ranges were delineated with the circle averaging 776 acres. Reproductive success of CSO pairs was determined during a different time period between 2006-2020 using data from Tempel 2022.

Results: 35% of prey were woodrats, 24% were deer mice, 22% were unidentified, 12% were gophers, and 3% were flying squirrels. There was a considerable degree of model uncertainty for all prey and woodrat capture rates as a function of vegetation, nevertheless these models suggest that owls captured more prey with higher canopy height, more canopy layers and

greater fine heterogeneity. And, owls captured more woodrats in areas with higher canopy height, more canopy layers and greater coarse heterogeneity. (Primary edge also fit with both models, however this was due to a single male). 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. Results consistent with Zulla 2022: CSO tend to capture prey particularly woodrat in areas with more large trees, heterogeneity and edge.

CSO reproductive success was unrelated to number of prey captures but authors nevertheless suggest that reproductive success is higher in areas with greater heterogeneity because of presumed increased prey acquisition.

“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 (Temple et al. 2015). Rather, fire and vegetation management that creates a mosaic of fuel and vegetation condition, including juxtaposed areas of higher resistance (eg. taller forests with minimal ladder fuels) and potential lower resistance (eg. areas of more shrub cover both independent of and under overstory trees) is more likely to improve owl fitness...we suspect that many smaller patches [of chaparral or shrubby vegetation] may benefit owls by providing more edge habitat with a lower risk of large severe fire that is associated with large, dense stands of chaparral...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).” (p.10)

Notes: This study (in D’s opinion) is evidence that CSO reproductive success must balance nesting and foraging habitat needs, and that simply managing for woodrat habitat is insufficient for CSO persistence, despite Jones 2024 claims. This study actually measured CSO reproductive success rather than postulate from woodrat biomass density like Jones 2024. This system was mostly woodrats, hardly any flying squirrels. Authors cite Smith et al. (1999) that woodrat comprise 75% of CSO diet by biomass (I think this actually varies quite a bit by elevation and site).

Williams, P.J., R.J. Gutiérrez, and S.A. Whitmore. 2011. Home range and habitat selection of spotted owls in the central Sierra Nevada. Journal of Wildlife Management 75:333-343.

Sample Size and Methods: Used radio telemetry to study foraging in 14 spotted owl territories in the Eldorado Study Area in the central Sierra Nevada in 2006.

Results: Home-range size variation was most correlated with the number of patches of distinct vegetation classes within home ranges (i.e., habitat heterogeneity), with home-range size

increasing as heterogeneity increased. Although owls selected mature forests with medium and high canopy cover most often relative to their availability, there was sparse distribution of large stands of mature forests outside of PACs.

Notes: None of the pairs successfully reproduced during the study, so it cannot be suggested that such foraging selection represents high quality foraging habitat.

Williams, P.J., S.A. Whitmore, and R.J. Gutierrez. 2014. Use of private lands for foraging by California spotted owls in the central Sierra Nevada. Wildlife Society Bulletin 38:705-709.

Sample Size and Methods: Primarily industrial private timber lands, for foraging by 14 radio marked spotted owls in the central Sierra Nevada in 2006.

Results: Spotted owls were more likely to select public land than private land for foraging.

Notes: The authors conclude that privately owned land is not equivalent to publicly owned land as a contributor to spotted owl conservation in the central Sierra Nevada.

Wood, C.M., Zulla, C., Whitmore, S., Reid, D., Kramer, H.A., Keane, J.J., Sawyer, S.C., Roberts, K.N., Dotters, B.P., Klinck, H. and Berigan, W. 2021a. Illuminating the nocturnal habits of owls with emerging tagging technologies. Wildlife Society Bulletin 45(1):138-143.

Sample Size and Methods: Central Sierra CSO diet study: 5 nesting CSO males with tail feather GPS tags for 4-12 days and infrared cameras focused on their nests. Acoustic study: 8 CSO with tail feather GPS tags for 3-5 days.

Results: CSO consumed 21 woodrats, 10 flying squirrels, 2 voles, 2 mice and 1 gopher. Non-nesting owls, especially males, produced more territorial vocalizations and were more likely to give calls throughout their home range. Nesting spotted owls produced mostly non-territorial contact calls from their nest areas.

Notes: Further study should investigate influence of habitat type on prey capture success.

Zulla, C.J., Kramer, H.A., Jones, G.M., Keane, J.J., Roberts, K.N., Dotters, B.P., Sawyer, S.C., Whitmore, S.A., Berigan, W.J., Kelly, K.G. and Wray, A.K., 2022. Large trees and forest heterogeneity facilitate prey capture by California Spotted Owls. *Ornithological Applications*, 124(3), p.duac024.

https://drive.google.com/file/d/1WmXkKETObExhgg61_koMiFUHcesHMIZL/view

Sample Size and Methods: CSO were monitored in 2019-2020 using GPS tracking and nest video to assess forest cover type influence on CSO prey capture rates and locations during the nestling provisioning stage at territory scale. Located at the Eldorado demography study area

(EDSA) on the ENF and the Stirling study area (SSA) on SPI land in the Sierra Nevada. Same study as Kuntze et al. 2023 except now authors examine prey capture success in relation to habitat type at much smaller scale. Vegetation classes included hardwoods, shrubs, young forest (6-11 inches dbh), medium trees/medium canopy cover (11-23.5 inches dbh trees with 30-69% canopy cover), medium trees/high canopy cover (11-23.5 inches dbh trees with >70% canopy cover), large trees/medium canopy cover (>24" dbh with 30-69% canopy cover) and large trees/high canopy cover (>24 inches dbh with >70% canopy cover).

Results: CSO all prey capture rates are highest in 5D and 5M at the territory scale. Woodrat capture rates were greatest in heterogeneous forest, 4M, edge, young forest at lower elevations near open or young forest. With each 10% increase in medium trees/medium canopy cover forest, the odds of prey capture increased by a factor of 1.20. The odds of prey capture increased by a factor of 1.3 and 1.16 with each 10% increase in large trees/medium canopy cover forest respectively. Successful hunting particularly for woodrats tends to occur in a broad range of conditions including in areas with more young forest and higher heterogeneity. Authors suggest promoting large trees, heterogeneity at the territory scale, gaps in canopy cover in 4D because it has less woodrats. Oaks weren't associated with more woodrats, just edge between conifer and hardwood. Prey included 43 dusky-footed woodrat, 29 flying squirrels, 11 mice, 3 voles, 2 moles and 2 gophers. Authors conclude different prey species achieve high densities in different habitat types.

Zulla, C.J., Jones, G.M., Kramer, H.A., Keane, J.J., Roberts, K.N., Dotters, B.P., Sawyer, S.C., Whitmore, S.A., Berigan, W.J., Kelly, K.G. and Gutiérrez, R.J., 2023. Forest heterogeneity outweighs movement costs by enhancing hunting success and reproductive output in California spotted owls. *Landscape Ecology*, 38(10), pp.2655-2673.

Sample Size and Methods: Eldorado demography study area and Sterling study sites in Central Sierra Nevada; 31 breeding male CSO GPS-tagged in 2019-2020; 15 of these males' nests were monitored using infrared video cameras. Home range estimated using 95% kernel density estimators for 2-15 nights during the nest provisioning stage between 2013-2020. Timber harvest and wildfire affected these territories but always <1% of home range. Forest cover was categorized into four types: 1) mature forest: QMD >23.6 inches, >40% canopy cover; 2) medium aged forest: QMD 11.8-23.6 inches, >40% canopy cover; 3) young forest: QMD <11.8 inches, <40% canopy cover; 3) open forest: <40% canopy cover. Reproductive data was from 151 owls on EDSA and SPI sites between 2013-2020. Reproductive success was related to forest cover data used in the first study, but there was no GPS-tagged data for this set of owls so vegetation data was examined across territories delineated 1.12km nearest neighbor distance.

Results: Prey was comprised of 41.5% woodrat and 40% flying squirrel, remaining 18% was unidentified, mice, etc. Breeding CSO travel twice as far as nonbreeding CSO. Prevalence of medium-aged forest reduced CSO nocturnal movements; edges between older and younger

forests increased rates of biomass delivered to nests (once an outlier was removed from data set). Reproductive output was highest for territories that contained both mature and open forest combined, but was lower for either one by itself.

Notes: Authors say results only apply in SN at low and mid-elevation in brushy and young forests where woodrat density is highest. Fire created heterogeneity in 47/151 CSO territories monitored for reproductive output. Authors note medium aged forests may help reduce energy expenditures during nocturnal activities that include foraging, but a mixture of forest types provide the greatest benefit to prey acquisition and fitness. Territories with more medium aged forests have potential to increase commuting distances to habitat where woodrats are more dense (open, younger forests). Authors caution that even though heterogeneity was beneficial for owls within territories, the open areas must have brush and young forest rather than being devoid of vegetation (ie. clear cuts). Habitat fragmentation may negatively impact NSO more than CSO because of prevalence of flying squirrels (hmm, but this isn't true in Marin County and possibly other areas, lots of NSO living off woodrat!!).

BARRED OWL RESEARCH IN SIERRA NEVADA

Hofstadter, D.F., Kryshak, N.F., Wood, C.M., Dotters, B.P., Roberts, K.N., Kelly, K.G., Keane, J.J., Sawyer, S.C., Shaklee, P.A., Kramer, H.A. and R. J. Gutiérrez. 2022. Arresting the spread of invasive species in continental systems. *Frontiers in Ecology and the Environment*

<https://doi.org/10.1002/fee.2458>

Sample Size and Methods: From 2018 to 2020, 76 owls were removed (63 BAOW and 13 hybrids). Most of these removals (69) occurred in the northern Sierra Nevada, 10 in central Sierra and one in southern Sierra.

267 PAM sites [regional multispecies passive acoustic monitoring program (PAM) using autonomous recording units (ARUs)] in Northern Sierra Nevada were surveyed 1-year pre- and 1-year post-removal.

Results: Early eradication was a success. 56% recolonization rate by CSO once BAOW removed. Of 27 former CSO territories invaded by BAOW, 15 sites had CSO back again within 1 year of BAOW removal.

BAOW site occupancy was reduced by a factor of six from 0.1 to 0.03. In 2018, there were 45 of 246 PAM sites with BAOW detections; after removal in 2020 there were 7 of 267 sites with BAOW.

These results are in contrast to NSO range where hundreds of BAOW removals were necessary to see even modest recolonization by NSO.

Notes: BAOW have narrow entry to SN from Klamath/ Cascade area across Pitt River. This makes SN like an island surrounded by non-habitat, aiding the effort to control invasion. Regional surveillance (PAM) was a strength. Private partnership also a strength. 'Forever management' is a possibility to manage BAOW invasion in Sierra Nevada. SPI was given assurances and 'flexibility' under ESA for their participation.

Hofstadter, D., Kryshak, N., Gabriel, M., Wood, C., Wengert, G., Dotters, B., Roberts, K., Fountain, E., Kelly, K., Keane, J. and Whitmore, S. 2021. High rates of anticoagulant rodenticide exposure in California Barred Owls are associated with the wildland–urban interface. *Ornithological Applications* 24(123):1-13.

Sample Size and Methods: Toxicology on livers of 115 Barred Owls (BO) and 12 hybrid (Northern or California Spotted Owl cross with BO) collected from the Sierra Nevada (Plumas and Lassen) and Klamath areas. Authors also collected 7 ovaries of female BO.

Results: BO in proximity of WUI were more likely to be exposed to AR. A total of 62% of BO and hybrids had anticoagulant rodenticide in liver; most were trace amounts, but 9 BO had significant amounts of AR that caused internal hemorrhaging in NSO and Golden Eagle in other studies. This is first reported potential AR exposure for California Spotted Owl.

Notes: Although most samples contained trace rodenticide, results could indicate dangerous and widespread exposure to AR in BO and CSO. Owls exposed to higher amounts of AR may not have shown up in study because they could be dead and unavailable for collection. CSO eat more rodents than BO, thus increasing potential of exposure for CSO. These results point to widespread exposure of forest raptors to AR banned in the state in 2014 except for licensed applicators. Could be AR is from illegal cannabis grows, or from illegal home use. WUI link points to illegal home use, but half-life of AR is long, so birds could move around after exposure.

Wood, C.M., Gutiérrez, R.J., Keane, J.J. and Peery, M.Z. 2020. Early detection of rapid Barred Owl population growth within the range of the California Spotted Owl advises the Precautionary Principle. *The Condor* 122(1):duz058.

Sample Size and Methods: LNF and PNF autonomous recording units (ARU) from 167 sites in 2017 and 346 sites in 2018; GPS tail feather tags on 10 Barred Owls (BO).

Results: Barred Owls (BO) were detected in 12% of sites in 2017 and 21% of sites in 2018 representing a 2.6-fold increase in BO site occupancy between 2017-2018 in core CSO range. Old forest cover (cc >40% and QMD >61cm) favored BO occupancy and colonization of CSO habitat. Medium forest cover (canopy cover >40% and QMD 31-61 cm) favored CSO occupancy (indicating CSO may be pushed out of high suitability habitat by BO, as happened with NSO in

PNW). Sites with steeper slopes had reduced probability of BO invasion. Mean BO home range in Sierra Nevada was 2,004 ha, mean territory size was 411 ha.

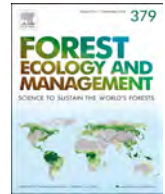
Notes: Rapid replacement of Northern Spotted Owl by BO was density-dependent and the Sierra Nevada may be experiencing the beginning stages of invasion before rapid colonization. The BO invaded Pacific Northwest 60 ys. ago, but rapid colonization only happened 20 ys. ago after BO population built up for 40 ys.

Wood, C.M., Kryshak, N., Gustafson, M., Hofstadter, D.F., Hobart, B.K., Whitmore, S.A., Dotters, B.P., Roberts, K.N., Keane, J.J., Sawyer, S.C. and Gutiérrez, R.J., 2021b. Density dependence influences competition and hybridization at an invasion front. *Diversity and Distributions* 27(5):901-912.

Sample Size and Methods: LNF and PNF autonomous recording units (ARU) from 167 sites in 2017 and 346 sites in 2018; GPS tail feather tags on 11 CSO and 10 Barred Owl (BO); feather isotopes (to determine diet) from 29 CSO and 34 BO in 2016 and 2019.

Results: BO and CSO site occupancy were negatively related to open forest cover (canopy cover <40%). Overlap in foraging habitat selection is high, with both species selecting young forest for foraging (> 40% cc and QMD < 31cm) perhaps because primary prey (woodrat and pocket gopher) are associated with this habitat. BO diet overlapped entirely with CSO diet (99%); CSO diet overlapped with BO by 52%. A total of 38 barred or hybrid owls were detected. Amount of hybrids (10) was 36% number of BO (28).

Notes: BO/CSO niche overlap for landscape-scale habitat selection is less than in Pacific Northwest because the Sierra Nevada is at the beginning of an invasion before rapid colonization. See Wood et al. (2020) for additional BO site occupancy patterns in Sierra Nevada. Diet overlap is also less than in the PNW diets where more advanced colonization is underway. Hybridization was observed at beginning of invasion because the phenomenon is density dependent and likely due to lack of conspecific mates. Hybridization is now rare in PNW where BO density is much higher and direct competition between NSO and BO displaces NSO to lower quality habitat.



Space use, forays, and habitat selection by California Spotted Owls (*Strix occidentalis occidentalis*) during the breeding season: New insights from high resolution GPS tracking

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ABSTRACT

Our current understanding of the relationship between imperiled species and forest management can benefit from global positioning system (GPS) technologies. Fauna of later seral stage forests have historically been difficult to detect and track in rugged terrain, leading to challenges in movement characterization and conservation. We investigated movement of California Spotted Owls (*Strix occidentalis occidentalis*) using automated GPS loggers affixed to 15 owls in the northern Sierra Nevada, California. We used > 17,000 locations from individual owls to characterize homerange size, movement distances, and roosting and foraging habitat selection at four spatio-temporal scales (landscape, home range, foray, nightly) during the breeding season (April–August). Additionally, we assessed owl use of Protected Activity Centers (PACs), which are designated by the U.S.D.A. Forest Service to protect nesting and roosting habitat. Our results corroborated some previous findings about habitat requirements of California Spotted Owls, while also revealing new nuances in space use and habitat selection. Roosting and foraging owls selected stands with high canopy cover and large trees at multiple spatio-temporal scales, with foraging owls showing strongest selection at the largest (landscape) scale investigated. Although owls selected for PACs while foraging and roosting, PACs protected less than one quarter of foraging space use (volume of use) and fewer than half of observed roosts during the breeding season. Female owl home ranges were double the size of male home ranges, and distances travelled from the nest by females were 1.3 times greater than distances travelled by males, with non-breeding females travelling farthest and visiting up to six PACs during a single breeding season. Foraging behavior of this sort has not been documented previously in California Spotted Owls. Our findings support protection of later seral stage forest attributes for roosting and foraging California Spotted Owls. Given their selection for later seral forest attributes, strongest evidence of foraging habitat selection at the landscape scale, long distances travelled by owls and limited habitat protection afforded by PACs, habitat connectivity across the landscape is likely an important component for owl conservation, and distribution of current protected areas may be inadequate for this wide-ranging species.

1. Introduction

Spotted Owls (*Strix occidentalis*) are threatened by loss and fragmentation of later seral forest and invasion by congeneric Barred Owls (*Strix varia*), which displace and hybridize with Spotted Owls (Keane, 2017). Consequently, Spotted Owls have been a focus of forest

conservation efforts in the western U.S. since the 1980s (Simberloff, 1987) and a primary factor in the development of some of the country's largest and most comprehensive management plans, including the Northwest Forest Plan which addressed management of 9.9 million ha in 3 states (Tuchmann et al., 1996). While the Northern Spotted Owl (*S. o. caurina*) and Mexican Spotted Owl (*S. o. lucida*) subspecies are

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federally protected, the California Spotted Owl (*S. o. occidentalis*) is currently under review for listing (U.S. Fish and Wildlife Service, 2017). The U.S.D.A. Forest Service, which manages lands where the majority of the California subspecies occurs, is currently reviewing a draft conservation strategy for the subspecies. While the California Spotted Owl is a high-profile and well-studied species, few of the management recommendations developed and implemented to protect it have been tested empirically (Berigan et al., 2012), and numerous questions remain on the most effective strategy to prevent its extinction (Stine and Manley, 2017).

California Spotted Owls are medium-sized owls that specialize in later seral stage forests (stands with high canopy cover and large trees) in montane regions of California (Tempel et al., 2016; Moen and Gutiérrez, 1997). They are socially monogamous central place foragers that defend territories around their nests, where they hunt at night and prey upon small mammals, birds, lizards and insects (Gutiérrez et al., 2017). Previous investigations established that spotted owls preferentially roost and nest in mature forest stands with later seral or old-growth characteristics (Moen and Gutiérrez, 1997; Bond et al., 2004; Tempel et al., 2016; North et al., 2017). Within mature forests, California Spotted Owls forage within a variety of habitats including stands with moderate to high canopy cover (Call et al., 1992; Williams et al., 2011), forest edges (Eyes et al., 2017; Williams et al., 2011), unlogged burned areas (Bond et al., 2016, 2009), and riparian corridors (Bond et al., 2016; Irwin et al., 2007).

Historically, conservation of California Spotted Owls has focused on protecting nesting and roosting habitat in later seral forests with high canopy cover and prevalence of large trees (Bond et al., 2004; Moen and Gutiérrez, 1997; North et al., 2017; Tempel et al., 2016). Habitat protection on National Forest lands generally occurs at the scale of “Protected Activity Centers” (PACs), where contiguous habitats are designated to protect core breeding and roosting behaviors for known pairs or territorial but unpaired owls (Berigan et al., 2012; U.S.D.A. Forest Service, 2004). Protected Activity Centers were proposed as part of an interim conservation strategy for the California Spotted Owl in 1992 (Verner et al., 1992b) to protect areas where owl use is concentrated within the home range, including nest and roost sites (Berigan et al., 2012). In practice, PACs are delineated as ≥ 121 ha polygons encompassing the best quality habitat (large trees and high canopy cover) around a California Spotted Owl nest or roost site. Stand-altering activities, except for chainsaw thinning small diameter material (< 15 cm diameter at breast height) and light under-burning, are generally prohibited within the PACs (Berigan et al., 2012). However, foraging California Spotted Owls in the Sierra Nevada utilize much broader areas than those encompassed by PACs, with individual owl home range estimates during the breeding season ranging from 500 to 2800 ha and year-round home range estimates exceeding 5000 ha (Williams et al., 2011; Zabel et al., 1992).

Habitat selection is dependent on spatial and temporal scales (Mayor et al., 2009; Orians and Wittemberg, 1991). For example, Blakesley et al. (2005) found that finer scale habitat features were better predictors of breeding site occupancy of California Spotted Owls, whereas LaHaye et al. (1997) reported that landscape scale features were better predictors of nest success. For foraging owls, Bond et al. (2016) found that the strength and direction of selection of burned habitat by owls was influenced by area designated as available habitat. Past assessments of habitat selection and space use by California Spotted Owls at multiple scales, and therefore evaluations of the efficacy of management, have been limited by available survey methods. For example, current knowledge of California Spotted Owl foraging behavior is based on auditory, and very high frequency (VHF) radio telemetry surveys, both of which are inherently biased toward areas that are more accessible to observers and are limited in spatial accuracy (Tomkiewicz et al., 2010).

Recent advances in animal tracking using Global Positioning Systems (GPS) and launch of the ICARUS satellite tracking program

permit collection of increasingly precise, detailed, and extensive data on movement and locations of highly mobile and cryptic species (Tomkiewicz et al., 2010; Wikelski, 2007). These technological developments have the potential to provide insights that will greatly improve our understanding of animal-habitat relationships and inform conservation planning (Morales-Reyes et al., 2017; Shimada et al., 2017). Forest-dwelling fauna have historically been difficult to detect and track in rugged terrain (Hollenbeck et al., 2018; Phoebe et al., 2017). This limitation has constrained the scope of research questions addressed, leading to a focus on conservation of habitat components in which species can be readily detected, and a neglect of life-history phases in areas where study subjects are more difficult to detect (Koenig et al., 1996). For example, movements and activities of central place foragers during nesting are a major research and conservation focus, but relatively little is known about movements of central place foragers during forays and dispersal (Clobert et al., 2012; Kesler and Walters, 2012; Rosenberg and McKelvey, 1999). Detailed information from high resolution GPS tracking can provide more robust support for existing forest management strategies, which are rarely empirically tested, or spur development of more refined and ecologically relevant approaches.

Our objective was to revisit current knowledge of California Spotted Owl habitat selection and space use by investigating movement of California Spotted Owls using GPS loggers that automate observations of movements at multiple temporal and spatial scales (Wilmers et al., 2015). Throughout three breeding seasons (April–August 2015–2017), we characterized California Spotted Owl homerange size, transit distances and straight-line distances from the nest, selection of roosting habitat, and selection of foraging habitat at four spatio-temporal scales. We used a model selection approach to evaluate whether owls selected for specific habitats and whether sex or breeding status influenced homerange, movement distance from the nest or habitat selection. We also assessed the proportion of each owl's observed roost sites and foraging volume of use within designated PACs and evaluated selection for these protected areas.

2. Materials and methods

2.1. Study area

We studied California Spotted Owls on the Mt. Hough Ranger District, Plumas National Forest (63,770 ha), within the Sierra Nevada mountain range in northern California (40°00'01"N 120°40'05"W, Fig. 1). The Forest has an elevation gradient of 311 to 2433 m and a Mediterranean and montane climate with dry, warm summers and cool, wet winters. Although conditions vary widely across the elevation gradient, mean annual precipitation within the Forest is c. 1036 mm, and mean temperature ranges from 1.3 ± 2.4 °C in January to 19.3 ± 1.5 °C in July (1895–2017, Western Regional Climate Center, 2017). Vegetation in Plumas National Forest is dominated by lower and upper montane forest with stands of ponderosa pine (*Pinus ponderosa*) – mixed conifer, white fir (*Abies concolor*) – mixed conifer, and red fir (*Abies magnifica*) (Fites-Kaufman et al., 2007). Common tree species include red fir, white fir, Douglas-fir (*Pseudotsuga menziesii*), ponderosa pine, Jeffrey pine (*P. jeffreyi*), sugar pine (*P. lambertiana*), black oak (*Quercus kelloggii*) and incense cedar (*Calocedrus decurrens*) (Fites-Kaufman et al., 2007). Fire is common throughout the region and mixed-severity fire regimes dominate, with tree scar records indicating composite fire return intervals on the forest ranging from 8 to 22 years at a site between 1454 and 2001 (Moody et al., 2006).

2.2. Owl movement surveys

During 2015–2017 we marked and tracked 8 females and 7 males from 8 territories and collected a mean of 805 (370–1072) locations per owl*season during 22 owl*seasons (15 individual owls were tracked, 5

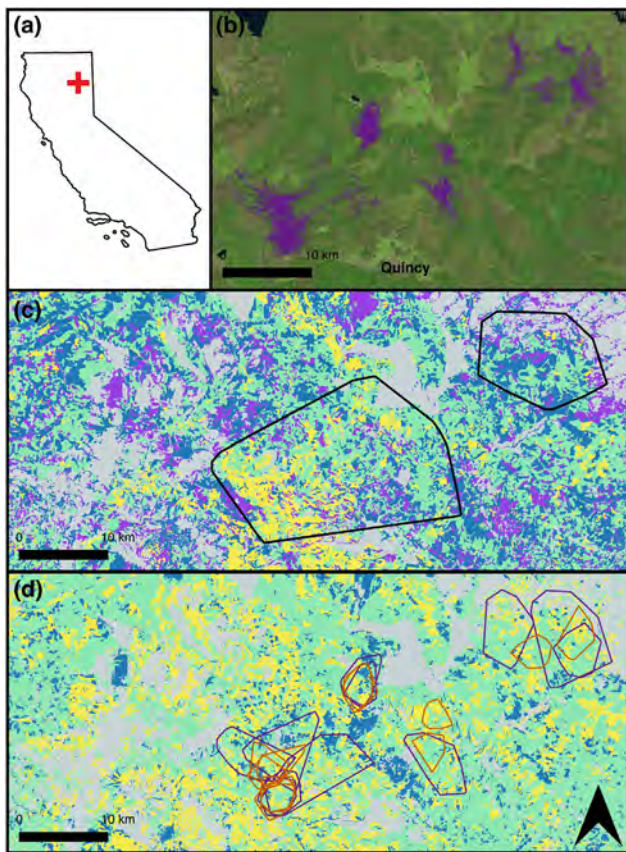


Fig. 1. Study area (a) in Plumas National Forest, California; (b) trajectories (purple traces) of 15 California Spotted Owls tracked during the 2015–2017 breeding seasons (April–August); (c) minimum convex polygons (MCPs) of all owl locations in east and west landscapes within the study area and overlaid on canopy cover (> 70% is yellow, 50–70% is green, 30–50% is blue, and < 30% is purple); (d) home ranges defined by MCPs for male (orange, 11 owl*seasons) and female (purple, 11 owl*seasons) in each season and overlaid on dominant tree size (DBH > 50 cm is yellow, 25–50 cm is green, < 25 cm is blue). Grey background in (c) and (d) show treeless areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of them during multiple breeding seasons) across > 45,000 ha of forest (Supplementary material, Appendix S1). We used Forest Service data on known nests coupled with surveys to locate owls in May and June of 2015, 2016, and 2017. We captured owls by hand and with snare and noose poles. Owls were tagged under authorization from the California Department of Fish and Wildlife (Scientific Collecting Permit #SC-8645) and the U.S.F.W.S. Bird Banding Laboratory (Permit #22423). We determined owl sex based on pitch of vocalizations or knowledge from prior banding efforts, and we classified owl age using plumage characteristics (Forsman, 1983; Franklin et al., 1996). When tracking began, one female owl was in its second year (SY, F) and 14 owls were after third year (ATY, 7F:7M). We attached an Alle-300 GPS-UHF GPS logger (Ecotone Telemetry, Sopot, Poland) and a VHF transmitter (Advanced Telemetry Systems, Isanti, U.S.A.) to each bird using a back-mounted Teflon ribbon harness (total package weight < 13 g) (n = 15, seven males and eight females). The GPS-UHF units recorded locations at defined intervals within daily duty cycles, and stored locations until a connection was established with a hand-held or stationary base station to which locations were then transmitted (EP-BS, Ecotone Telemetry). We placed base stations near nests or in areas commonly transited by owls. Additionally, owls were tracked on foot to within 50–200 m using VHF radio telemetry and data were downloaded from the GPS-UHF units using a wireless link to the base station.

These GPS-UHF units can be remotely reprogrammed, enabling use of multiple sampling regimes over time on individual owls. During the breeding season, batteries on the GPS-UHF units allowed approximately 3 months of tracking after marking (c. 10 May), with hourly locations collected daily between c. 1800 h and 600 h the following day. We also programmed GPS-UHF units to collect 3–7 nights of higher-resolution movement data for each owl, with locations collected at 1–6 min intervals. Herein, we truncated movement data to align with the California Spotted Owl breeding season from 1 April–31 August (García-Feced et al., 2011; Lee et al., 2012; Tempel and Gutiérrez, 2013). Foraging location observations were defined as position coordinates recorded between 1 h after sunset and 1 h before sunrise. We defined roost locations as locations recorded between 2 h after sunrise and 2 h before sunset. We determined the breeding status (breeding or non-breeding) of owls during each season through survey efforts or direct observation.

2.3. Homorange size

We calculated homorange size using the minimum convex polygon (MCP) method (Worton, 1987), so that our calculations would be comparable to the majority of literature on California Spotted Owl home range (see Roberts, 2017 and references therein). MCPs were derived for each owl*season using all available locations. For robustness, we also calculated home ranges using the 95% isopleth of the kernel density utilization distribution (Worton, 1989). We compared homorange size between sexes and breeding status classes using a model selection process to test specific hypotheses about homorange size (Table 1). We used an information-theoretic approach to model selection (Burnham and Anderson, 2003) and evaluated support for 4 hypotheses related to homorange size (Table 1). For each dataset, we compared candidate models using the Akaike information criterion, adjusted for sample size (AIC_c), and retained the best approximating model with the lowest AIC_c value, or the best set of models, if top models were within 2 ΔAIC_c (Burnham and Anderson, 2003). As a final step, we assessed the effect of survey year (2015, 2016, 2017) by adding it to the best approximating model as a categorical fixed variable and evaluating whether it significantly improved model fit (reduced $AIC_c > 2$). We interpreted variables using parameter estimates from the best approximating model, or model-averaged estimates from the best model set. Models were fit using log-transformed homorange size (ha) as the response variable, to satisfy the assumption of normality. We included *territory* as a random effect only (not individual) because a parametric bootstrap test showed that when *individual* was added to the final model it was not significantly different from the model containing only *territory* (LRT = 74.22, $P = 0.500$). We conducted all analysis within the R environment for statistical computing (R Development Core Team, 2016). We used the *adehabitatHR* v3.3.0 (Calenge, 2006) package to fit MCPs and kernel density utilization distributions, packages *lme4* v1.1-12 (Bates et al., 2013) and *lmerTest* v2.0-33 (Kuznetsova et al., 2017) to fit linear mixed effects models and *MuMIn* v1.40.4 was used for model averaging and to calculate R^2 of all models using methods described in Nakagawa and Schielzeth (2013). We considered differences significant at $\alpha < 0.05$, and we report test statistics (TS) and 95% confidence intervals (95% CI) where appropriate; test statistics were t values for single models and z values for model-averaged sets.

2.4. Distance travelled

We calculated nightly distance transited (sum of all nightly movements) using only high resolution data (1–6 min position interval) for full nights (> 6 h data collection). We also calculated maximum distance travelled from the nest (straight-line distance) for each owl*season and each night. We defined nest locations as active nests for breeding birds and nest site from prior year for non-breeding birds, due

Table 1

Hypotheses and corresponding models developed to explain variation in California Spotted Owl homerange size and distance travelled from nest during breeding seasons of 2015–2017. Homerange size (ha) was defined by MCP for each owl*season and models were linear mixed effects models with territory included as a random effect. Distance travelled from nest was the maximum straight-line distance from the nest for each night and models were Gaussian mixed effects models with a log-link and with individual owl included as a random effect. Nest locations represented active nests for breeding birds and nest sites during prior years for non-breeding birds.

Hypothesis	Model equation
<i>Homerange size</i>	
1. Owl homerange size was not influenced by sex or breeding status	Homerange size $\sim \beta_0 + (1 \text{territory})$
2. Home range size differed between males and females	Homerange size $\sim \beta_0 + \beta_1 \cdot \text{sex} + (1 \text{territory})$
3. Home range size differed between non-breeding and breeding birds	Homerange size $\sim \beta_0 + \beta_1 \cdot \text{breeding_status} + (1 \text{territory})$
4. Sex and breeding status influenced homerange size	Homerange size $\sim \beta_0 + \beta_1 \cdot \text{sex} + \beta_2 \cdot \text{breeding_status} + (1 \text{territory})$
<i>Distance travelled from nest</i>	
1. Nightly maximum distance from the nest was not influenced by sex or breeding status.	Distance from nest $\sim \beta_0 + (1 \text{individual})$
2. Distance travelled from nest differed between sexes	Distance from nest $\sim \beta_0 + \beta_1 \cdot \text{sex} + (1 \text{individual})$
3. Distances travelled from nest differed between breeding and nonbreeding birds	Distance from nest $\sim \beta_0 + \beta_1 \cdot \text{breeding_status} + (1 \text{individual})$
4. Sex and breeding status influenced distances travelled from the nest	Distance from nest $\sim \beta_0 + \beta_1 \cdot \text{sex} + \beta_2 \cdot \text{breeding_status} + (1 \text{individual})$
5. Sex and breeding status interacted to influence distance travelled from the nest	Distance from nest $\sim \beta_0 + \beta_1 \cdot \text{sex} + \beta_2 \cdot \text{breeding_status} + \beta_3 \cdot (\text{sex} \cdot \text{breeding_status}) + (1 \text{individual})$

to high nest site fidelity (Berigan et al., 2012). We compared distance travelled from the nest between sexes and between breeding and non-breeding birds, using the same methods and hypotheses used for the homerange size analysis described above, except that distance traveled was the response variable and individual owl was included as a random effect (Table 1). Models were fit using distance from nest as the response variable and the Gaussian family with a log-link.

2.5. Foraging habitat selection

To evaluate foraging habitat selection, we tested whether owls used habitats disproportionately to the amount available (Johnson, 1980) by comparing intensity of habitat use to availability of habitat (Thomas and Taylor, 2006). We restricted our analysis to two measures of forest structure (canopy cover and dominant tree size) that are known to be highly important for California Spotted Owls (Call et al., 1992; Williams et al., 2011), however we acknowledge that habitat selection for this species comprises a much wider range of factors including other components of habitat structure (North et al., 2017), fire history (Bond et al., 2016, 2009), prey availability, habitat configuration (Eyes et al., 2017), and presence or water or riparian areas (Bond et al., 2016), as well as conspecific and interspecific interactions. We assessed habitat selection by foraging owls at four spatio-temporal scales: landscape (2nd order), home range (3rd order), foray, and nightly (Johnson, 1980). We analyzed all owl movements using the R packages *BBMM* v3.0 (Nielson et al., 2015), *adehabitatLT* v3.3.0 (Calenge, 2006) and *adehabitatHR* v3.3.0 (Calenge, 2006).

2.5.1. Landscape scale

To evaluate foraging habitat selection at the landscape scale, we tested whether owls used habitats disproportionately to the amount available by comparing habitat use at the home range scale to availability of habitat within the eastern or western (Fig. 1c) study areas. We characterized habitat using vegetation mapping data (U.S.D.A. Forest Service, 2015) based on the CALVEG (“Classification and Assessment with Landsat of Visible Ecological Groupings”) classification (Nelson et al., 2015). From these spatial data we selected two habitat variables that have been associated with California Spotted Owl habitat use, are widely quantified, and are often targeted for manipulation by forest managers: percent canopy cover and dominant tree size (Blakesley et al., 2005; North et al., 2017). Areas of non-forested land, roads, water, and cleared or naturally open areas were categorized as “open treeless areas”.

We treated four categories of canopy cover, three categories of

dominant tree size, and open treeless areas as eight separate datasets. Canopy cover categories included high (> 70%), medium (50–70%), low (30–50%) and very low (< 30%). Dominant tree size was based on the mean size of the dominant trees in the stand, measured as diameter at breast height (DBH), categorized as large (> 50 cm), medium (25–50 cm), or small (< 25 cm). We delineated the landscape available to owls as the MCP of every foraging location obtained for all the owls in our study, separated into eastern and western landscapes to account for a substantial gap in used habitat near the center of our study area (Fig. 1c).

To quantify habitat use, we calculated volume of the Brownian bridge utilization distribution (UD) for each owl*season (Horne et al., 2007; e.g. Cox and Kesler, 2012a). The Brownian bridge method extends traditional methods of quantifying animal space use (e.g. kernel density, MCPs) by accounting for temporal autocorrelation among locations to estimate the probability density function (PDF) and utilization distribution (Calenge, 2006). When calculating UD, we excluded time lags longer than 62 min (our longest nightly sampling interval), reduced our data to one location per hour (higher resolution data addressed below) and used a spatial accuracy of 30 m (corresponding to accuracy of our GPS units) and a grid cell size of 50 m. Within each UD, we calculated the volume of use within eight habitat categories (Fig. 1c, d) for each owl*season, and within available landscape (i.e., east or west). We produced a landscape-scale dataset for each of the 8 habitat categories, each with 22 owl*seasons of proportional used habitat, and 22 measurements of proportional owl*season available area (representing either the east or west landscape). We developed seven generalized linear mixed effects models to test hypotheses on foraging habitat selection (Appendix S2, models 1–7) and used model selection to determine the most parsimonious model. Territory was included as a random effect in all models. We retained the model with the lowest AIC_c as the best approximating, or the best set of models, if top models were within 2 ΔAIC_c (Burnham and Anderson, 2003). We evaluated the effect of survey year (2015, 2016, 2017) by adding it to the best approximating model as a categorical fixed variable and assessed whether it significantly improved model fit (reduced AIC_c > 2). We interpreted variables using parameter estimates from the best approximating model, or model-averaged estimates from the best model set. Test statistics were t values for single models and z values for model-averaged sets. Models were fit using proportion as the response variable, with the Gaussian family and the log link.

2.5.2. Home range scale

We used methods similar to those described above to compare

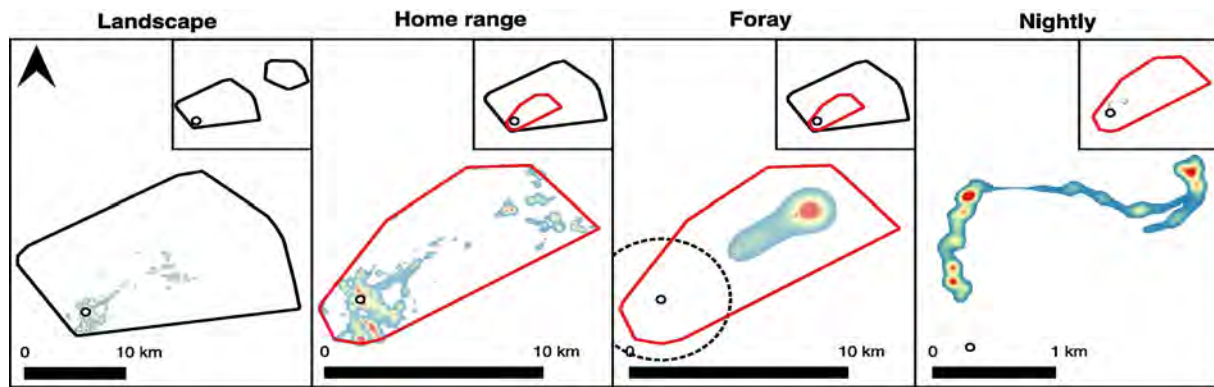


Fig. 2. Example of foraging habitat selection analysis at four spatio-temporal scales (landscape, home range, foray and nightly) for a nonbreeding female California Spotted Owl (1177–40374, Appendix S1) tracked during the 2016 breeding season (April 1–August 31) in the Sierra Nevada, California. At the landscape scale, the volume of use by owls in each habitat category, based on a utilization distribution (UD) for each owl*season (high use red to low use blue), was compared to the proportion of area for each habitat category (see text) within the western landscape of the study area (black polygon – see inset for both landscapes). Habitat use (volume of UD in each habitat category) was also compared to available habitat within the home range minimum convex polygon (MCP) for the owl*season; (red polygon). The foray scale compared volume of use by owls in each habitat category based on the UD of owls during forays to the proportion of habitat categories within the home range (red polygon). We defined forays as movements outside a 3.2-km buffer around the nest (dotted circle), the mean distance to nearest neighboring nest of study subjects. Foray and nightly scale insets show location of the home range within the western landscape. The nightly scale compared habitat use within the UD, for each night of high resolution data, to habitat availability within the home range (red polygon, see inset). Nest location is denoted by a black circle on all panels. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

proportional habitat use within the UD and available habitats within the MCP home range (Fig. 2). We produced a home range dataset for each of the eight habitat categories in the MCPs (available area) and 22 owl*seasons of proportional habitat use. We used the same habitat variables described above, and the same alternative models (Appendix S2, models 1–7) and model selection process. Mixed effect models were fit using proportion as the response variable, with the Gaussian family and the log link.

2.5.3. Foray scale

We examined habitat selection during forays, which occurred in six non-breeding females in our study. The mean distance to nearest neighboring nest of study subjects was 3.2 km, so we defined forays as movements farther than 3.2 km from the nest and temporally extending for ≥ 10 locations and 10 h. We estimated the proportional used area for each habitat with UD for each foray*night ($n = 18$ in 6 owl*seasons), and compared those to the proportional area of each habitat within the MCP home range for the owl*season using a generalized linear mixed effects model that included individual as a random effect, using the Gaussian family and the log link. We used the same habitat categories described above with a similar model fitting and selection process, but examined only the effect of the habitat category (Appendix S2, models 1–2). Most birds were sampled hourly during forays, however we also included four foray nights with high resolution sampling (every 5 min). As a final step, we tested our models with and without the high resolution data and as we found no difference in the direction or significance of results, we retained the high resolution data.

2.5.4. Nightly scale

For 21 of the 22 owl*seasons, high resolution location data (locations recorded every 1–6 min) were available, enabling analysis of habitat use at the nightly scale. Nightly records ranged from 2.4 to 7.4 h periods over 103 nights (mean 6.4 h, 1.5 SD) and 88% of nights had > 6 h sampling. We obtained a mean of 87 (SD 12.6, range 72–126) locations within each sampling period. We derived a UD for each owl night and estimated the proportional used area by habitat. We used the same available area as for home range analysis, the MCP, and included individual owl as a random effect. We used the same habitat categories described above, the same model fitting and selection process, and similar alternative models (Appendix S2, all models).

2.6. Roost habitat selection

We evaluated owl selection of roost habitat by comparing used and available habitat with package *adehabitatHS* v0.3.13 (Calenge, 2006). Roost locations were defined by the location temporally closest to 1200 h for each owl from the set of locations recorded between 2 h after sunrise and 2 h before sunset. We summed the number of roost locations within each habitat category for each owl*season to define use. Available roost habitats were defined as the proportion of each habitat category within the corresponding MCP home range. We then calculated Manly selectivity measures for each habitat category and tested overall habitat selection using a log-likelihood test statistic (Khi2L) (Manly et al., 2007). We treated canopy cover and dominant tree size as separate categorical variables, both of which included open treeless areas as a variable level. Manly selection ratios were interpreted as indicating selection for a habitat if the ratio and its confidence interval was > 1 and selection against a habitat if the ratio and its confidence interval were < 1 . We used a type III test because the use and availability were measured for each owl*season (Thomas and Taylor, 1990).

2.7. Protected activity center analysis

We analyzed overlap between PACs and owl home ranges, and selection for or against PACs, using foraging space use (volume of use) and roost locations. PACs (designated to comprise the best available 121 ha of owl habitat surrounding known and suspected nest stands) were delineated in previous years by Forest Service biologists. For each owl*season we identified the “nest PAC” as the PAC that contained the nest, or the previous year’s nest for non-breeding birds, and “all PACs”, or sections of PACs, intersected by the MCP home range.

We compared PAC use (UD volume within PAC/s) with the percent area of PACs within each owl’s MCP home range (available) for all owls, regardless of reproductive status (22 owl*seasons). We used a method similar to the foraging habitat selection analysis to test for selection for or against PACs. To assess the overlap of PACs with roost locations, we used a similar approach, but rather than intersecting PACs with volume of foraging space use, we intersected PACs with roost locations for 15 out of the 22 owl*seasons for which there were > 20 roost locations. We used Manly selectivity measures to compare proportional use of PAC and non-PAC areas, using number of roost sites within and outside PACs (used) and percent area of PACs within each owl’s MCP home

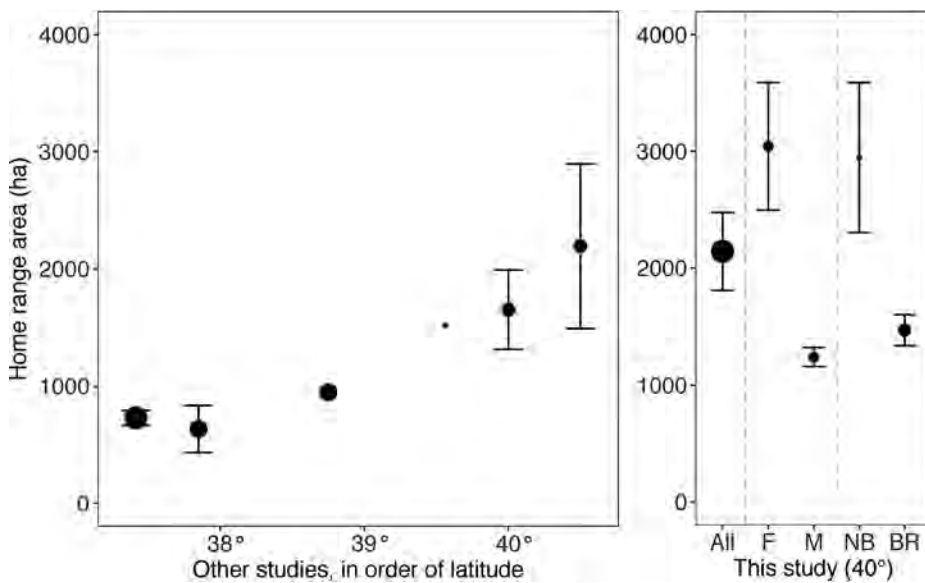


Fig. 3. California Spotted Owl breeding season (1 April–31 August) home range (MCP) estimates and SE (whiskers) reported elsewhere in the Sierra Nevada (left) (from Roberts, 2017, references listed below), and reported herein [this study] for the Plumas National Forest during 2015–2017 (right). Other studies, ordered by latitude, were conducted in Sierra National Forest (Zabel et al., 1992); Yosemite National Park (Eyes, 2014); Eldorado and Tahoe National Forests (Williams et al., 2011); Tahoe National Forest (Call et al., 1992); Plumas National Forest (Gallagher, 2010); and, Lassen National Forest (Zabel et al., 1992). Dot-size represents sample size, which ranged from $n = 5$ (Tahoe National Forest) to $n = 22$ (this study). We report estimated homerange sizes by sex and breeding status for birds evaluated herein as arithmetic means and SE of observed data for comparison to other studies, though this differs from least squared means reported in the text. Only studies using the 100% minimum convex polygon method to calculate home range were included to facilitate comparisons.

range (available), using the same test statistic as for roost selection analysis (Khi2L).

3. Results

3.1. Homerange size

Mean California Spotted Owl homerange size (2143 ha, 334 SE) was similar to estimates from previous studies within the Plumas National Forest (1653 ha, 336 SE) and the adjacent Lassen National Forest (2195, 701 SE; Fig. 3). Mean kernel density estimates of home range (2319 ha, 442 SE) were 8% higher than minimum convex polygon estimates. Homerange sizes differed significantly by sex ($TS = 3.74$, $p < 0.001$) and breeding status ($TS = 1.97$, $p = 0.049$) (Appendix S3). For the sex-only model, least squared mean home range of female owls (2611 ha, 95% CI 1961–3476) was more than double mean male home range (1216 ha, 95% CI 914–1619). Survey year did not influence home range size as the best models outranked the models including year.

3.2. Distance travelled

Breeding owl maximum nightly transit distances (sum of all nightly movements) ranged from 12.3 (7.0 ± 1.9) km for males to 17.9 (8.3 ± 3.0) km for females. Nightly maximum transit distances for non-breeding owls ranged from 7.9 km for males (6.2 ± 1.1) to 32.1 km for females (8.6 ± 4.8). All non-breeding females travelled outside the home range of their mate (Fig. 4) and visited (location points were recorded within) a mean of 4.5 (range 3–6) PACs (Appendix S1), while their home ranges overlapped with 4.7 (3–8) PACs. One non-breeding female (1177–40,374; Fig. 4b, green) left her territory and forayed to locations > 10 km from the previous year's nest on her home territory on four occasions between 17 May and 31 August for periods of 2, 8, 21 and 2 days. During the forays she visited six PACs in total and passed through the adjacent home ranges of another marked owl pair (Fig. 4b).

Distances travelled from the nest (straight-line distance, not transit distance) by non-breeding owls differed between sexes, with sex and breeding status interacting significantly (Appendix S3). Female owls travelled 1.3 times farther from the nest ($TS = 4.70$, $p < 0.001$) than male owls (respective mean distances of 2.3 km, 95% CI 1.84–2.91; and 1.76 km, CI 1.38–2.25). Breeding status alone was not a reliable predictor of maximum distance travelled from nest ($TS = 1.25$, $p = 0.221$); however, the interaction between sex and breeding status

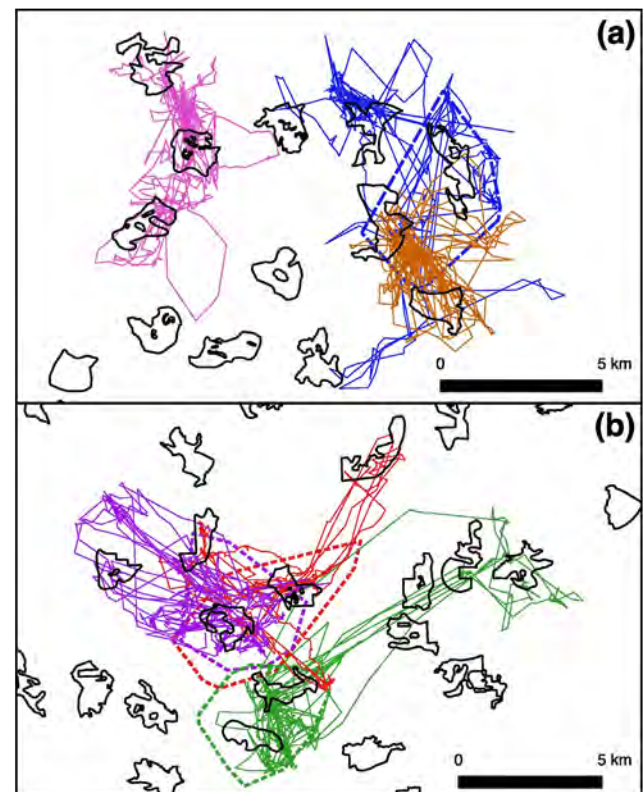


Fig. 4. Movement paths of six non-breeding female California Spotted Owls (traces), home ranges of mates in the same year (if tracked, dashed polygons) and Protected Activity Centers (black polygons). All owls presented in this figure were either non-breeding or had their nest fail in the season tracked and were tracked during breeding seasons (1 April–31 August) of 2016 and 2017. Panel (a) shows three non-breeding females in the eastern landscape (pink traces depict a female whose mate was not tracked, while blue and brown depict two females that paired with the same male, but in a different year). Panel (b) illustrates three non-breeding female seasons from two territories in the western landscape (red and purple traces are from two separate female owls that paired with the same male in different years). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

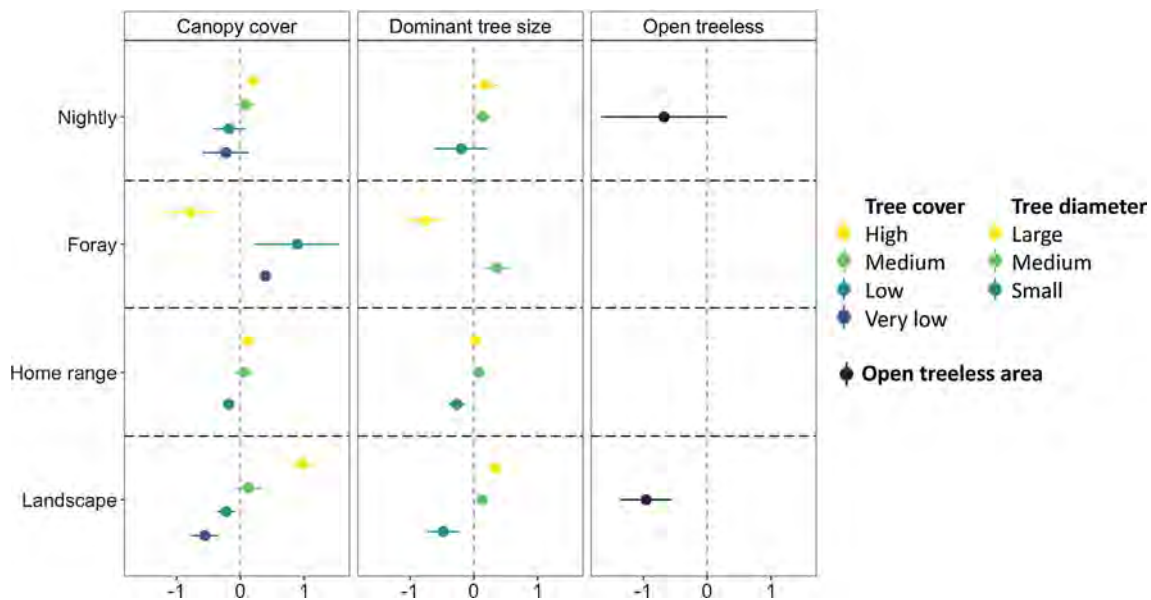


Fig. 5. Summary of best models describing habitat selection by California Spotted Owls during breeding seasons of 2015–2017 at four spatio-temporal scales, including landscape, home range, foray and nightly. Coefficients and 95% CI (whiskers) from top ranked models (or model-averaged model sets) that included the used/available categorical variable are shown. Positive coefficients indicate selection for a habitat category and negative coefficients indicate selection against. Three habitat categories are shown: canopy cover [high (> 70%), medium (50–70%), low (30–50%), very low (< 30%)], dominant tree size [large (> 50 cm), medium (25–50 cm), small (< 25 cm)] and open treeless areas (one category).

was significant ($TS = -7.74$, $p < 0.001$) due to greater distances travelled by female non-breeding owls (Appendix S4). Male owls travelled similar distances from the nest irrespective of breeding status (Appendix S4). Survey year did not influence distance travelled from the nest as the best model outranked the model including year.

3.3. Foraging habitat selection

After accounting for differences between sexes and breeding status, California Spotted Owls used habitats selectively at landscape, home range, foray and nightly scales. Survey year did not appear to influence foraging habitat selection, as only 3 models were improved by adding year (home range: open treeless area, nightly: very low cover, small dominant tree size), none of which demonstrated significant habitat selection (Fig. 5, Appendix S6). Landscape scale best approximating models indicated that owls selected for high canopy cover ($TS = 10.1$, $p < 0.001$), selected against low ($TS = 3.1$, $p = 0.002$) and very low canopy cover ($TS = -5.1$, $p < 0.001$) and used medium canopy cover in proportion to availability (Fig. 5, Appendices S5 and S6). Owls selected habitat at the landscape scale that was dominated by large ($TS = 6.2$, $p < 0.001$) and medium ($TS = 2.7$, $p = 0.007$) diameter trees, and selected against stands dominated by small trees ($TS = -3.7$, $p < 0.001$) or open treeless areas ($TS = 4.7$, $p < 0.001$). The best approximating landscape models for large trees included breeding status, however no landscape scale models included sex (Appendices S5 and S6). Models at the landscape scale had the greatest explanatory power among the three scales that included all owls (Landscape, home range, nightly; Appendix S5).

At the home range scale, after accounting for differences between sexes and breeding status, we found that owls selected for high canopy cover ($TS = 3.7$, $p < 0.001$), selected against low canopy cover ($TS = 4.8$, $p < 0.001$) and used medium and very low canopy cover in proportion to availability (Fig. 5, Appendix S6). Owls also selected habitat within the home range that was dominated by medium-sized trees ($TS = 2.3$, $p = 0.022$) and against stands dominated by small trees ($TS = 4.1$, $p < 0.001$), whereas stands dominated by large trees and open treeless areas were used in proportion to their availability (Appendices S5 and S6). The best fitting home range models for seven

variables included breeding status and sex (Appendices S5 and S6).

In contrast to habitat selection at other spatio-temporal scales, six non-breeding females in our study selected against high canopy cover ($TS = -3.6$, $p < 0.001$) and large dominant tree size ($TS = -5.7$, $p = 0.003$) during forays, while selecting for areas with low ($TS = 2.6$, $p = 0.009$) and very low ($TS = 12.3$, $p < 0.001$) canopy cover dominated by medium sized trees ($TS = 3.5$, $p < 0.001$) (Appendices S5 and S6).

At the nightly scale, accounting for differences between sexes and breeding status, owls selected for high canopy cover ($TS = 4.0$, $p < 0.001$) and stands dominated by medium-sized ($TS = 2.2$, $p = 0.025$) but not large ($TS = 1.7$, $p = 0.087$) trees. All of the best approximating models or model sets for the nightly scale contained interaction terms with sex and/or breeding status, indicating differential selection between sexes and breeding/non-breeding owls (Appendices S5 and S6).

3.4. Roost habitat selection

Owls selected roost sites based on canopy cover ($TS = 319$, $df = 28$, $p < 0.001$) and dominant tree size ($TS = 264$, $df = 23$, $p < 0.001$). Owls selected for high canopy cover (Manly selection ratio = 1.61 [1.39–1.82]) and against areas with canopy cover < 50% (Fig. 6; Manly selection ratio for low = 0.10 [0.02–0.19], Manly selection ratio for very low = 0.06 [–0.02 to 0.13]). Owls also selected against stands dominated by small trees and open treeless areas for roosting (Fig. 6, Manly selection ratio for trees < 25 cm = 0.20 [0.12–0.28] and Manly selection ratio for open treeless areas = 0.09 [–0.08 to 0.27]). Habitat with medium canopy cover (50–70%) or dominated by either medium or large dominant tree sizes (> 25 cm), was used by roosting owls in proportion to availability in the home range (MCP), indicated by Manly selection ratios with intervals overlapping 1.0 (Fig. 6).

3.5. Protected activity center analysis

The PACs that contained the nest (or previous year's nest) encompassed a mean of 14.6% (range 3.7–31.6%, 1.5 SE) of owl*season UD. When all PACs were considered, they accounted for a mean of

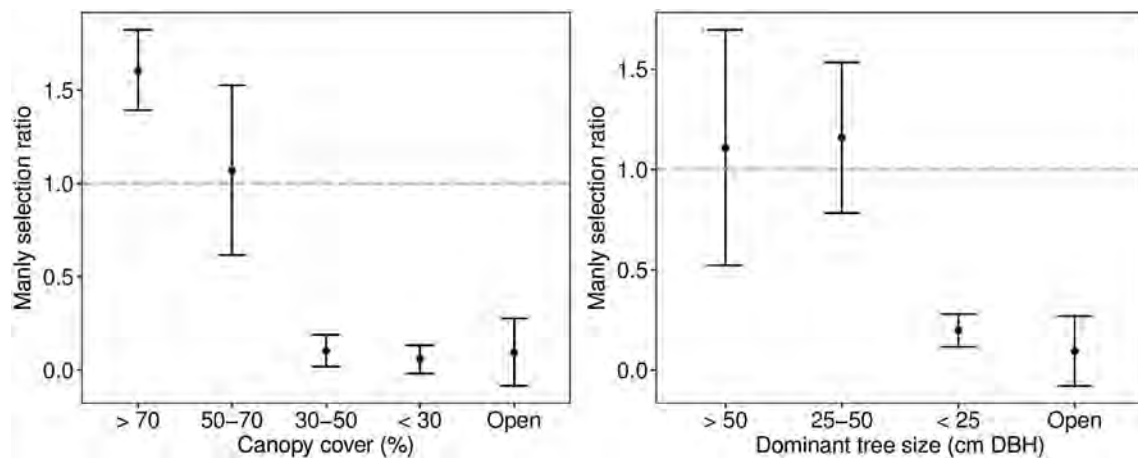


Fig. 6. Manly selection ratios showing positive (> 1) and negative (< 1) selection of canopy cover and tree size categories by roosting California Spotted Owls across 22 owl*seasons, during breeding seasons of 2015–2017.

22.1% (range 4.3–39.2, 1.6 SE) of owl*season UD. Owls used multiple PACs throughout the breeding season with Owl*season UD overlapping a mean of 2.7 PACs (range = 1–6), regardless of breeding status or sex [mean (range) number of PACs within owl UD: breeding females = 2.2 (2–3), breeding males = 2.1 (2–3), non-breeding females = 4.5 (3–6), non-breeding males = 1.8 (1–2); Appendix S1]. The PACs containing nests (or containing nests during previous year) contained an average of 48% of roost sites used per owl (range 2.3–90.4, 8.0 SE), and the average proportion of roost sites contained within PACs did not increase significantly when all PACs were considered (mean of 49.8%, range 4.7–92.0, 8.0 SE). Owls selected for PACs while foraging, whether considering only the PACs containing their nest ($TS = 3.8$, $p < 0.001$) or all PACs ($TS = 4.0$, $p < 0.001$). Owls also selected for PACs while roosting, considering PACs containing their nest ($TS = 638$, $df = 15$, $p < 0.001$; Manly selection ratio = 6.35 [4.67–8.03]) or all PACs ($TS = 372$, $df = 15$, $p < 0.001$; Manly selection ratio = 3.13 [2.27–3.99]).

4. Discussion

High resolution GPS observations of the movements of California Spotted Owls confirmed the importance of late seral stage habitat (high canopy cover and large trees) for roosting and foraging at multiple scales and revealed previously undocumented foraging behaviors by non-breeding females during the breeding season. Our findings also highlight potential limitations of existing PACs in protecting owl habitat, as individual PACs overlapped with only 48% of roosts and 14.6% of foraging space use for owls that nested within them and individual owls visited up to 6 different PACs during one season.

The tendency of owls to select roost sites with greater canopy cover and larger diameter trees than foraging sites corroborates previous findings (Gutiérrez et al., 1992; Irwin et al., 2007; Kramer et al., 2016; North et al., 2017; Tempel et al., 2016). We found strongest evidence of foraging habitat selection at the landscape scale, where owls selected for substantial canopy cover ($> 70\%$) and stands with medium to large trees (> 25 cm DBH), while selecting against low to very low canopy cover ($< 50\%$), stands dominated by small (< 25 cm) trees, or open treeless areas (Fig. 5). Habitat selection at home range and nightly scales exhibited similar but weaker patterns, due to a stronger influence of sex and breeding status on habitat availability and selection, as well as variability among individual owls (Fig. 5, Appendices S5 and S6). Selection at finer scales (home range and nightly) may be limited by selection occurring at larger scales (Johnson, 1980), and others have reported strongest habitat selection at broader scales (Boyce et al., 2003; Stolen et al., 2007). We hypothesize that owls select high quality habitats at the landscape scale, potentially masking the importance of

finer-scale habitat selection. However, weaker habitat selection relationships at finer scales also may be due to preferences for habitat features outside the focus of this study, such as forest edges (Eyes et al., 2017; Williams et al., 2011), burned areas (Bond et al., 2016, 2009), or riparian corridors (Bond et al., 2016; Irwin et al., 2007) or other factors including conspecific and interspecific interactions. In contrast to other spatio-temporal scales, our results indicated that California Spotted Owls selected for less dense vegetation ($< 50\%$ canopy cover) during forays. Foraging birds could have been attempting to minimize transit to known distant locations, or attempting to avoid encounters with other territorial birds during forays. Mobile species, such as Spotted Owls, rely on multiple patches of suitable habitat within their home range and often traverse environments that are unsuitable for some activities (Holloway and Miller, 2017). California Spotted Owl movement patterns indicated birds are likely able to acquire environmental information (e.g., food and nest site availability, mortality risk) on alternative habitat choices across the landscape, when the costs of gathering such information does not outweigh the benefits.

Our estimates of California Spotted Owl breeding homerange sizes were comparable with those observed for this subspecies in nearby Lassen National Forest (Zabel et al., 1992; Fig. 3). Our estimates were larger than breeding home range estimates of Mexican Spotted Owls (regional means of 228–562 ha; U.S. Fish and Wildlife Service, 2012) and of Northern Spotted Owls (regional means of 388–1150 ha; Carey et al., 1992; Forsman et al., 2015), with which they hybridize in the Northern part of their range (Miller et al., 2017). We found differences attributable to sex and breeding status (Fig. 3, Appendix S3), which have not previously been reported for California Spotted Owls (Roberts, 2017). Non-breeding females had the largest home ranges, the greatest of which was a 6496 ha breeding-season MCP, 5 times the mean reported in the literature (Roberts, 2017). Larger female home range is partially attributable to foraging behavior, wherein females left home territories and visited multiple (up to 6) surrounding PACs. One female transited > 30 km in a night, and undertook multiple forays of > 10 km while repeatedly visiting areas where she nested in previous years (Fig. 4b, green traces). Males may incur relatively greater costs (e.g. reduced territory defense) compared to females when using areas at great distances from the nest site, which could explain why we did not observe male forays. Foraging females are not likely seeking current year or future extra-pair copulations, as California Spotted Owls exhibit synchronous biennial cycles in reproductive output (Blakesley et al., 2010) and extra pair fertilizations are not commonly reported among owl species (Arsenault et al., 2002; Koopman et al., 2007; Lawless et al., 1997; Marks et al., 1999; Saladin et al., 2007). Rather, foraging may represent prospecting for future opportunities, an exploratory behavior pattern not previously documented in this species.

Prospecting, or gathering advanced information about potential breeding habitat within an area before settling there, has been described in > 100 bird species (Reed et al., 1999 and references therein). Accurate assessment of quantity, quality and configuration of available habitat is important to individual fitness, population dynamics and distribution (Howard, 1920; Lack, 1971; Reed et al., 1999; Wiens, 1976). Individuals must be able to acquire reliable environmental information (e.g., food and nest site availability, mortality risk) on alternative habitat choices across a landscape without costs of information gathering outweighing the benefits (Cox and Kesler, 2012b; Kesler et al., 2010; Johnson, 1989; Reed and Oring, 1992). Our documented foraging behavior may be a precursor to dispersal, given 7% of breeding California Spotted Owls in a nearby study dispersed into new territories between breeding seasons and 42% of breeding dispersals were into adjacent territories (Blakesley et al., 2006). A recent study noted observations of California Spotted Owls in multiple PACs during a breeding season, but did not examine the behavior in detail nor report sex or breeding status of birds (Berigan et al., in press). To our knowledge, foray behavior has not been recorded for the Mexican Spotted Owls and has been noted but not studied for the Northern Spotted Owl (Forsman et al., 2002). Investigations using VHF telemetry typically have not reported the frequency or duration of periods when birds went undetected, but inability to locate birds during VHF studies could indicate foraging behavior. Recent declines in Northern Spotted Owl natal dispersal distances of 1 km per year, alongside habitat fragmentation and increases in Barred Owl populations, indicate a more detailed understanding of multi-scale movements of all Spotted Owl subspecies afforded by GPS-tracking is likely an important component for their conservation (Hollenbeck et al., 2018).

Protection of owl core use areas (nesting and roosting sites) through exclusion of stand-altering activities within designated PACs is currently the management focus for California Spotted Owls. In addition to establishing PACs, the U.S.D.A. Forest Service designates up to 971 ha of the best available California Spotted Owl habitat in the closest proximity to a PAC as a “Home Range Core Area” (HRCAs) (U.S.D.A. Forest Service, 2004), where owl habitat needs are to be considered in management decisions, but stand-altering vegetation management practices are allowable and routinely undertaken. Berigan et al. (2012) reported high overlap between PACs and core use areas based on long-term roosting and nesting data. Although our results indicated positive selection for PACs by foraging and roosting California Spotted Owls on the Plumas National Forest, we found relatively low overlap between PACs and both roost locations (< 50%) and foraging space use (< 25%). Indeed, for some owls < 5% of their foraging or roost locations were contained within the PAC in which they nested (or nested in the previous year). Furthermore, our estimates of owl home range size and distance travelled were restricted to the breeding season. Owls are likely to range over much wider distances annually, with PACs and even HRCAs consequently protecting only a small fraction of habitat used for complete annual life-history needs.

PACs were developed specifically to protect nesting and roosting sites, rather than the much broader foraging areas used by Spotted Owls. Nevertheless, California Spotted Owl populations continue to decline, particularly within study areas on National Forest lands (Blakesley et al., 2010; Conner et al., 2016; Tempel et al., 2016) for reasons that are not well understood but may include past and ongoing forest management activities (Jones et al., 2018; Tempel et al., 2017). Based on the relatively low overlap between PAC areas and roosting and foraging habitat use by the owls we studied, we hypothesize that insufficient habitat protection from stand-altering activities outside PAC areas could partially explain ongoing population declines. Most of the habitat used by owls for roosting and foraging in our study was outside of PACs and therefore available for stand-altering forestry activities. Even where PACs protect nesting stand conditions conducive to successful reproduction, stand-altering activities elsewhere in owl home ranges may reduce occupancy or reproductive success. For example, a

simulation study by Tempel et al. (2015) found that stand-wide fuel-reduction treatments that reduced canopy cover had a negative effect on owl nesting habitat and demographic rates 30 years into the future in the absence of fire. The same study predicted positive effects of fuel reduction treatments on owl nesting habitat and demographic rates if fire occurred in the study area (Tempel et al., 2015). While limited research to date has not indicated negative effects of timber harvest on California Spotted Owl foraging (Irwin et al., 2015), harvesting can reduce populations of key California Spotted Owl prey (Lehmkuhl et al., 2006; Williams et al., 1992). Relationships between prey dynamics and owl fitness are still poorly understood (Roberts, 2017).

Cumulatively, past results combined with our findings suggest that habitat conditions throughout individual California Spotted Owl home ranges – but beyond the boundaries of PACs – may be critical for fulfilling life history needs, and if inadequate, could be contributing to ongoing declines. Additionally, even habitat outside usual home ranges may be more important than has been previously considered. Non-breeding female owls traveled great distances (forays), sometimes roosting and spending over a week > 10 km from their territory centers before returning. Although it would seem obvious that connectivity of later seral forest across the landscape is important for this species, our finding that foraging owls selected habitat attributes (< 50% cover) in contrast to those selected during non-foray movements requires further study. Understanding the role of long distance foray movements in facilitating breeding dispersal, as well as genetic and demographic connectivity, and more generally, the importance of habitat well outside what has historically been considered the activity center of California Spotted Owls, is likely important for addressing ongoing population declines.

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Data accessibility

Data will be available by request from Plumas National Forest at the conclusion of this ongoing study.

Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2018.10.017>.

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Habitat Use and Selection by California Spotted Owls in a Postfire Landscape

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ABSTRACT Forest fire is often considered a primary threat to California spotted owls (*Strix occidentalis occidentalis*) because fire has the potential to rapidly alter owl habitat. We examined effects of fire on 7 radiomarked California spotted owls from 4 territories by quantifying use of habitat for nesting, roosting, and foraging according to severity of burn in and near a 610-km² fire in the southern Sierra Nevada, California, USA, 4 years after fire. Three nests were located in mixed-conifer forests, 2 in areas of moderate-severity burn, and one in an area of low-severity burn, and one nest was located in an unburned area of mixed-conifer-hardwood forest. For roosting during the breeding season, spotted owls selected low-severity burned forest and avoided moderate- and high-severity burned areas; unburned forest was used in proportion with availability. Within 1 km of the center of their foraging areas, spotted owls selected all severities of burned forest and avoided unburned forest. Beyond 1.5 km, there were no discernable differences in use patterns among burn severities. Most owls foraged in high-severity burned forest more than in all other burn categories; high-severity burned forests had greater basal area of snags and higher shrub and herbaceous cover, parameters thought to be associated with increased abundance or accessibility of prey. We recommend that burned forests within 1.5 km of nests or roosts of California spotted owls not be salvage-logged until long-term effects of fire on spotted owls and their prey are understood more fully. (JOURNAL OF WILDLIFE MANAGEMENT 73(7):1116–1124; 2009)

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KEY WORDS California spotted owl, fire severity, foraging habitat, forest structure, resource selection function, southern Sierra Nevada, *Strix occidentalis*, telemetry error.

Forest fire is a natural disturbance event and prominent management issue that can affect habitat of California spotted owls (*Strix occidentalis occidentalis*; Weatherspoon et al. 1992), a species that has driven many forest-management decisions in the Sierra Nevada and southern California, USA, for the past decade (U.S. Forest Service [USFS] 2001, 2004, 2005). Sierran mixed-conifer forests are a particularly important vegetation type for California spotted owls and are characterized by mixed-severity fire regimes, where complexes of lightly to severely burned patches at intermediate scales are common (Weatherspoon et al. 1992, Minnich et al. 1995, Centers for Water and Wildland Resources 1996, Tefler 2000). California spotted owls evolved in an environment that included a heterogeneous landscape partially shaped by fires that produced mixed patches of unburned, low-, moderate- and high-severity burned forest (Weatherspoon et al. 1992, Centers for Water and Wildland Resources 1996). Vital rates of spotted owls are positively associated with forest characteristics, including the amount of older conifer-dominated forest in an area (Blakesley et al. 2005, Seamans 2005).

Beginning in the early 20th century, natural and human-caused processes changed fire regimes of forests in the western United States. Changes in climate resulted in periods of increased moisture and warmer temperatures (Centers for Water and Wildland Resources 1996). Extensive harvesting shifted the size distribution of trees within forested stands from larger, older trees with greater inter-tree gaps to denser forests with more smaller sized

trees (McKelvey and Johnston 1992, Centers for Water and Wildland Resources 1996). By the mid-20th century, policies of vigorous fire suppression led to exclusion of this once more frequent and widespread disturbance process (Weatherspoon et al. 1992).

Because California spotted owl nests and roosts are associated with older forests and high tree-canopy cover (Bias and Gutiérrez 1992, Call et al. 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997, Bond et al. 2004), many forest managers postulate that high-severity fires could have a negative impact on persistence of the species and, therefore, believe that fire poses the greatest risk to owl habitat (Weatherspoon et al. 1992; USFS 2001, 2004, 2005). Reducing fire risk by modifying owl habitat is considered necessary to help conserve the species. In addition, burned forests that once provided habitat for spotted owls may be presumed unusable and trees harvested as salvage.

Results from past studies of fire impacts on spotted owls are equivocal. Fires with large patches burned at high severity seemed to adversely affect occupancy rates in some owl territories, whereas in other territories experiencing high-severity fire, spotted owls have remained and continued to reproduce (see e.g., MacCracken et al. 1996, Gaines et al. 1997, Bond et al. 2002, Jenness et al. 2004). Franklin et al. (2000) hypothesized that fire could enhance prey abundance and access to prey by creating patchy openings within otherwise closed forest canopy and by increasing habitat edges.

Although spotted owls continue to occupy burned landscapes, few data have been published that describe how owls use burned landscapes. Managing burned

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landscapes for the benefit of California spotted owls requires understanding how owls use burned portions of their territories for nesting, roosting, and foraging. We report on habitat use and selection by 7 California spotted owls occupying a landscape that burned 4 years previously in the 2002 McNally Fire in the southern Sierra Nevada, California. Our study objectives were to determine whether this sample of California spotted owls nested, roosted, and foraged differentially according to vegetation burn severity. Specifically, we sought to 1) characterize nesting and roosting sites of California spotted owls relative to burn severity and conventional microhabitat descriptors, 2) quantify the probability that a spotted owl in our sample would select a roost site according to burn severity, 3) develop and contrast multiple resource selection probability functions (RSPF; Manly et al. 2002) to quantify the probability of foraging habitat use by owls according to burn severity and other ecologically pertinent covariates, and 4) quantitatively describe and compare structural characteristics of vegetation within the burn-severity categories.

STUDY AREA

We conducted our study at 2 areas, the Greenhorn Mountains and the Kern Plateau, both in Sequoia National Forest, southern Sierra Nevada Mountains, California. The Greenhorn Mountains are approximately 20 km northwest, and the Kern Plateau is approximately 20 km north-northeast, of the town of Kernville, California. These 2 areas are separated by Kern River Canyon and are approximately 13 km apart.

Elevations at both areas ranged from 1,500 m to 2,500 m. The nearest National Weather Service weather station at Johnsondale (1,427 m) recorded an annual average precipitation of 57 cm from 1971 to 2000 (National Climate Data Center 2008). Vegetation was classified as Sierran Mixed Conifer (Allen 1988), dominated by ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), and white fir (*Abies concolor*). Above 2,100 m, a transition zone was dominated by red fir (*A. magnifica*). Other common tree species included sugar pine (*P. lambertiana*), incense cedar (*Calocedrus decurrens*), canyon live oak (*Quercus chrysolepis*), and California black oak (*Q. kelloggii*).

In July and August 2002, the McNally Fire burned approximately 60,985 ha in the Sequoia and Inyo National Forests, including 33,704 ha of conifer-dominated forests (Odion and Hanson 2006). Like most fires, the McNally Fire burned with variable severity, leaving a mosaic in the 2 study areas. Using USFS vegetation burn-severity maps (USFS 2006), we estimated that 31% of conifer forest types remained unburned in foraging ranges of the spotted owls that we studied, whereas 29%, 27%, and 13% were burned at low-, moderate-, and high-severities, respectively.

METHODS

Spotted Owl Habitat Use

We collected location data from sites used by California spotted owls for roosting, nesting, and foraging, and vegetation data from sites available to owls. We defined

selection as use of a particular forest burn-severity class at a greater frequency than expected given its availability.

Our field procedures for sampling habitat use by California spotted owls entailed 1) surveying and locating spotted owls at previously occupied sites near or within the McNally Fire, 2) capturing owls and affixing radiotransmitters, and 3) relocating owls at daytime roosts or in nests and at nighttime foraging sites using radiotelemetry. Prior to our study, USFS personnel surveyed for and located California spotted owls occurring within and adjacent to the McNally Fire perimeter during 3 consecutive breeding seasons 2003–2005 (W. Rannals and R. Galloway, USFS, unpublished data). We selected 4 territories confirmed to be occupied by pairs of spotted owls during the 2006 breeding season. We selected these 4 territories because 1) territory juxtaposition was inside or within 1 km of the fire perimeter, giving occupying owls access to burned and unburned forest; 2) these territories were occupied by spotted owls continually since the fire; and 3) there was sufficient road access for effective radiotracking.

We located, captured, and classified sex of California spotted owls using standard techniques (Forsman 1983, Franklin et al. 1996). We also affixed backpack-style radiotransmitters designed to minimize contact with the owl's back (AVM Instrument Company, Ltd., Colfax, CA; J. P. Ward, New Mexico State University, unpublished data) using Kevlar ribbon (0.63-cm wide; Bally Ribbon Mills, Bally, PA). Our transmitter units with harness weighed <20 g, or <4% of each owl's body mass.

We considered individual owls as sampling units because previous studies of California spotted owls found that males and females foraged independently (Call et al. 1992, Zimmerman et al. 2001). We located each owl nightly or every other night between 2130 hours and 0400 hours. We also located each owl during the day every 7–10 days to obtain roosting locations and measure our telemetry-location error. We used a systematic design with a random start to collect a representative sample of foraging locations. We randomly assigned each individual owl to a 1-hour time block in the first night that we tracked the owl, then we systematically shifted each owl's time block by 1 hour (or back to the first time block when the sequence was completed) on each subsequent sampling night.

We estimated owl locations by triangulation on signals from the affixed radiotransmitters. We used ≥ 3 compass bearings of the strongest signals with all bearings taken within approximately 30 minutes for estimating each owl location (Guetterman et al. 1991). We used handheld 3-element collapsible directional Yagi antennas and portable receivers supplied by AVM Instrument Company, Ltd. and Telonics (Telonics, Inc., Mesa, AZ) for deciphering signal strength and direction. We used a Geographic Positioning System (error <10 m) to determine Universal Transverse Mercator (UTM) coordinates of telemetry monitoring stations and spotted owls visually observed at roosts or nests and Program LOCATE III (Pacer Computing, Tatamagouche, NS, Canada) to estimate the most likely point-location of the radiomarked owls from observer location and direction of the radio signals using a

maximum likelihood estimator (Nams 2006). We plotted and analyzed all spatial data using ArcMap 9.1.

Available Habitat Types

To quantify habitat selection, we needed to estimate the amount of different habitat types available to owls during the study. We used spatially explicit data generated by the USFS (USFS 2006) to estimate amounts of habitat and vegetation burn severity within foraging ranges of owls that we approximated for the primary period for rearing young (May through mid-Aug) using a circle with radius that extended from a nest or roost center to the furthest documented foraging location for each radiomarked owl. We used a nest location as the center of the approximated foraging range if young were produced and fledged during the study. Otherwise, we used a harmonic mean of roost locations for each individual owl generated in Animal Movement Program (Hooze et al. 1999). For analyzing selection of foraging sites, we quantified available habitat by intersecting a systematic sample of grid-points in each owl foraging range with the digital habitat maps (see Foraging Habitat Selection).

We classified habitat within foraging ranges according to digital data layers of existing vegetation type and burn severity from the McNally Fire using Geographic Information System (GIS) maps. The vegetation map we used (EVEG Tile; Goudy and Smith 1994) was updated by USFS analysts in 2001 using a combination of automated-systematic procedures, remote sensing classification, photo editing, and ground surveys. Minimum mapping size was 1 ha and 30-m pixel size (Allen 1988). California Wildlife Habitat Relations (CWHR; Mayer and Laudenslayer 2002) vegetation type was derived from EVEG data.

To create a GIS layer of severity of vegetation burned by the McNally Fire, USFS analysts used Landsat Thematic Mapper data before and after the fire and field data on vegetation collected 1 year following several Sierra Nevada fires that occurred from 2001 to 2004 for ground verification of the remote sensing data. The resulting map showed 4 classes of fire severity: 1) Unburned-unchanged—areas in which conditions 1 year after the fire were indistinguishable from prefire conditions; 2) Low severity—areas of surface fire with little change in cover and little mortality of dominant vegetation; 3) Moderate severity—areas between low- and high-severity classes and representing a mixture of effects on dominant vegetation; and 4) High severity—areas where dominant vegetation had high to complete mortality due to fire. We considered including clearcut areas as an additional category because there were scattered pre- and postfire clearcuts within 5 of the owl foraging ranges. However, we calculated after mapping that <3% of all available habitat as defined by our owl foraging ranges had been clearcut and considered this habitat class too limited for detecting use given our sample of foraging sites for each owl.

Available Habitat Structure

We described vegetation in each burn-severity category using structural measures of owl habitat (e.g., Gutiérrez et al. 1992).

We measured structural features at 5 randomly selected sites within each of the 4 GIS-classified burn-severity categories of conifer and mixed-conifer forest types within the largest foraging range of each of 4 owl pairs. Ground-truthing of GIS-classifications indicated slight errors, which resulted in unequal sample sizes among burn-severity categories, mostly between the unburned and low-severity burn ($n = 15$, unburned; 26, low severity; 20, moderate severity; 19, high severity; for 80 sites across all 4 pairs).

At each of the 80 sites, we measured tree-canopy cover, tree size by condition (dead or alive), herb and shrub cover, and size and number of fallen logs, and we assessed vegetation burn severity. We established a center for each sampling plot at a tree ≥ 30 cm diameter at breast height nearest to the random UTM location because we assumed that large trees provided perches for foraging spotted owls. At each center tree, we centered 2 perpendicular transects 25 m long with the direction of the first transect determined by a spin of a handheld compass. We measured canopy cover by taking a spherical densitometer reading every meter for 50 readings. We recorded species and number of all live trees and fire-killed or prefire snags >15 cm diameter at breast height within a variable circular plot using a 20-basal-area-factor prism from the center tree. We measured the diameter of each tallied tree or snag with a Biltmore stick (Forestry Suppliers, Inc., Jackson, MS) or diameter tape. We measured herb and shrub cover by recording the length (cm) of transect intersected by shrub, bare ground, and herbaceous vegetation. We indexed amount of downed wood in each plot by counting the number of segments in each of 3 diameter categories (15–29 cm, 30–59 cm, ≥ 60 cm) that intersected the transect. Lastly, we assigned burn severity of the stand based on a visual, qualitative estimation of the amount of vegetation burned and the definitions used by the USFS to produce the burn-severity map.

We measured the same microhabitat vegetation characteristics at all 4 nest sites and a sub-sample of 33 roost sites distributed among all 4 owl territories. At these sites, we used the actual nest or roost trees as plot-center.

Data Analyses

To quantify accuracy of burn-severity mapping, we constructed an error matrix (Story and Congalton 1986, Congalton and Green 1993) structured to report user and producer errors for each burn-severity class. We combined accuracy values from each class to determine overall accuracy of the burn-severity map.

We assessed accuracy of telemetry methods by first estimating locations of radiomarked owls while they were stationary at roosts or nests every 7–10 days using telemetry signals and compass bearings and then by subsequently finding the actual locations by following the strongest radio signal until we observed owls visually. We then used distance and direction vectors from estimated to actual observed radio locations to calculate radiotelemetry bias. From the distance–direction vectors, we estimated the long-axes (m) of a 95% Hotelling's confidence ellipse (Batschelet 1981) for each of 5 owls for which we amassed ≥ 5

distance–direction samples. We used overall mean of the 5 mean values for each owl as a radius of a telemetry-error circle, which we circumscribed around each estimated foraging location. Establishing the telemetry-error circle around each point also allowed us to account for instances where owls foraged at habitat edges (Zabel et al. 1995, Ward et al. 1998). We classified foraging sites that included <90% of the same habitat within an associated telemetry-error circle as an edge site.

We described nesting and roosting habitat according to the burn-severity class that defined the location of the observed nest or roost tree for each individual or pair of owls. We tested for selection of roosting habitat using resource selection ratios ($\hat{w}$), which in this case were ratios between the proportion of roost sites found in a burn-severity class divided by the proportion of that class estimated to be available (Manly et al. 2002). We took the latter proportions from GIS maps of estimated owl foraging ranges. We used Bonferroni-corrected 95% confidence limits to denote selection ($\hat{w} > 1$), use equal to availability ($\hat{w} = 1$), or avoidance ($\hat{w} < 1$) of a burn-severity class. We based this analysis on combined use of all 7 owls in the sample.

We analyzed selection of foraging habitat by California spotted owls by comparing frequency of used and available habitat utilizing logistic regression to estimate a RSPF (Manly et al. 2002). We quantified used habitat with telemetry-estimated foraging locations. We calculated available habitat for each owl from a systematic sample of all telemetry-error circles within its approximated foraging range with centers spaced at twice the error-circle radius.

For the RSPFs, we developed a series of logistic regression models to estimate probabilities that a particular burn severity was used (Manly et al. 2002) using Stata 8.0 (Stata Corporation, College Station, TX). Our model structure identified each individual owl's data as a group of used and available sites with owl treated as a random effect, with distance, burn severity, and other covariates as fixed effects. Thus, we compared each owl's foraging points only with its own available habitat. In addition to owl identity and burn severity, we analyzed other variables believed to affect the owls' selection of foraging habitat. Spotted owls are central-place foragers during the breeding season (Carey and Peeler 1995) so we modeled foraging-habitat selection as a function of distance and distance² from the center of the foraging-range circle (Rosenberg and McKelvey 1999, Glenn et al. 2004). Laymon (1988) found that random sites had steeper slopes than foraging sites, so we included percent slope as a variable. Franklin et al. (2000) reported that northern spotted owl survival and reproduction were positively associated with amount of edge in the territory, so we also included an edge effect as a binomial variable indicating that a foraging point telemetry-error circle included <90% of one burn-severity class. Lastly, although Zimmerman et al. (2001) found evidence that members of a California spotted owl pair foraged independently, we included a sex effect to account for possible negative association, sex-specific foraging patterns, or within-territory habitat partitioning. Thus, our global model included effects of owl, burn severity,

distance from center of foraging range, this distance², edge, and slope. We also included 2-way interactions of owl, burn severity, and distance to investigate whether selection of different burn severities varied independently according to owl and distance.

We established 30 a priori models that included various nested and nonnested subsets of the global model. Our primary focus was to assess the influence of burn severity on foraging site selection. This model set also included sex, slope, and edge effects mainly as possibly confounding parameters to be controlled for, but we did not model these parameters with great complexity. We followed an information-theoretic approach (Burnham and Anderson 2002) using Akaike's Information Criterion corrected for small sample sizes (AIC_c) and assigning AIC_c weights to rank candidate models and formalize evidence that a particular model is supported by the underlying data.

We limited our analysis of structural conditions in burn-severity classes to those variables that previous researchers determined to be key components of spotted owl foraging habitat. California spotted owl foraging locations have been characterized by greater basal area of medium (28 cm) to large trees (>61 cm), high canopy cover, lower basal area of smaller trees (<28 cm), higher snag basal area, gentler slopes, greater conifer basal area, greater shrub cover, and more coarse woody debris than random sites (Gutiérrez et al. 1992). Northern spotted owls (North and Reynolds 1996, McDonald et al. 2006) and California spotted owls (Call et al. 1992, Gutiérrez et al. 1992, Irwin et al. 2007) also selected foraging sites with greater hardwood basal area and multiple canopy layers. Shrub and herbaceous ground cover and downed wood are associated with prey of spotted owls like woodrats (*Neotoma* spp.), northern flying squirrels (*Glaucomys sabrinus*), and white-footed mice (*Peromyscus* spp.; Williams et al. 1992, Block et al. 2005, Innes et al. 2007). Thus, our independent variables included tree-canopy, shrub, and herbaceous cover, coarse woody debris >15 cm diameter, basal areas of various combinations of live and dead conifer and hardwood trees of different size classes, mean and variance of tree diameter at breast height, and percent slope.

Using an information-theoretic approach, we described differences in habitat structure among burn-severity categories with a parsimonious model that best fit the microhabitat data we collected in the field. According to AIC_c and associated weights, we selected a top model from a set of 26 a priori candidate models developed from previous studies on spotted owl foraging habitat and biological knowledge. We modeled the 4 burn-severity categories as a function of multiple continuous or discrete independent variables (microhabitat measurements) with multinomial logistic regression, also known as polytomous logistic regression (North and Reynolds 1996).

RESULTS

We located, captured, and radiomarked 4 male and 3 female California spotted owls on 4 territories between 22 May and 12 June 2006. From 22 May through 15 August 2006, we identified all 4 nest trees and 60 roost sites (range = 4–11

Table 1. California Wildlife Habitat Relationship (CWHR) vegetation type, burn severity, number of spotted owl foraging locations in each burn-severity category, percent of foraging points and 4.1-ha circles in each category, and mean percent of each category that was available within foraging ranges of 7 California spotted owls in the McNally Fire, Sequoia National Forest, California, USA, during the 2006 breeding season. Blank indicates quantities <1%. We excluded 17 locations from vegetation types that comprised <4% of total available habitat.

CWHR vegetation type	Burn severity	Total no. of foraging points in category	% of foraging sites		Average % available in foraging ranges
			Points	Error circles	
Sierran mixed conifer	Unburned	26	9	10	15
	Low	107	35	34	16
	Moderate	69	23	23	14
	High	35	12	12	7
Montane hardwood	Unburned	10	3	3	4
	Low	3	1	2	3
	Moderate	6	2	2	4
	High	1			2
Red fir	Unburned	2	1		5
	Low	1		1	3
	Moderate	0			2
	High	0			1
Montane hardwood-conifer	Unburned	4	1	2	2
	Low	4	1	2	2
	Moderate	7	2	2	2
White fir	Low	7	2	2	2
	Moderate	1			1
	High	1			

roosts/owl) and estimated 301 foraging locations (range = 32–53 locations/owl). Distance from nest or harmonic mean of roost locations to the owl's farthest foraging point during this period ranged from 1,149 m to 3,444 m ($\bar{x}$ = 2,149 m). Areas within owls' foraging ranges that we calculated from these distances ranged from 415 ha to 3,726 ha ($\bar{x}$ = 1,451 ha) for this period.

Overall accuracy of the burn-severity map was 93% correct (n = 80 sites). User's accuracy of the 4 burn-severity classes on this map ranged 75–100% and producer's accuracy ranged 81–100%. We observed 6 misclassifications in the field. Of 20 sites classified as unburned 5 were actually burned at low severity and 1 of 20 sites classified as moderate severity was actually burned at high severity.

Average telemetry error (linear distance between estimated and actual roost locations) among all owls was 82 m (SD = 65.4 m, n = 34 locations among 7 owls). Population mean value of the long-axis of the 95% Hotelling's confidence ellipse from 5 owls with ≥ 5 locations each was 114 m (SE = 60.6 m). We used the 114-m error-radius to calculate a 4.1-ha telemetry-error circle around each estimated owl foraging location and we used 2 times the radius (228 m) to space the systematic sample of circle centers for obtaining available habitat amounts.

All burn-severity classes were utilized by spotted owls for roosting. We classified 17 of 60 roosts on the GIS vegetation burn-severity map as unburned (28%), 34 as burned at low severity (57%), 9 as burned at moderate severity (15%), and none in high severity. Vegetation surveys at a sub-sample of roost sites (n = 33) documented one roost classified on the GIS map as moderate severity that was actually in high-severity burned forest. Selection ratios indicated that forest burned at low severity was selected for roosting (95% CI of $\hat{w}$ = 1.31–2.60), unburned forest (0.36–1.46) was used for roosting in proportion to its availability, and forest burned at moderate severity (0.02–

0.97) was avoided for roosting. We recorded only one incidence of roosting in the high-severity burn class. Sampled roost sites averaged tree-canopy cover of 63% (SE = 3.5), similar to unburned forests, a mean tree diameter at breast height of 63 cm (SE = 3.6), and a high basal area of large trees, averaging 30 m²/ha (SE = 3.2).

Spotted owl pairs in all 4 territories attempted to nest in spring 2006 as determined by behavior and evidence of brood patches on females. Nests in 3 territories were located within the boundaries of the fire, and the nest in one territory was located approximately 500 m outside the fire boundary. We documented one nest tree in unburned mixed conifer-hardwood, one in conifer forest burned at low severity, and 2 in conifer forest burned at moderate severity. One pair, nesting in a stand burned at moderate severity, produced the only fledgling of the 4 nesting attempts. All 4 nest trees were large (≥ 72 cm) conifers, including one apparently killed by the fire within a moderately burned stand.

Twelve CWHR vegetation types were used by foraging owls, but most (78%) foraging locations were in Sierran Mixed Conifer vegetation, with 12% in Montane Hardwood and Hardwood-Conifer vegetation (Table 1). We assessed 301 foraging sites, an average of 43 (SD = 7.6) sites/owl, and an average of 305 available sites/owl (SD = 195.5) for a total of 2,433 sites. All burn-severity classes were utilized by foraging spotted owls. Proportions of availability for the 4 burn-severity classes were not highly variable among individual owls (CVs were $\leq 29\%$ in all categories, mean CV = 19%).

Our global model with individual owl effects, including owl $\times$ distance, owl $\times$ burn severity, and distance $\times$ burn severity interactions, fit best (AIC_c wt = 1.0; all other models were >13 AIC_c values of the top model). The RSPFs indicated that selection probabilities varied among owls, with all burn-severity classes influencing selection of foraging habitat. A mean RSPF generated by combining RSPFs from individual

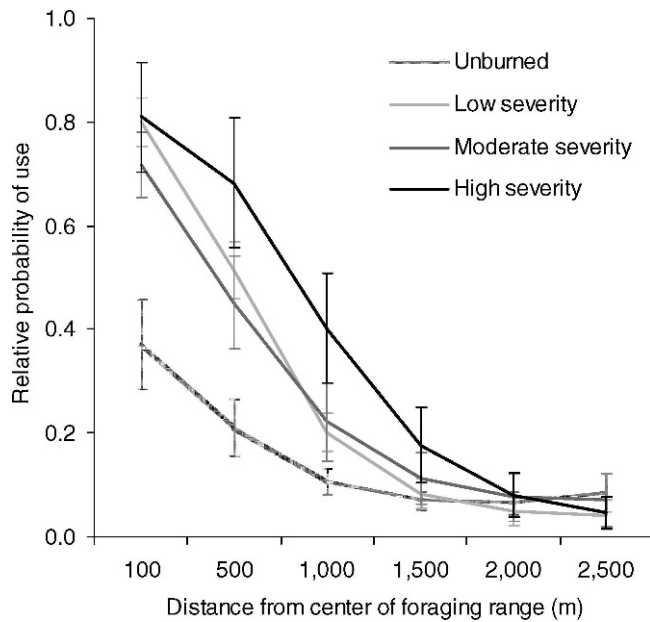


Figure 1. Mean resource selection probability functions ($\pm$ SE) for 7 California spotted owls foraging at different distances from the center of the owls' breeding foraging range in forest burned at different severities (unburned, low, moderate, and high) in the McNally Fire, Sequoia National Forest, California, USA, 2006. Probabilities generated from coefficients in top-ranked model.

owls includes a curvilinear reduction in probability of use with distance from the center of foraging range that varied with severity of burn (Fig. 1). Probability that any of these 7 owls would use a site for foraging was greatest when the site was burned and was located within approximately 1 km of a nest or roost center (Fig. 1). For 5 of 7 owls, strongest selection for foraging areas was in high-severity burned forest within 1.5 km from the center of their foraging ranges. Although selection of burned forest for foraging was strong, high standard errors indicate selection was variable among owls. Conversely, unburned forest generally had lower probability of use for foraging, although 2 owls showed increased use of unburned forest at locations furthest from the center of their foraging ranges. No discernable difference in use patterns

among burn severities was evident beyond 1.5 km. Both steepness of slope and edge affected selection of foraging sites, as they were included in the top model; probability of a foraging site being used was negatively related to steepness of slope and positively related to presence of an edge between burn-severity classes.

The model that best described differences in habitat variables among the 4 burn severities (AIC_c wt = 0.99) included percent tree-canopy cover, percent shrub and sapling cover, percent herbaceous cover, amount of coarse woody debris, basal area of snags, mean tree diameter at breast height, variance of tree diameter at breast height, and percent slope (Table 2). Canopy cover was highest at unburned sites and lowest at high-severity burned sites. Unburned sites were characterized by many pieces of coarse woody debris >15-cm diameter and small live trees 15–27-cm diameter at breast height. Low-severity burned sites had the highest basal area of large live trees with diameter at breast height >53 cm, although this metric was not included in the top-ranked model. Moderate-severity burned sites were characterized by the highest mean diameter at breast height and greatest variance of diameter at breast height of all trees, live and dead. High-severity sites had the highest herb and shrub cover, highest basal area of snags, and steepest slopes (Table 2).

DISCUSSION

The California spotted owls we studied used all severities of burned forest for nesting, roosting, and foraging during the breeding season 4 years after a large forest fire. We detected a negative effect of distance from the center of an owl's foraging range on utilization of habitat for foraging, regardless of burn severity, as expected for central-place foragers. However, we documented one owl traveling >3.4 km from the center of a foraging range, indicating that an owl will travel at least this distance while foraging during the breeding season. After accounting for distance, spotted owls selected burned areas for foraging over unburned forest, with the greatest selection for high-severity burned areas.

Vegetation characteristics of different burn-severity categories provide insight into why these spotted owls might be

Table 2. Conventional measures of spotted owl microhabitat estimated ($\bar{x}$ with SE) from a sample of randomly selected plots in each of 4 burn categories available to 7 California spotted owls for roosting, nesting, or foraging in the McNally Fire, Sequoia National Forest, California, USA, from May to August 2006.

Habitat variable	Burn severity							
	Unburned		Low		Moderate		High	
	$n = 15$		$n = 26$		$n = 19$		$n = 20$	
	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE	$\bar{x}$	SE
% canopy	62.5	4.76	51.4	3.26	27.9	3.64	14.7	2.26
% herb	14.5	4.41	12.6	2.13	17.8	5.11	32.3	5.72
% shrub and sapling	19.5	2.70	11.2	1.99	12.4	2.94	39.8	5.80
No. of pieces coarse woody debris >15 cm	4.3	1.02	1.7	0.41	1.9	0.43	1.8	0.39
Basal area of live trees 15–27 cm (m^2/ha)	11.4	2.83	2.7	0.81	1.9	1.01	0	0
Total snag basal area (m^2/ha)	5.8	2.96	15.0	3.94	13.8	2.65	48.4	5.15
Basal area of live trees and snags >53 cm (m^2/ha)	23.9	5.96	34.3	6.02	24.5	3.05	19.9	4.39
Mean dbh (cm)	53.2	5.04	58.5	3.54	72.5	4.34	54.0	4.17
Variance of dbh (cm)	756.4	199.36	713.6	101.26	1,224.4	208.02	1,033.3	306.30
% slope	14	1	16	2	16	1	24	2

selecting burned forest for foraging and low-severity burned forest for roosting 4 years postfire. Several of the parameters in our best model for distinguishing owl habitat structure among burn-severity classes may be associated with increased abundance or accessibility of prey. Spotted owl prey species, including dusky-footed woodrats (*N. fuscipes*), are more abundant in plant communities with greater understory hardwood, shrub, and herbaceous cover (Carey et al. 1992, Williams 1992, Lee and Tietje 2005, Innes et al. 2007). Understory plants, particularly shrubs and forbs, provide food for woodrats (Williams et al. 1992) and dense shrubs provide excellent cover. Both of these factors may contribute to greater abundance of this key prey species and stimulate attraction by spotted owls to high-severity burned sites after postfire vegetation regrowth has produced a modest understory. In the northern Sierra Nevada, northern flying squirrels and deer mice (*P. maniculatus*) are most abundant in areas with open canopy and high shrub cover (Coppeto et al. 2006). Deer mice have also shown strong affinity to forest openings where conifer seeds may become more accessible or stronger competitors may be limited in number (Gashwiler 1979, Galindo and Krebs 1985).

Another important vegetation difference among burn-severity categories in our study was the greater number of snags in high-severity burned areas relative to other categories. Snags provide shelters for prey species like woodrats and flying squirrels. In the southern Sierra Nevada, dusky-footed woodrat nests are common where shrubs encircle rock outcrops or snags (Lawrence 1966). Bushy-tailed woodrat (*N. cinerea*) densities in dry forests of eastern Washington, USA, were strongly correlated with arboreal and terrestrial cover in the form of large snags, mistletoe, and large soft logs (Lehmkuhl et al. 2006). Northern flying squirrel population densities in Oregon, USA, were correlated with the occurrence of suitable nesting cavities in trees and early decay-stage snags with diameters >50 cm (Volz 1986).

Although we found no reports on the direct effects of fire on common spotted owl prey in Sierran mixed-conifer habitat, we suspect on the basis of habitat requirements that northern flying squirrels may suffer the greatest or take longer to recover than woodrats or forest-dwelling mice (Waters and Zabel 1995). Adult dusky-footed woodrats do not suffer reduction in survival or abundance from understory fire of low to moderate intensity and patchy distribution in oak woodlands (Lee and Tietje 2005), but reductions in survival and abundance can occur immediately after hotter, more complete burns for chaparral-dwelling (Wirtz 1977, Wirtz et al. 1988) and desert-dwelling (Simons 1991) woodrats. However, low-severity burned or unburned patches may serve as refugia from which animals can recolonize areas with a recovering understory like that observed in patches of forest that burned at high severity. In addition, a number of studies have concluded that populations of deer mice increase after fire (Tevis 1956, Gashwiler 1959, Bendell 1974, Ream 1981, Converse et al. 2006). In summary, the most likely explanation for the greater probabilities of use by spotted owls of forest patches burned at high severity was increased presence of prey

promulgated by enhanced habitat conditions, which we documented as increased shrub and herbaceous cover, and number of snags. Additional research is needed to determine precise effects of different severities of fire and associated patch sizes on populations of California spotted owl prey, whether increased prey abundance or access ultimately provides an ecologically significant benefit to spotted owls or other predators, and the duration of any such effects.

Spotted owls in our study area selected low-severity burned forest for roost sites, avoided roosting in higher severity burns, and used unburned roost sites in proportion to their availability. Our field-sampled roost sites had an average tree-canopy cover >60% and were dominated by large trees. California spotted owl roost sites in previous studies also were characterized by higher canopy cover and larger diameter trees (Call et al. 1992, Gutiérrez et al. 1992, Moen and Gutiérrez 1997). These characteristics may serve such functions as predator avoidance, protection from mobbing, and thermoregulation (Gutiérrez et al. 1992, Franklin et al. 2000).

The range of burn severities used by spotted owls in our study illustrates that a mosaic of burn severities in California spotted owl territories apparently can satisfy owl habitat requirements for ≥ 4 years postfire. Investigations into the influence of spatial characteristics of different burn severities such as patch size and shape on probability of postfire occupancy from a larger sample of spotted owls may provide insight into the reason results from previous studies on impacts of fire on this species were equivocal.

Although RSPFs describe habitat selection, habitat conditions identified by our modeling should not necessarily be considered definitive indicators of population requirements. Longer term studies should be conducted to quantify vital rates of spotted owls in burned versus unburned landscapes over multiple years in conjunction with prey studies and without the confounding effect of postfire salvage-logging. Evaluating long-term impacts of fire on spotted owls will also require a better understanding of postfire habitat change over time and whether those changes will further affect habitat suitability for spotted owls.

MANAGEMENT IMPLICATIONS

California spotted owls whose territories included unburned and burned Sierran mixed-conifer forest of low- to high-severity made use of all burn severities, with high probability of foraging in burned areas, including high severity, within 1.5 km of nests or roosts, and selectively roosted in low-severity burned areas. Accordingly, we implore restraint in assuming all fire has a negative impact on late-seral forest habitat specialists like spotted owls. The assumption that moderate- and high-severity burned forest is not suitable spotted owl habitat has provided a basis for risk assessments of timber harvesting as fuels treatments (e.g., Lee and Irwin 2005) but may be inappropriate in the development of pre- and postfire management prescriptions. Because our sample of California spotted owls in the McNally Fire did not avoid burned areas for nesting, roosting, and foraging, burned forest may have provided some benefits to this species. We

recommend that burned forests within 1.5 km of nests or roosts of California spotted owls not be salvage-logged until long-term effects of fire on spotted owls and their prey are understood more fully.

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RESEARCH ARTICLE

California Spotted Owl (*Strix occidentalis occidentalis*) habitat use patterns in a burned landscape

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ABSTRACT

Fire is a dynamic ecosystem process of mixed-conifer forests of the Sierra Nevada, but there is limited scientific information addressing wildlife habitat use in burned landscapes. Recent studies have presented contradictory information regarding the effects of stand-replacing wildfires on Spotted Owls (*Strix occidentalis*) and their habitat. While fire promotes heterogeneous forest landscapes shown to be favored by owls, high severity fire may create large canopy gaps that can fragment the closed-canopy habitat preferred by Spotted Owls. We used radio-telemetry to determine whether foraging California Spotted Owls (*S. o. occidentalis*) in Yosemite National Park, California, USA, showed selection for particular fire severity patch types within their home ranges. Our results suggested that Spotted Owls exhibited strong habitat selection within their home ranges for locations near the roost and edge habitats, and weak selection for lower fire severity patch types. Although owls selected high contrast edges with greater relative probabilities than low contrast edges, we did not detect a statistical difference between these probabilities. Protecting forests from stand-replacing fires via mechanical thinning or prescribed fire is a priority for management agencies, and our results suggest that fires of low to moderate severity can create habitat conditions within California Spotted Owls' home ranges that are favored for foraging.

Keywords: California Spotted Owl, fire severity, habitat selection, Yosemite National Park

Patrones de uso de hábitat de *Strix occidentalis occidentalis* en un paisaje con incendios

RESUMEN

Los incendios son procesos dinámicos de los ecosistemas de bosques mixtos de coníferas de la Sierra Nevada, pero la información científica que evalúa el uso de hábitat de la fauna en paisajes quemados es limitada. Estudios recientes presentan información contradictoria con respecto a los efectos de los incendios forestales que reemplazan rodales de bosque sobre poblaciones de *Strix occidentalis* y su hábitat. Mientras que los incendios promueven paisajes de bosque heterogéneos que son preferidos por estos búhos, los incendios de alta severidad pueden crear grandes claros en el dosel que pueden fragmentar el hábitat de dosel cerrado preferido por *S. occidentalis*. Usamos telemetría de radio para determinar si los *S. o. occidentalis* del parque nacional Yosemite exhiben selección por un tipo particular de severidad en los incendios en su ámbito hogareño mientras forrajea. Nuestros resultados sugieren que *S. o. occidentalis* presentó selección de hábitat en su ámbito hogareño para sitios cerca de los nidos y hábitats de borde, y selección débil por áreas con incendios menos severos. Aunque los individuos seleccionaron bordes de alto contraste con mayores probabilidades relativas que los bordes de bajo contraste, no detectamos una diferencia estadística en estas probabilidades. La protección de los bosques contra los incendios forestales usando podas o incendios controlados es una prioridad para las agencias de manejo y nuestros resultados sugieren que los incendios de intensidad baja a moderada pueden crear condiciones de hábitat preferidas para el forrajeo en los ámbitos hogareños de *S. occidentalis*.

Palabras clave: parque nacional Yosemite, selección de hábitat, severidad de los incendios forestales, *Strix occidentalis*

INTRODUCTION

In the multilayered, structurally complex, and large tree–dominated forests (hereafter, ‘old forests’) occupied by the California Spotted Owl (*Strix occidentalis occidentalis*),

fire is critical for maintaining forest structure and function (Collins et al. 2011). Currently, California Spotted Owl populations are declining due to habitat loss and fragmentation (Tempel et al. 2014). The role of stand-replacing fires is complex and research has produced

conflicting results, with some studies suggesting that large stand-replacing fires may pose a new threat to Spotted Owl habitat (Spies et al. 2010, Tempel et al. 2014, Jones et al. 2016) and others indicating limited negative effects on the owls (Bond et al. 2009, 2016, Lee and Bond 2015a). Fire has an essential role in forests inhabited by Spotted Owls, yet that role is changing as the spatial extent and behavior of fire increases and intensifies, respectively, due to a warming climate (Stephens et al. 2013) and decades of fire suppression (Collins et al. 2011). Therefore, it is critical for land managers to understand the effects of fire on California Spotted Owl habitat selection, especially if they want to develop a conservation strategy for a changing forest.

Patterns of fire severity (magnitude of change in vegetation, often measured as tree basal area removed by fire) affect important characteristics of owl nesting and roosting habitat, such as canopy closure and cover, forest structure, and persistence of large trees (Collins et al. 2011, Roberts et al. 2011). However, because the foraging habitat of owls has greater structural variability than their nesting and roosting habitats (Bias and Gutiérrez 1992, Call et al. 1992), the influence of fire severity on owl foraging habitat is complex. Foraging sites are typically moderately dense forest stands ($\geq 40\%$ canopy closure) close to nests and small streams, with trees greater than 15 cm diameter at breast height, large hardwoods (Call et al. 1992, Irwin et al. 2007, Williams et al. 2011), and higher woody debris and greater snag presence than expected by chance (Gutiérrez et al. 1992). Foraging habitats often contain more variable characteristics than nesting and roosting habitats, such as different forest types or gaps in the canopy where shrubs may be abundant, due to the distribution and range of habitat needs of primary owl prey, which include woodrats (*Neotoma* spp.), northern flying squirrels (*Glaucomys sabrinus*), and mice (*Peromyscus* spp.; Call et al. 1992).

Diversity in vegetation and fuels composition and structure, weather, and topography results in a mosaic of postfire forest patches burned at varying fire severities, including interspersed areas untouched or measurably unchanged by fire (Miller and Urban 1999, Collins et al. 2007). This postfire spatial habitat complexity can increase a foraging owl's access to different types of habitat and number of habitat edges, including high and low contrast edges (Miller and Urban 1999, Franklin et al. 2000, Collins et al. 2007). Research examining how different edge types affect owl foraging habitat quality is limited, but some studies have revealed that Northern Spotted Owls (*S. o. caurina*) avoid high contrast edges (sharply defined edge between 2 different habitat patches, e.g., a patch burned at low fire severity adjacent to a patch burned at high severity) and prefer low contrast edges (blended edges between different habitat types, e.g., a habitat patch unchanged postfire adjacent to patch burned at low fire

severity), depending on the spatial scale used to examine habitat selection (Glenn et al. 2004, Clark 2007, Comfort et al. 2016). Therefore, by creating a patchwork of stands of different ages, fire may enhance foraging opportunities for Spotted Owls by increasing the number or amount of edges present in the landscape (Franklin et al. 2000). However, others have argued that patch edges fragment habitat, decrease owl survival (Blakesley et al. 2005), and increase owl home range size (Schilling et al. 2013), although differences in primary prey species may contribute to these differences.

We examined California Spotted Owl habitat use patterns in a landscape with a range of fire severities, patch edge types, and fire ages in Yosemite National Park (hereafter, Yosemite), California, USA. The forests in Yosemite, unlike surrounding private timberlands and areas administered by the U.S. Forest Service (USFS), have not been managed and harvested for timber, which allows the examination of fire effects without the confounding influence of plantations or logging. Learning how sensitive species, such as the California Spotted Owl, respond to fire is critical for implementing future management plans. Specifically, we wanted to know how owl foraging patterns may be influenced by (1) fire severity, (2) fire-created edges, and (3) other factors such as topography or distance to a stream or nest or roost site. We hypothesized that fire severity would be important to owl habitat use because of changes in forest structure and canopy cover (Shaffer and Laudenslayer 2006, Beaty and Taylor 2007). Further, we postulated that fire-created edges would influence owl habitat use (Clark 2007, Comfort et al. 2016). We also speculated that abiotic factors, such as slope, aspect, and distance to streams and nests or roosts, would influence owl foraging habitat use, based on earlier work (Clark 2007, Irwin et al. 2012). By providing insight into owl use of fire severity patch type patterns, this study may help to inform future fuels reduction efforts and prescribed burning programs in similarly managed public lands (i.e. National Parks).

METHODS

Study Area

Yosemite spans 302,688 hectares (ha) in the central Sierra Nevada of California. We surveyed California Spotted Owls in the 87,200 ha of lower montane forest dominated by California black oak (*Quercus kelloggii*), ponderosa pine (*Pinus ponderosa*), incense cedar (*Calocedrus decurrens*), sugar pine (*Pinus lambertiana*), and white fir (*Abies concolor*; Figure 1). Monthly average temperatures for the Yosemite Valley range from -3°C to 32°C , and precipitation, which mostly occurs as snow at high elevations, varies from 0.8 cm to 15.7 cm (<http://www.nps.gov/yose/planyourvisit/climate.htm>). A Mediterranean

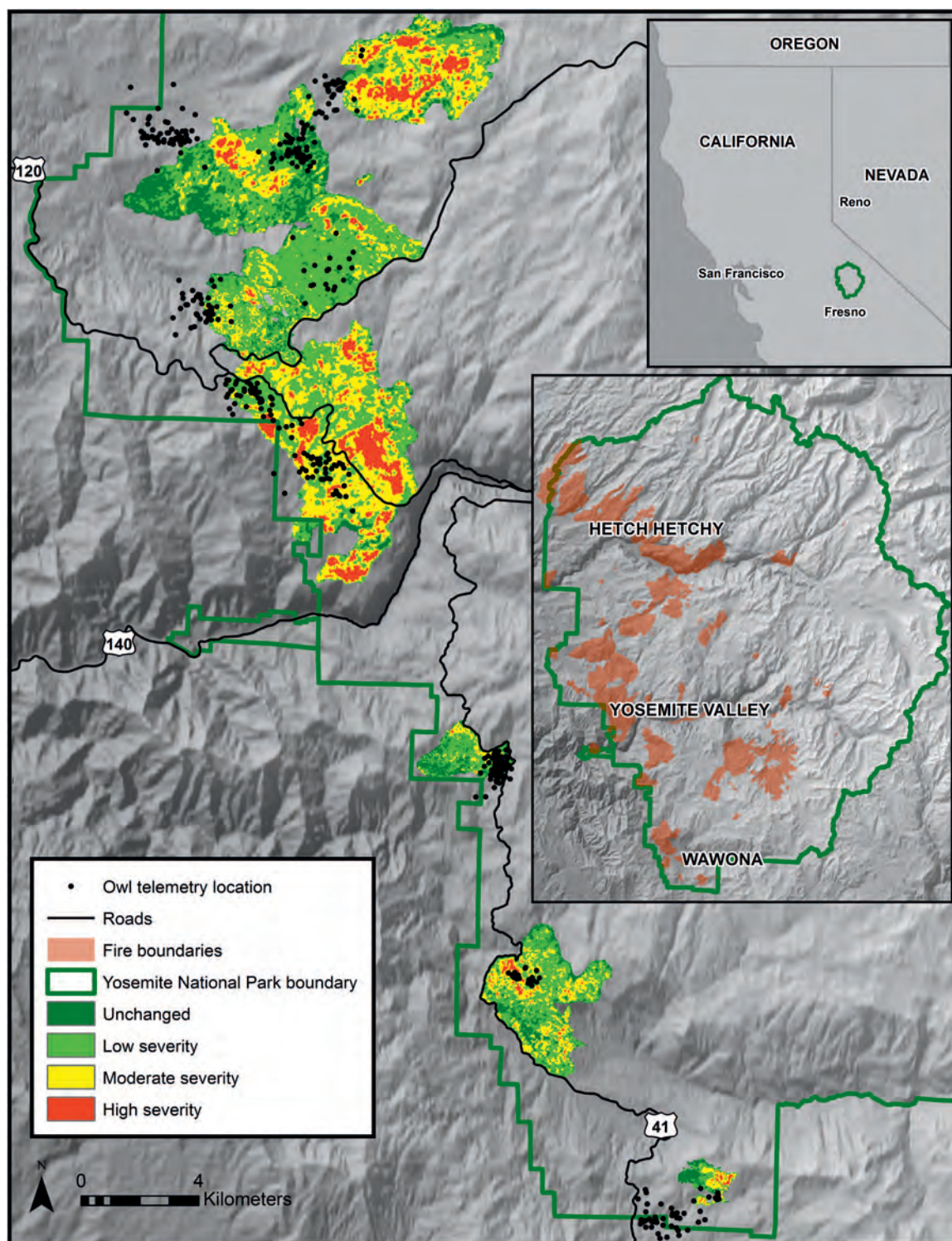


FIGURE 1. Study area used to examine California Spotted Owl foraging habitat use patterns within California, USA, and Yosemite National Park, 2010–2012. Inset map of Yosemite National Park shows all fires that have burned in Yosemite since 1997. Large map shows fire severity patterns for specific fires near owl locations.

climate of cool, wet winters and warm, dry summers characterizes Yosemite's climate.

Field Methods

We located owls following established protocols (Forsman 1983) at previously known nest or roost sites (Roberts et al. 2011). We selected 10 sites based on (1) the occurrence of a recent (since 1997) wildfire or prescribed fire, (2) the presence of a known owl pair, and (3) site accessibility (the crew needed to be able to rapidly hike or drive to the telemetry stations at night). We conducted all fieldwork from June through September, 2010–2012, so the extremely large 'Rim Fire' that burned portions of Yosemite in 2013 did not form part of this analysis. We attached a backpack-mounted radio-transmitter (AVM Instrument Company, Colfax, California, USA) to captured owls following established procedures (Forsman 1983, Bull and Henjum 1990, Guetterman et al. 1991). Because Glenn et al. (2004) showed that Spotted Owl mates do not forage independently, we only radio-tagged one member of a pair in a given year.

We performed nocturnal telemetry surveys from 30 min after sundown to 30 min before sunrise to determine foraging locations. We used Communications Specialists receivers (model R-1000; Communications Specialists, Orange, California, USA) and 3-element Yagi antennas (Advanced Telemetry Systems, Isanti, Minnesota, USA) to track all radio-tagged owls. We triangulated owl foraging locations with compass bearings from georeferenced monitoring stations and collected one foraging location per owl each night to avoid pseudoreplication (Guetterman et al. 1991). To ensure that we sampled each owl at different times throughout the sampling period, we randomly assigned telemetry survey start times to each owl.

Home Range Analysis

We used the arithmetic mean estimator in Program LOAS (Location of a Signal) 4.0b (Ecological Software Solutions, Hegymagas, Hungary, <http://www.ecostats.com/web/LOAS>) to generate owl point locations from our triangulated compass bearings recorded from the georeferenced telemetry stations. To reduce location signal bias, we only used location polygons ≤ 5 ha (this excluded only 4% of our locations).

To assess the accuracy of our telemetry locations, we followed the same techniques as have been used in other owl telemetry studies (Glenn et al. 2004, Bond et al. 2009, Wiens 2012). We triangulated to stationary owls at diurnal roosts visually located by an independent observer. We also placed transmitters in locations unknown to technicians. A naïve technician then performed triangulation to estimate the location of the hidden transmitter. We calculated telemetry bias as the

linear distance between locations estimated by triangulation and actual locations.

We plotted owl locations in ArcGIS 10.0 (ESRI, Redlands, California, USA), and created a buffered owl location using the median error distance as our radius (Figure 2). From these telemetry locations, we calculated a home range for each owl with ArcGIS and Geospatial Modelling Environment (GME 0.6.0.0; Beyer 2012) using 100% minimum convex polygons (MCP) including the error buffer. We then calculated home range size by summing the area contained within the MCP. In order to conform to a normal distribution, we log-transformed the home range sizes and used the geometric mean, which provides a better measure of the middle of a dataset than the arithmetic mean (Sheskin 2003).

Habitat Selection Analysis

We applied logistic regression to compare used habitat (owl telemetry locations) with available habitat and to estimate a resource selection function (Manly et al. 2002) at the within-home-range scale (i.e. third order selection; Johnson 1980). Because we could not ensure that our sample of owls was truly random across the broader landscape, we did not attempt to examine the selection of home ranges within a larger study area (i.e. second order selection). We defined available habitat within the MCP, rather than within a fixed kernel home range estimate, because MCPs may more accurately represent available area (Gillies et al. 2006, Kauhala and Auttila 2009, Comfort et al. 2016). Depending on the particular habitat variable, we used the point center location or the entire telemetry circle (point location with error buffer) in our estimations (see below).

We randomly generated ~ 3 times as many available locations as used locations within each owl's home range in ArcGIS to minimize rates of contamination and overlap. Contamination refers to having both used and unused units in the pool of available units (Johnson et al. 2006), and overlap occurs when a random (available) sample falls in the same location as a used location. We buffered available locations with a radius of our median error distance to account for the same spatial error as the used locations, and estimated the same habitat variables for both used and available locations. For the final candidate model set, we fit generalized linear mixed-effects models (GLMM) allowing for both fixed and random effects. We used the `glmer` function in the `lme4` package (Bates et al. 2015) in R (R Core Team 2015) to fit all models and considered owl ID as a random effect. Therefore, we fit a model with a varying-intercept group effect using the variable 'owl ID,' which allowed used and available locations to be compared at the level of each individual owl. We considered all other habitat variables as fixed effects (see below).

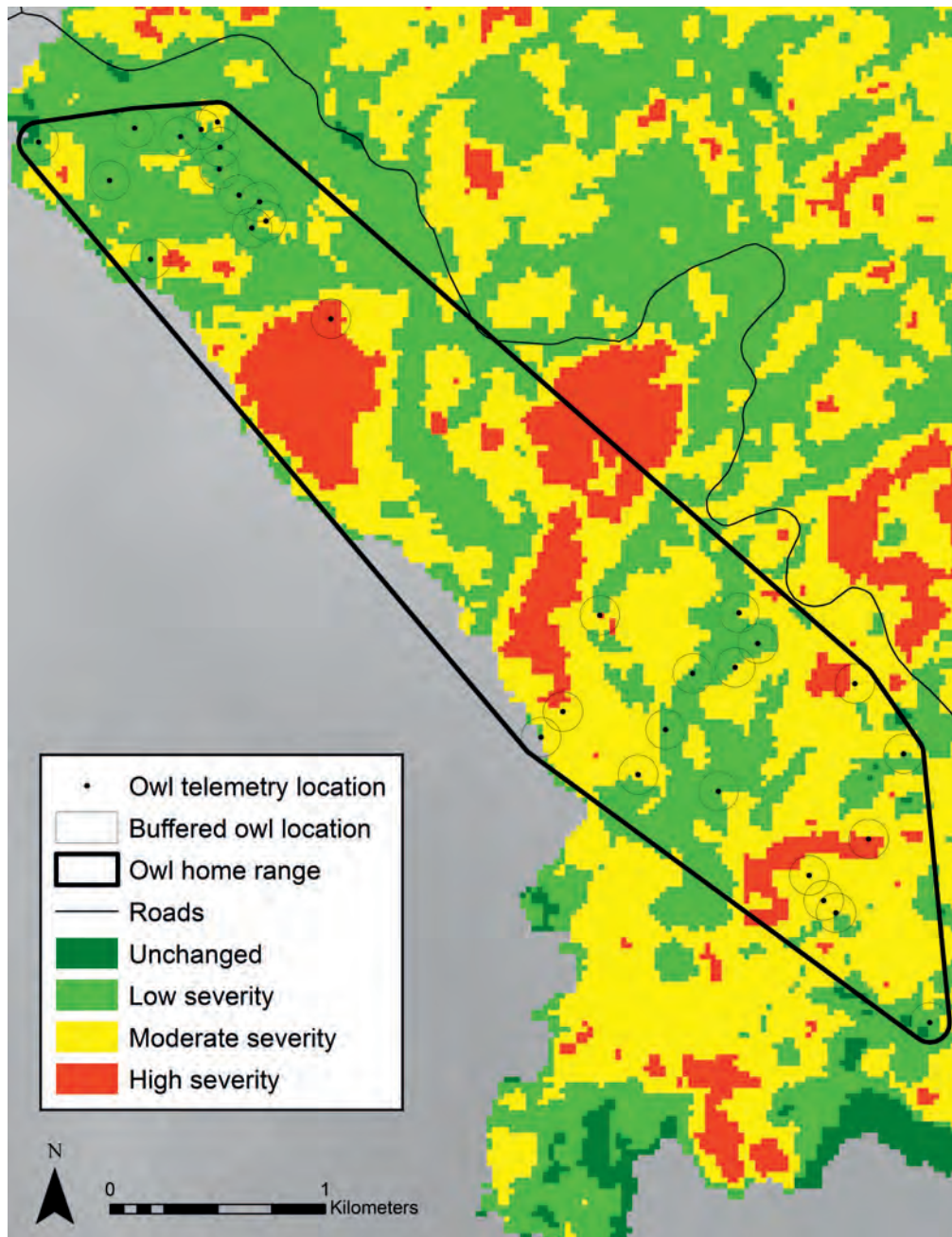


FIGURE 2. An example of one California Spotted Owl home range showing fire severity patterns within a home range in Yosemite National Park, California, USA, 2012. Black dots represent owl telemetry locations and circles show the buffered owl location with a 92-m radius to represent telemetry error.

Habitat Variables

We calculated all predictor variables using ArcGIS and GME and used fire severity maps generated by Yosemite fire specialists to describe the extent and boundaries of fires in each owl's home range. To quantify fire severity, we used the relative differenced Normalized Burn Ratio (RdNBR), which measures the amount of spectral (reflectance) change in vegetation after fire (Miller and

Thode 2007). Miller and Thode (2007) created relative thresholds to classify all RdNBR values into 4 fire severity patch types: no detectable change (hereafter, unchanged); low; moderate; and high. Following van Wagtenonk and Lutz (2007), we reclassified these types with integer values of 2, 3, 4, and 5, respectively, to aid in the calculation of a total fire severity index (FSI) for each buffered owl location. Reclassification with integer values allowed every

combination of fire severity patch composition within each buffered owl location to have its own unique value.

We overlaid the used and available locations onto the fire severity maps to determine fire severity composition at each location (Figure 1). We calculated the proportional area of each fire severity patch type within the buffered owl location using ArcGIS and GME and then multiplied the area of each patch type by its corresponding RdNBR integer value. We calculated a total FSI for each foraging location by summing all of these values (Roberts et al. 2008). Our FSI ranged continuously from 2 (i.e. a buffered owl location that was entirely unchanged) to 5 (i.e. an area completely burned at high severity). Values between these extremes corresponded to buffered owl locations burned at moderate severity or, since some buffered owl locations contained multiple fire severity types, burned at a combination of higher and lower fire severities. This FSI summation within a buffered location thus collapsed heterogeneity within a buffered location to a single value, but we feel that this appropriately acknowledged the uncertainty of the owl's actual location within the buffered location circle and resulted in a conservative analysis (i.e. owls less likely to show strong selection for high or low FSI values). We believe that simply using the centroid of the error polygons as the owl's assumed location, common in some studies, fails to reflect the imprecision typical in radio-telemetry studies. Nonetheless, we did not want to ignore heterogeneity of habitats within an estimated location, so we also included edge effects in our analysis.

We classified all used and available locations as an edge (no edge, low contrast edge, or high contrast edge) if they contained more than one fire severity category. Edge locations that contained patches burned at high fire severity were considered high contrast edges, and edge locations without patches burned at high fire severity were categorized as low contrast edges (Clark 2007).

Our abiotic covariates included horizontal distance to roost (m); horizontal distance to stream (m); slope (degrees); elevation (m); and aspect (north, northeast, east, southeast, south, southwest, west, and northwest) as a categorical variable. Employing the point location, or the center of the error-buffered owl location, we generated all abiotic covariates in ArcGIS using a 10-m digital elevation model for the study area.

Because slope, elevation, and distance to roost were on different scales (e.g., degrees vs. hundreds of m), we rescaled these variables to make coefficients more comparable by subtracting the mean of each variable from an individual value and dividing the difference by the standard deviation. Logistic regression does not require that predictor or response variables be normally distributed (Johnson 1998), and, to avoid multicollinearity, we confirmed that all correlation coefficients between variables in candidate model sets were <0.2 .

Model Development and Selection

Based on previous Spotted Owl research, we developed a priori candidate models incorporating 3 sets of covariates: (1) fire, (2) edge, and (3) abiotic, and proceeded through model development in stages (Olson et al. 2004, Irwin et al. 2012). Applying an information-theoretic approach based on Akaike's Information Criterion (AIC) to evaluate candidate models, we used second-order AIC (AIC_c) to account for small sample sizes and ranked models according to Akaike weights (w_i ; Anderson 2008). The model with the lowest AIC_c value and the greatest Akaike weight represented the best fit to the data, and we considered models with ΔAIC_c (difference in AIC_c value between the candidate model and the best-fit model) <2 as plausible alternative models (Anderson 2008).

We hypothesized that topographical characteristics (slope, aspect, and site elevation) would be important because of differing forest structure and composition associated with these characteristics. Topography can affect forest structure, microclimate, and fire behavior, with higher canopy cover, cooler microclimates, and lower fire severity and frequency at northern aspects, and more open canopies, warmer microclimates, and higher fire severity and frequency at southwestern aspects (Lydersen and North 2012). Further, forest structure and composition can influence owl prey abundance (Coppeto et al. 2006, Roberts et al. 2008, 2015). To determine whether owls were selecting intermediate elevations or slopes, we incorporated quadratic forms for these variables.

We postulated that distance to the roost site would be influential because Spotted Owls are central-place foragers and have high site fidelity to roost locations (Carey and Peeler 1995). We speculated that distance to a perennial stream would affect owl foraging because riparian areas are important for primary prey species such as the northern flying squirrel (Meyer et al. 2007). Because the relationship with distance may be nonlinear, we incorporated quadratic terms for all distance covariates.

We hypothesized that fire severity would be pivotal to owl habitat use because of corresponding changes in forest structure (Shaffer and Laudenslayer 2006, Beaty and Taylor 2007). We postulated that edge would be important because it has been found to affect life history traits (Franklin et al. 2000, Tempel et al. 2014); therefore, the final candidate model set included edge type as a predictor.

We translated the above hypotheses into a final candidate model set in various combinations along with the best models from the abiotic predictor variable model sets. We created a 95% confidence set of models by including models for which Akaike weights summed to 0.95. We applied model averaging to the entire candidate model set, not just the 95% confidence set, to calculate logistic regression coefficients for all predictor variables using R package AICcmodavg (Mazerolle 2016). We

TABLE 1. Fire severity proportions, patch sizes for patches used more than once by California Spotted Owls, and mean patch sizes available in Yosemite National Park, California, USA, 2010–2012.

Fire severity patch type ^a	Percentage contained in owl home range (mean $\pm$ SE)	Patch size (ha) used by owls (mean $\pm$ SE)	Patch size (ha) used by owls (range)	Patch size (ha) intersecting home range (mean $\pm$ SE)
Unburned	42 $\pm$ 8	**	**	**
Unchanged	6 $\pm$ 2	4.4 $\pm$ 17.9	0.1–118.4	2.2 $\pm$ 0.7
Low	26 $\pm$ 4	99.7 $\pm$ 391.1	0.1–2,035.5	30.5 $\pm$ 13.7
Moderate	21 $\pm$ 4	56.2 $\pm$ 159.3	0.1–696.9	10.6 $\pm$ 4.7
High	6 $\pm$ 1	6.5 $\pm$ 10.5	0.1–36.0	2.9 $\pm$ 0.8

^a Unburned = area untouched by fire outside the fire perimeter; Unchanged = no detected change in vegetation, relative differenced Normalized Burn Ratio (RdNBR) threshold <42; Low = surface fuels consumed with little change to overstory structure, RdNBR threshold $\geq$ 42 and <220; Moderate = understory vegetation, midstory shrubs, and small trees consumed and $\sim$ 0.5% canopy trees killed, RdNBR threshold $\geq$ 220 and <566; High = nearly all mature plants killed ($\sim$ 75% of canopy trees), RdNBR threshold $\geq$ 566.

** Unburned mean and range of patch sizes were not calculated because unburned areas consisted of large, contiguous patches of forest.

evaluated logistic regression coefficients for the model-averaged estimates by calculating 95% confidence intervals to determine the strength of estimates. We used odds ratios to examine the change in the relative probability of selection for every 1 unit change in the covariate (Manly et al. 2002). Odds ratios >1 indicate increased likelihood of owl use with each unit increase of the predictor variable. Odds ratios <1 indicate a decreased likelihood of owl use with each unit increase of the predictor variable. Use-availability designs are unable to estimate the true probability of selection (Johnson et al. 2006), therefore we refer to our findings as relative probability. We evaluated the full model using both marginal and conditional R^2_{GLMM} (Nakagawa and Schielzeth 2013). Marginal R^2 accounts for the variance explained by fixed factors, while conditional R^2 accounts for the variance explained by fixed and random factors. For all statistical analyses, including AIC_c estimations and evaluations, we used R (R Core Team 2015).

RESULTS

From June through September, 2010–2012, we captured 13 owls (8 females and 5 males) from 8 unique territories within Yosemite. We monitored the same territories for multiple years, but captured a different member of the pair each year, except in one situation in which we caught the same female in 2010 and 2012. We therefore had 14 sets of used and available location data to consider as random effects. We calculated 480 ($\bar{x}$ = 35 per owl) owl foraging locations (used points) and generated 1,431 random (available) points for the logistic regression analysis. Based on the 18 distance error samples that we collected across all 8 of our sampled territories, our median error distance was 92 m, which we used as the error buffer for our analyses.

Home Range Analysis

Home range size ranged from 65 ha to 1,136 ha for male owls and 90 ha to 2,983 ha for female owls, averaging 302 ha (95% CI: 119–787 ha) and 451 ha (95% CI: 175–1,293 ha), respectively. There was no statistically significant difference in log-transformed home range size between males and females ($F_{1,13} = 0.5$, $P = 0.5$); therefore, we pooled the data for the analyses and the mean pooled home range size was 391 ha. Mean home range size also did not differ between years using MCP estimates ($F_{1,13} = 0.2$, $P = 0.7$).

In our study area, nearly 75% of most owl home ranges burned in one or more fires that occurred between 1997 and 2009. However, 2 owl home ranges contained $<5\%$ burned area, although both of these territories were immediately adjacent to large burns. Overall, the proportion of the home range in each fire severity category declined with increasing severity, and the average size of patches used more than once by owls varied depending on fire severity, with the largest used patches burned at low to moderate severities (Table 1).

Habitat Selection Analysis

Across all owl locations, the mean ($\pm$ 1 SE) FSI was 2.8 ± 0.8 and distance to roost was $1,310 \pm 1,518$ m. The mean slope and elevation of all owl locations were $12.1 \pm 5.9^\circ$ and $1,692 \pm 161$ m, respectively.

We collected data for 3 yr and treated year as a categorical variable, blocking this factor to account for any variability across years and including it as an interaction term to examine whether the effect of a predictor differed across years. Because models with the year of data collection and its interaction with predictor variables showed little evidence of support from the data, we dropped year from our candidate models and combined data for all years in subsequent analyses.

TABLE 2. Models within the 95% confidence set that best explained California Spotted Owl habitat use patterns in Yosemite National Park, California, USA, 2010–2012. K is the number of model parameters, $-2\text{Log}_e(\mathcal{L})$ is the $\log_e$ (likelihood), ΔAIC_c is the difference from the top model in Akaike's Information Criterion corrected for small sample size, and w_i is the Akaike model weight. Models highlighted in bold are within $2 \Delta\text{AIC}_c$ of top model.

Model ^a	K	$-2\text{Log}_e(\mathcal{L})$	ΔAIC_c	w_i
DistRoost + DistRoost² + FSI + EdgeType	7	2133.95	0.00 ^b	0.27
Slope + Elev + DistRoost + DistRoost² + FSI + EdgeType	9	2130.59	0.69	0.19
Slope + DistRoost + DistRoost²	5	2138.91	0.94	0.17
Slope + Elev + DistRoost + DistRoost ²	6	2138.26	2.31	0.09
DistRoost + DistRoost ²	4	2142.53	2.55	0.08
Slope + Elev + DistRoost + DistRoost ² + EdgeType	8	2135.88	3.95	0.04
Elev + DistRoost + DistRoost ²	5	2141.96	3.99	0.04
DistRoost + DistRoost ² + FSI	5	2142.01	4.13	0.03
Slope + Elev + DistRoost + DistRoost ² + FSI	7	2138.15	4.21	0.03

^a DistRoost = distance to roost, i.e. distance (m) from center of buffered owl location for used and available points to roost; DistRoost² = quadratic term for distance to roost; FSI = fire severity index, i.e. index value for fire severity proportions within buffered owl location for used and available points, with values ranging from 2 (low) to 5 (high); EdgeType = 3 values of edge type: high contrast edge, low contrast edge, and no edge. High contrast edges contained high severity fire, while low contrast edges did not contain high severity fire; Slope = slope (degrees) at center of buffered owl location for used and available points; Elev = elevation (m) at center of buffered owl location for used and available points.

^b $\text{AIC}_c = 2148.00$.

Our analysis of topographic variables indicated that slope and elevation were the most important factors to consider in the final candidate model set. Because slope was strongly significant and the 95% confidence interval did not overlap zero, we placed more emphasis on including it in the final candidate models. Aspect and a quadratic effect of slope had poor support and we excluded them from subsequent analyses (Anderson 2008).

We determined that the model with the quadratic form of distance to roost (distance + distance²) had the lowest AIC_c value, and no other models that included distance to stream or other forms of distance to roost were within $2 \Delta\text{AIC}_c$ of this top model. Therefore, we incorporated only this nonlinear effect of distance to roost in the final candidate set of models.

After selecting the best models from the abiotic variables candidate model sets, the models with the strongest support included a combination of quadratic distance to roost, FSI, edge type (high contrast, low contrast, and no edge), slope, and elevation. The top model contained the fixed effects of quadratic distance to roost, fire severity index, and edge type (Table 2). All models in the 95% model set had substantially higher support than the null model, which had <1% of model weight (Table 2). The null model includes the intercept only, and if it is ranked highly indicates that predictor variables explain little about owl habitat use patterns. The marginal and conditional R^2_{GLMM} for the full model were both 0.02, indicating that little additional variance was explained by the random effect of individual owl ID.

Two models were within $2 \Delta\text{AIC}_c$ units of the top model and together all 3 carried 63% of the Akaike weight (Table 2). Because no model had a substantial amount of weight

(i.e. >0.75), we model-averaged all models in the set and report odds ratios from this averaged model (Table 3). Confidence intervals for the odds ratio estimates did not overlap 1 for distance to roost predictors, low contrast edge, and no edge, while those for fire severity index, slope, and elevation included or slightly overlapped 1 (Table 3). However, in estimates from the top model only, the 95% confidence interval for the odds ratio for FSI did not overlap 1 (Table 3).

Distance to roost had the highest relative variable importance (0.97), followed by FSI (0.55), edge type (0.54), slope (0.54), and elevation (0.40), when Akaike weights were summed across all models. Further, all models that did not contain the distance to roost variable had 0% of the Akaike model weight and thus were not included in the 95% confidence set of models. Confidence intervals did not overlap 1 and the odds of use were highest closest to the roost, with a slight increase again at distances far from the roost (Figure 3). The relative probability of use was highest for high contrast edge, followed by low contrast edge, and then no edge sites (Figure 4). The odds of owls using the high contrast edge type were 2.78 times greater than odds for the low contrast edge type and 3.5 times greater than for the no edge type. However, 95% confidence intervals for use of all 3 categories of edge type overlapped. The odds of nonuse increased by 1.25 for each 1 unit increase in FSI (odds ratio = 0.80), however the 95% confidence interval included 1 (Table 3), indicating less confidence in the estimate. The 95% confidence intervals for the odds ratios for slope and elevation overlapped 1, however the relative probability of use increased in areas with gradual slopes and higher elevations. Post hoc, we conducted an analysis that included an interaction term between FSI and

TABLE 3. Estimates, standard errors (SE), and lower (LCL) and upper (UCL) 95% confidence limits for odds ratios from model-averaged model of California Spotted Owl habitat use patterns in Yosemite National Park, California, USA, 2010–2012. Estimates from the top models (Table 2) are included for comparison.

Predictor variable	Estimate	SE	95% LCL	95% UCL	Top model estimate	Second-best model estimate
High contrast edge	0.51	0.32	−0.11	1.14	0.91	0.89
Distance to roost	0.84 ^a	0.08	0.68	0.99	0.84 ^a	0.86
Distance to roost ²	1.12 ^a	0.04	1.04	1.21	1.13 ^a	1.12
Fire severity index	0.80	0.10	0.61	1.00	0.77 ^a	0.79 ^a
Low contrast edge	0.36 ^a	0.18	0.01	0.72	0.40	0.38 ^a
No edge	0.28 ^a	0.12	0.04	0.51	0.22 ^a	0.23 ^a
Slope	0.91	0.05	0.81	1.01	N/A	0.92
Elevation	1.05	0.06	0.93	1.17	N/A	1.06

^a 95% CI does not overlap 1.

edge type in the top model, with no change to model interpretation.

DISCUSSION

Overall, California Spotted Owls in our study area selected foraging sites close to their roosts and avoided areas containing no habitat edges created by fire (Tables 2 and 3). The top model also suggested that owls showed an avoidance of areas with a high FSI (Figure 4), although the 95% confidence interval for the model-averaged estimate included 1 (Table 3). Model selection indicated strong support for the variables in the top models.

Our study joins several others that have documented that distance to the roost or nest is important for foraging habitat selection by Spotted Owls (Glenn et al. 2004, Irwin

et al. 2007, 2012, Wiens 2012, Bond et al. 2016). Spotted Owls have high site fidelity to nest sites and tend to roost near the eventual nest site, which is typically used for many years (Forsman et al. 1984). Furthermore, Spotted Owls are central-place foragers and often remain near the nest site in the nonbreeding season, so nest and roost locations may play a significant role in owl foraging habitat selection throughout the year (Forsman et al. 1984, Carey and Peeler 1995). Rosenberg and McKelvey (1999) argued that not including distance to the nest or roost in habitat selection models might bias selection for habitat characteristics near the central place, perhaps resulting in a false suggestion that it is the habitat type that the owls are selecting rather than merely its adjacency to the nest. In our study, support was strongest for a nonlinear effect of distance to the roost, with a slight flattening at intermediate distances from the

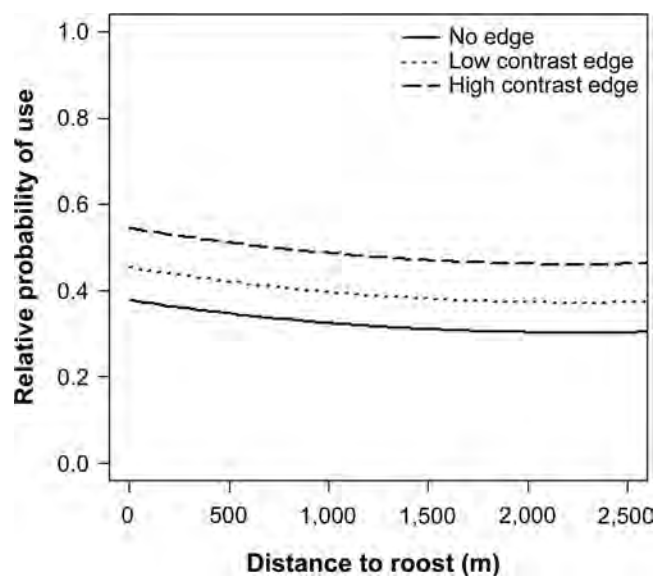


FIGURE 3. Modeled relative probability of California Spotted Owl habitat use as a function of distance to roost and edge type in Yosemite National Park, California, USA, 2010–2012.

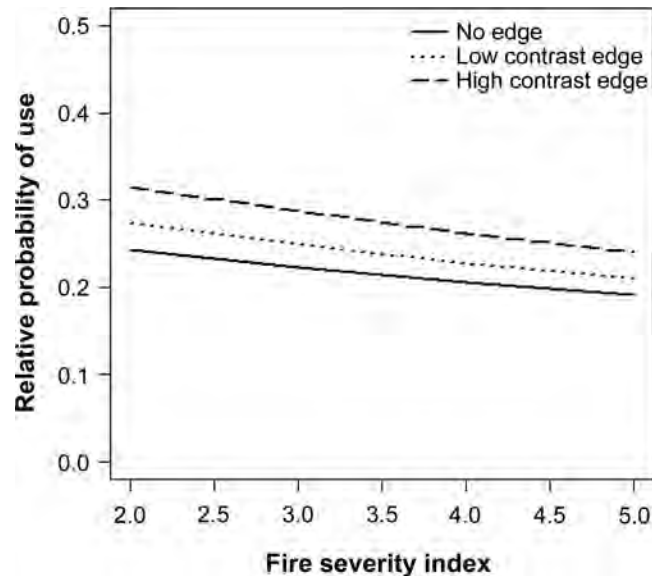


FIGURE 4. Modeled relative probability of California Spotted Owl habitat use as a function of fire severity index and edge type in Yosemite National Park, California, USA, 2010–2012.

roost and a slight increase at distances far from the roost (Figure 3). This nonlinear effect suggests that, while owls show a preference for areas in close proximity to the roost, they will also actively use more distant foraging sites, perhaps where there may be greater access to high contrast edges and/or higher prey availability.

Our results suggest that owls show a higher relative probability of selection for fire-created edge habitats than contiguous habitats. Collectively, recent research has revealed that Northern and California spotted owl survival and reproductive rates are higher in areas with a mosaic of vegetation types and edges (Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005, Keane 2014), which may explain owl use of habitat edges associated with fire. In our study system, fire, rather than logging, was the main cause of forest change, and we found that selection was strongest for high contrast edges. In the Klamath Mountains of southern Oregon and northern California, Comfort et al. (2016) found that Northern Spotted Owls foraged in edges and, at large spatial scales (12.9–207.0 ha), appeared to select diffuse or low contrast edges created by fire, whereas at smaller spatial scales (3.2 ha), owls selected hard edges. However, Schilling et al. (2013) associated larger Spotted Owl home ranges with habitat fragmentation from increased edges in southwestern Oregon, where most edges were artifacts of past logging. A recent study that investigated foraging habitat selection in burned forests in southern California found no evidence of edge selection (Bond et al. 2016). The disparity in these results suggests that there may be a threshold level of habitat patch edges, where some edge habitat can have neutral to positive effects, but too many edges may lead to negative effects on owl habitat quality. Although not a focus of our analysis, it appears that owls used small patches burned at high severity, but used a much larger size range of patches burned at low and moderate severity, which implies that owls may have more flexibility in the latter burned patch types (Table 1). Further, it appears that burned patches used more than once by owls may be larger than the average available burned patch size (Table 1), suggesting that patch size could influence selection of burned habitat and warrants future investigation. The complexities of these results from different studies suggest that, to find a balance between high-quality edge habitat and potentially detrimental fragmentation, more research addressing Spotted Owl use of habitat edges is necessary, especially in burned landscapes.

Our analyses showed that California Spotted Owls in our study area also had a weak negative relationship with FSI (Figure 4). This negative relationship with FSI suggests that, while owls in Yosemite frequently used edges created by high severity fire, they may have avoided the interiors of large patches burned at high fire severity, a result similar to that from research on California Spotted Owls in megafires

(Jones et al. 2016) and Northern Spotted Owls (Comfort et al. 2016). Therefore, perhaps small proportions of patches burned at high fire severity embedded in a larger matrix of areas burned at low and moderate fire severities may be beneficial for owl foraging habitat by creating high contrast edges.

Frequent low and moderate severity fires, characteristic of the mixed-conifer zones of the Sierra Nevada, have shaped these forests for millennia (Collins et al. 2011, Thode et al. 2011). Therefore, the native forest inhabitants, such as the California Spotted Owl, have evolved with the fire regime of these forests and should be adapted to fire that burns within the natural range of variation for this habitat type. Low severity fires typically result in minimal overall tree mortality and can maintain the closed canopy conditions favored by California Spotted Owls (Blakesley et al. 2005, Roberts et al. 2011). In fire-suppressed (unburned) forests, California Spotted Owls forage in mature forest with an abundance of large trees, multiple canopy layers, and 40–70% overstory canopy cover (Williams et al. 2011). Forests where fire is allowed to burn within the natural range of variation (at low and moderate severities), such as in Yosemite, typically retain all of these characteristics (Thode et al. 2011) and may explain the Spotted Owl foraging patterns that we observed in this study.

The effect of fire on California Spotted Owl habitat selection is complex and incompletely understood, with some studies finding contradictory results. For example, Bond et al. (2009) used radio-telemetry to examine the foraging habitat selection of California Spotted Owls in Sequoia National Forest, California, USA, and found that owls selected patches burned at high fire severity for foraging, perhaps due to a higher density of snags and increased shrub cover that provided refuge for their prey. In Bond et al.'s (2009) study, all owl territories experienced a fire with severity patterns that were not representative of the natural range of variation typical for those habitats (Meyer 2015). Our study encompassed a larger area and more than a dozen fires that burned with a considerable range of variation, yet still within the natural range of variation for the area. Bond et al. (2009) collected habitat use data during a single year, 4 yr after a single fire, while our study included many fires that burned 2–15 yr before data collection. Overall, fire severity proportions also differed between the 2 study areas because, on average, only 5% of owl home ranges in Yosemite contained patches burned by high severity fires, while foraging ranges in the study area of Bond et al. (2009) contained 13% high severity fire areas. The unburned forest matrix differed between the 2 study areas as well. The Sequoia National Forest, where the Bond et al. (2009) study occurred, had a history of timber harvest and much more aggressive fire suppression programs, whereas our study area in Yosemite

experienced minimal harvesting from the 1900s to the 1930s and, since 1970, managers have implemented prescribed fires and allowed many wildfires to burn un-suppressed (van Wagtendonk 2007, Lutz et al. 2009). Also, we used MCP to estimate available area, while Bond et al. (2009) used capture radius, which may have led to different estimated proportions of areas burned at high fire severity (Bond et al. 2016). Furthermore, Yosemite's complex fire history may have confounded the effects of any one fire, since past fires often drive the location and behavior of future fires. This makes it difficult to isolate the importance of repeated burning in owl foraging habitat selection without having a much larger sample size of owl foraging locations.

Other recent work has also suggested that Spotted Owls are not negatively affected by stand-replacing high severity fires. For example, Lee et al. (2012) examined colonization probabilities and concluded that fires that burned up to 32% of the total affected area at high severity had no effect on extinction or colonization probabilities of California Spotted Owls in burned forests of the Sierra Nevada. A further demonstration of uncertainty surrounding owl response to fire comes from Lee and Bond (2015a), who found high occupancy rates (modeled burned site occupancy probability for pairs = 0.87) 1 yr following a large fire in the Sierra Nevada. However, this occupancy probability may have been high because only historically occupied sites were monitored, compared with another study that randomly selected sites in burned and unburned forest to calculate occupancy rates (modeled burned site occupancy probability for pairs = 0.46; Roberts et al. 2011). Likewise, California Spotted Owls in southern California with <50 ha of severely burned habitat within core areas had extinction probabilities similar to those in unburned sites, but extinction probability increased if severely burned habitat exceeded 50 ha (Lee et al. 2013). Another consideration is that owl site occupancy is influenced by the previous year's reproductive state, making it difficult to separate the effects of disturbance vs. reproductive status (Lee and Bond 2015b).

Although we discovered that distance to roost, patch edge metrics, and fire severity patterns explained California Spotted Owl foraging habitat selection, we recommend that our top models be interpreted with caution, since it is likely that there are other factors that affect Spotted Owl foraging that we did not measure, such as prey availability. The tests that we used to evaluate our models assume that we measured all of the effects that may influence Spotted Owl foraging, which this study never intended to do; therefore, the low variability explained by the 'best' model is not unexpected. Incorporating owl ID as a random effect did not explain any of the variance in the model, meaning that the probability of use was not influenced by individual owls, a

result also seen in 2 other studies (Gillies et al. 2006, Williams 2008). Future research investigating microscale habitat characteristics associated with foraging locations or prey abundance and movement could help to shed more light on owl habitat use patterns. Our low model evaluation values indicate that other variables that we did not measure may be more important to patterns of Spotted Owl foraging habitat selection.

Conclusion

Protecting old forests in the Sierra Nevada from stand-replacing fires via mechanical thinning or prescribed fire is a priority for management agencies (Roloff et al. 2012, Kane et al. 2015). Researchers have concluded that active management, such as prescribed fire and silvicultural treatments, that promotes a matrix of tree age classes can reduce fire threat, promote forest resiliency, and decrease owl habitat loss to stand-replacing fire (Irwin et al. 2004, Roloff et al. 2012, Winford et al. 2015). For example, the Rim Fire, one of the largest fires in California's history, burned 5 of our study sites and 2 owl nest trees, demonstrating the need to incorporate fire as a management tool to avoid large stand-replacing fires. However, it is important to balance the benefits of fire for hazard reduction with the potential impacts of fire on sensitive wildlife, since long-term gains may result in short-term habitat loss for California Spotted Owls (Tempel et al. 2014, 2015, Jones et al. 2016). Our study found that edge type and fire severity index were important for explaining owl habitat selection, which suggests that maintaining closed canopy forest within owl home ranges that includes variably sized patches burned at low and moderate fire severity and small patches (<36 ha) burned at high severity may be beneficial for owls. Our results also suggest that sustaining forests burned in a mosaic of lower fire severities in different years interspersed with large unburned patches may help to preserve California Spotted Owls in Yosemite National Park.

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Data deposits: Our data will be deposited through the National Park Service Research Permit and Reporting System on the Integrated Resource Management Applications Portal.

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ABSTRACT Western dry conifer forests continue to experience increased severe, stand-replacing wildfire that is outside of historical precedent. Fuels treatments, landscape-scale modifications of forest fuels and structure, are likely to remain a management tool to modify fire behavior and restore ecological resilience. The impacts of fuels treatments to listed species such as spotted owls (*Strix occidentalis*) remain uncertain and are contested because of limited available information. To evaluate spotted owl foraging habitat selection in a landscape recently modified by forest fuels-reduction treatments, we radio-marked and tracked 10 California spotted owls (*S. o. occidentalis*) for 2 years immediately following fuels treatment installation in the northern Sierra Nevada, California, USA. We categorized fuels treatments into 3 types: mechanical thin, installed within the study area as landscape-scale fire breaks characterized by even tree spacing, open understory, and low canopy cover, or group selections; understory thin, a hand-removal of small trees and shrubs; and understory thin followed by underburn, a controlled surface-fuel burn that left the overstory intact. We described post-treatment habitat using forest structural metrics derived from a Light Detection and Ranging (LiDAR) dataset that was collected 1 year after fuels treatments were completed. We collected 436 spotted owl foraging locations during 2 breeding seasons and evaluated breeding season home range size and composition using a resource selection function. We assessed possible contributors to owl foraging patterns by comparing *a priori* hypotheses in an information-theoretic approach and using randomly generated points that estimated available habitat. Spotted owl breeding season home ranges contained fuels treatments in proportion to their availability on the landscape and averaged 17.1% treated area. Within the home range, owl foraging locations in the post-treatment landscape were best predicted by lower proportions of gaps than anticipated at random, steeper slopes, and minimized distance from the owl's site center. Our results suggest that moderate to high proportions of gaps, typically a feature of forest fuels reduction and restoration treatments, may reduce the probability of spotted owl foraging. © 2018 The Wildlife Society.

KEY WORDS California spotted owl, foraging, forest restoration, fuels management, fuels treatment, habitat use, home range, LiDAR, Sierra Nevada, *Strix occidentalis occidentalis*.

Ecosystem restoration of historically mixed-severity fire regime forests is a primary concern and management goal across western North America, particularly amidst increasing trends in the size and severity of wildfire and insect mortality disturbances (Westerling et al. 2006, North et al. 2009, Safford et al. 2009, Hessburg et al. 2016). In the Sierra Nevada of California, USA, a century of fire suppression, timber harvest, and grazing practices have fundamentally changed forest structure, composition, and function, resulting in forests with a reduced large tree component and

increased homogeneity, fuel loads, and vulnerability to high-severity wildfire compared with historical records (Miller et al. 2009, North 2012, Stephens et al. 2012, Knapp et al. 2013, Dolanc et al. 2014). These changes have affected forest resilience and rendered these forests vulnerable to stand-replacing wildfire and insect mortality, both of which are projected to increase in size and severity under future climate predictions (Westerling et al. 2006, Millar et al. 2007, Liu et al. 2013, Hessburg et al. 2016). Methods to mediate severe wildfire events and restore Sierra Nevada forests in the face of climate change have been controversial (North 2012); current management guidelines for the United States Forest Service (USFS) lands in the Sierra Nevada adopt landscape-scale fire and fuels treatments (e.g., forest thinning) as an approach to reduce higher fuel loads, modify fire behavior,

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promote stand resilience, restore forest ecosystems, and protect civic and economic interests (USFS 2004, Stephens and Moghaddas 2005, North et al. 2009, Safford et al. 2009). The potential benefits of fire and fuels treatments (i.e., fuels treatments) to both ecosystem improvement and reduction of catastrophic fire risk has led federal land management agencies to invest in fuels treatments as a forest management strategy (Kalies and Kent 2016).

Fuels treatments, which include mechanical thin, understory manual thin, pile burning, and prescribed fire, are currently the primary management activities affecting forest ecosystems and species of concern, such as California spotted owls (*Strix occidentalis occidentalis*), on USFS lands in the Sierra Nevada (USFS 2004, Keane 2017, North et al. 2017b). The general prescription for fuels treatments is to reduce stand-replacing wildfire risk and create an open forest structure using a reduction of forest canopy cover to $\leq 40\%$, retention of trees ≥ 76 cm diameter at breast height (dbh), and a reduction of tree density, ladder fuels, and surface fuels (USFS 2004), prescribed according to site conditions and topography. Although resulting modifications in fire behavior are documented (Stephens and Moghaddas 2005, Schmidt et al. 2008, Stephens et al. 2009), broader ecological implications of fuels treatments are less clear, particularly for reductions in structure and diversity in late seral forests and effects on associated species such as spotted owls (Kalies and Kent 2016). In the case of the spotted owl, this is an important information need because long-term demographic monitoring indicates California spotted owl populations have declined over the last 20 years on USFS lands (Blakesley et al. 2010, Tempel and Gutiérrez 2013, Tempel 2014, Conner et al. 2016).

Although federal land management in the Sierra Nevada incorporates standards to manage for spotted owl habitat, little empirical information is available that assesses the effects of the structural modifications of fuels treatments on spotted owls or their habitat (Stephens et al. 2014, Tempel et al. 2014, Kalies and Kent 2016). Studies using habitat quality to model northern spotted owl (*S.o. caurina*) response to fuels treatments have reported reductions in habitat suitability, accompanied by positive long-term effects from reduction of nesting habitat loss to high-severity and stand-replacing fire (Gaines et al. 2010, Ager et al. 2012, Roloff et al. 2012). Similarly, effects of fuels treatments on California spotted owl demographics and territory quality have suggested that treatments may reduce the effects of high-severity fire but, in the absence of fire, can result in long-term reductions in habitat quality (Tempel et al. 2015). In an empirical study in the northern Sierra Nevada, the number of California spotted owl territories declined following implementation of a landscape fuels treatment strategy, although this was a single, observational case study (Stephens et al. 2014).

California spotted owl habitat selection at nest and roost sites is documented as favoring multi-layered understories with high canopy closure, dominated by large-diameter trees (Gutiérrez et al. 1995, LaHaye et al. 1997, Moen and Gutiérrez 1997, Bond et al. 2004). California spotted owl

foraging habitat use has received less research attention (Keane 2014); available studies report foraging habitat as occurring close to nest trees, with more open canopies and greater structural and compositional heterogeneity compared with nesting habitat, including late seral forest, broadleaf forest, and post-burn areas (Call et al. 1992, Irwin et al. 2007, Bond et al. 2009, Williams et al. 2011, Eyes et al. 2017). Analyses of spotted owl foraging habitat use have previously been limited by coarse-resolution habitat data that categorizes vegetation into broad categories based on tree species composition, size classes, and canopy-cover classes, precluding opportunities to describe finer-resolution habitat use patterns at the patch-scale used by owls (Kramer et al. 2016a). However, recent availability of vegetation data from remotely sensed Light Detection and Ranging (LiDAR) provides high-resolution imaging of forest structure and pattern, and holds promise for improved understanding of spotted owl habitat use (García-Feced et al. 2011, Ackers et al. 2015, Kramer et al. 2016a, North et al. 2017a).

Information on the effects of fuels treatments on California spotted owls is needed to inform forest management in the Sierra Nevada and contributes to broader discussions of the direction of fire and fuels management in Sierra Nevada forests. Our objective was to assess the foraging patterns of California spotted owls in a post-treatment landscape, by characterizing individual owl breeding season home range (i.e., home range) configuration and foraging site selection immediately following fuels treatment installation. We hypothesized that spotted owls would forage less frequently within fuels treatments because of structural modification of habitat components that are important to the owls' mammalian prey. We also hypothesized that spotted owls would forage close to their site center in areas with large-diameter trees (≥ 76 cm dbh), $>40\%$ canopy cover, and a mosaic of small gaps, where small-mammal abundance at early seral forest edges is combined with increased protection and movement offered by mature forest.

STUDY AREA

We conducted our study within the 23,823-ha Meadow Valley Project (MVP) area located on the Plumas National Forest in the northern Sierra Nevada Mountains, California, USA (Fig. 1) from 2007 to 2008. Elevation ranged 950–2,150 m in mountainous terrain, with dominant vegetation types of Sierra mixed conifer (35%) and montane hardwood-conifer (20%), consisting primarily of ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), Jeffrey pine (*P. jeffreyi*), Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), incense-cedar (*Calocedrus decurrens*), California black oak (*Quercus kelloggii*), dogwood (*Cornus* spp.), and willow (*Salix* spp.). Pockets of white fir and red fir (*A. magnifica*) forest occurred at higher elevations. The Mediterranean climate consisted of warm, dry summers and cool, wet winters; precipitation (105 cm/year) occurred as snow and rain primarily during winter and spring months. Average daily low and high temperatures were 9 °C to 31 °C during summer and –3 °C to 7 °C during winter. Dominant fauna included mule deer (*Odocoileus hemionus*),

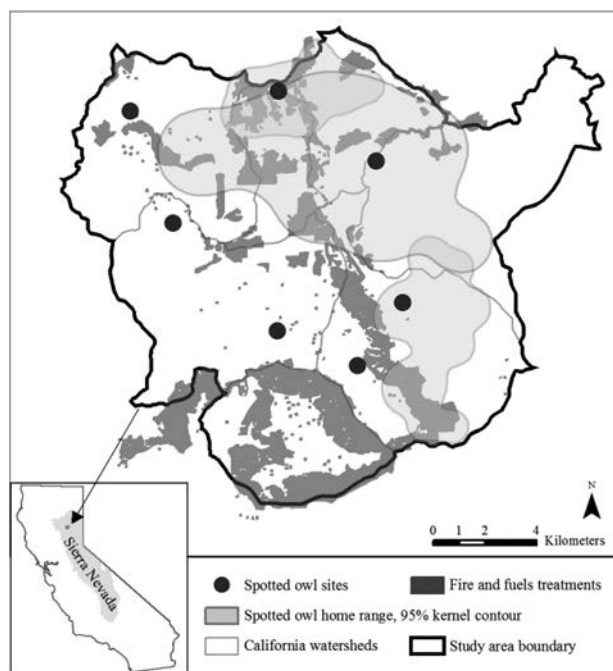


Figure 1. The 238-km² spotted owl study area located in the Plumas National Forest, in the northern Sierra Nevada of California, USA, 2007–2008. For clarity, we show 3 spotted owl home ranges illustrating the minimum (northernmost), maximum (center), and an intermediately sized home range (southernmost).

American marten (*Martes americana*), mountain lion (*Puma concolor*), American black bear (*Ursus americanus*), Humboldt's flying squirrel (*Glaucomys oregonensis*), dusky-footed woodrat (*Neotoma fuscipes*), and northern goshawk (*Accipiter gentilis*). The historical fire regime for the study area was a return of low to moderate severity fires every 7–19 years, prior to fire suppression (Moody et al. 2006).

Forest management during the study was guided by the Herger-Feinstein Quincy Library Group Forest Recovery Act of 1998 (HFQLG Act), which mandated a landscape-scale fuels management strategy consisting of Defensible Fuel Profile Zone (DFPZ) and group selection timber harvests; DFPZs are landscape-scale (400–800 m wide) linear fuel thins strategically located to function as wildfire breaks and characterized by a reduction of ground and ladder fuels, even tree spacing, and $\leq 40\%$ canopy cover. Group selections are ≤ 0.8 -ha patch cuts in which all trees < 76 cm diameter are harvested, to create vegetation heterogeneity and generate revenue. The HFQLG Act prohibited fuels and timber harvest treatments within spotted owl Protected Activity Centers (PACs), 121-ha units of late seral forest delineated by forest biologists around spotted owl nests and roosts; other areas of spotted owl home ranges were treated.

The Meadow Valley Project was the only landscape-level HFQLG Act forest treatment suite fully implemented in an area containing suitable spotted owl habitat. Under HFQLG Act guidelines, contracting parties had ≤ 5 years from the date of sale to complete fuels treatments. The MVP treatment and harvest operations began in 2003 and were 80% complete by January 2007; all project treatments and harvests were completed by October 2008.

We created a perimeter for the study area by overlaying the MVP area with the California Watershed Map (CALWATER version 2.2, California Interagency Watershed Mapping Committee) in a geographic information system (GIS). Seven watersheds contained most of the MVP treatments, and had been surveyed for spotted owls for 5 years prior to this study. We delineated the perimeter of these 7 watersheds as the perimeter of the study (Fig. 1). The resulting 23,823-ha study area encompassed 4,160 ha of fuels treatments. We collected spotted owl foraging data during the breeding seasons of 2007 and 2008. The breeding season was 1 April to 30 September, based on the expected return of territorial birds from wintering grounds, and the juvenile fledging period extending into August and September (Gutiérrez et al. 1995). These *a priori* dates were later supported by winter habits of the radio-tagged owls, which remained on territory through early November, and returned to territories in mid-March of the following year.

METHODS

We grouped treatments into 3 broad categories: large-scale mechanical thin and biomass removal implemented across the study area as DFPZs and group selections; understory thins, prescribed as a non-commercial removal of shrubs and trees < 25 cm dbh; and understory thin followed by prescribed underburn, a controlled surface-fuel burn that did not affect the forest overstory. The MVP area contained 1,784 ha of DFPZ treatments and 272 ha of group selections, which were typically located near or embedded within DFPZs. The MVP area also contained 1,440 ha of understory thin and 665 ha of underburn.

Spotted owl sites within the study area boundary were identified by annual surveys conducted by the Pacific Southwest Research Station, USFS. For site selection, we constrained sites to those that had been occupied for > 1 year prior to this study and were occupied by pairs at the time of the study. This limited our site selection to 6 sites in the first post-treatment year (2007) and a different configuration of 6 sites in the second post-treatment year (2008).

We radio-marked owls at these sites with backpack radio-transmitters (Holohil Systems, Model RI-2C, Ontario, Canada) fitted to each owl with Teflon[®]-coated Kevlar[®] ribbon (Bally Ribbon Mills, Bally, PA, USA). Total mass of the radio-transmitters was 14 g, or 2.5% of the body mass of an average spotted owl male (Gutiérrez et al. 1995). We radio-tagged females in June, after young fledged from the nest; we removed radio-transmitters from all owls at the conclusion of the study.

Radio-Telemetry

Two observers, working together, derived owl locations using standard radio-telemetry triangulation techniques (White and Garrott 1990, Kenward 2001, Millsbaugh and Marzluff 2001). We separated sequential locations for each owl by ≥ 24 hours to reduce temporal autocorrelation; this resulted in a maximum sampling regime of 5 locations per bird every 2 weeks, or 10 locations per bird per month. We continuously varied the owl tracking sequence to sample

across the full nocturnal activity period for each owl, and gathered all owl locations between 1 hour after sunset and 1 hour before sunrise. We followed protocols in accordance with the Guidelines for the Use of Wild Birds in Research (Fair et al. 2010), and all procedures were part of a study plan approved by the USFS.

Observers gathered bearings as close together in time as possible to reduce the probability of bird movement; once near the owl, mean elapsed time of the triangulation process was 16 ± 0.5 (SE) minutes ($n = 465$). After collecting ≥ 3 bearings, observers checked data in the field using Palm LOCATE (Pacer Computing, Nova Scotia, Canada). We accepted locations when the 95% confidence ellipse was < 1.5 ha; similar spotted owl telemetry studies have used a 95% confidence ellipse of 2 ha (Clark 2007) or 5 ha (Glenn et al. 2004, Williams et al. 2011). If the owl was ≤ 200 m from the surveyors, surveyors attempted to observe the bird and verify location; surveyors abandoned this effort if they detected a signal change indicating bird movement.

We used LOAS 4.0b software (Ecological Software Solutions, Urnäsch, Switzerland) to calculate the 95% confidence ellipse of each owl location with the maximum likelihood estimator. We assessed accuracy of triangulation estimates using daytime owl locations; working individually while owls were roosting, observers triangulated on the owl and then moved in on the signal to directly observe the bird. Surveyors recorded the owl's true location with a global positioning system unit accurate to ≤ 5 m and noted the difference between the estimated location and true location.

We rejected the datum if, upon observing the owl, the owl appeared disturbed or awake, or if we detected changes in the radio-signal indicating bird movement while the observer approached. Mean bearing error between estimated and true locations was 7.25 ± 0.85 degrees and mean distance error was 68.5 ± 38 m. Similar studies on spotted owls report accuracy estimates of 7.2–9.6 degrees bearing error and mean distance errors of 68–164 m (Carey et al. 1992, Glenn et al. 2004, Forsman et al. 2005, Williams et al. 2011).

Habitat and Fuels Treatment Mapping

To create a study-wide map of fuels treatments (MVP map), we combined the 2009 USFS Region 5 Remote Sensing Laboratory map for the Meadow Valley Project area, derived from aerial photographs and satellite data captured in August 2009, with Plumas National Forest harvest records. The resolution of the MVP map was 5 m, based on the remote sensing imagery used in its creation (C. M. Ramirez, USFS Remote Sensing Laboratory, personal communication).

Watershed Sciences (Corvallis, OR, USA) collected aerial LiDAR imagery for the MVP area in July and August 2009. The imagery was captured with an average point density of 4.68 points/m², and an average vertical and horizontal accuracy of 2.6 cm and 7.2 cm, respectively. We extracted 21 LiDAR metrics that we thought could be biologically important to spotted owls (Table 1) using LasTools (Isenburg 2011) and Fusion (McGaughey 2012). Metrics included topography, direct forest structural metrics such as

Table 1. Post-treatment landscape metrics derived from Light Detection and Range (LiDAR) for spotted owl foraging locations and random locations within owl breeding season home ranges, Meadow Valley Project area, northern Sierra Nevada, California, USA, 2007–2008.

Abbreviation	Description	Resolution (m)	Owl foraging ($n = 413$)		Random ($n = 2,100$)	
			($\bar{x}$)	SE	($\bar{x}$)	SE
Slope	Slope at point location	10	20.36	0.45	17.49	0.19
Aspect	Aspect at point location	10	169.68	5.59	162.80	2.36
CH _{max}	Maximum canopy height (m) across ellipse, mean	1	13.73	0.37	11.74	0.12
CH1	Canopy height class 1 (0–2 m; proportion in ellipse)	1	0.24	0.01	0.27	0.00
CH2	Canopy height class 2 (2–8 m; proportion in ellipse)	1	0.16	0.01	0.15	0.00
CH3	Canopy height class 3 (8–16 m; proportion in ellipse)	1	0.17	0.01	0.19	0.00
CH4	Canopy height class 4 (16–32 m; proportion in ellipse)	1	0.29	0.01	0.27	0.00
CH5	Canopy height class 5 (32–48 m; proportion in ellipse)	1	0.10	0.01	0.06	0.00
CH6	Canopy height class 6 (> 48 m; proportion in ellipse)	1	0.01	0.00	0.00	0.00
LargeTree	Density of large trees (> 76 cm dbh), trees/ha	10	29.77	1.80	20.10	0.71
Cover _{>70%}	Proportion of ellipse that is $> 70\%$ total cover	30	0.64	0.02	0.55	0.01
Cover _{40–70%}	Proportion of ellipse that is 40–70% total cover	30	0.27	0.02	0.30	0.01
Cover _{>70%, 16m}	Above 16 m minimum canopy height, proportion of ellipse that is $> 70\%$ cover	30	0.11	0.01	0.09	0.00
Cover _{40–70%, 16m}	Above 16 m minimum canopy height, proportion of ellipse that is 40–70% cover	30	0.38	0.02	0.30	0.01
Cover _{>70%, 32m}	Above 32 m minimum canopy height, proportion of ellipse that is $> 70\%$ cover	30	0.002	0.001	0.001	0.000
Cover _{40–70%, 32m}	Above 32 m minimum canopy height, proportion of ellipse that is 40–70% cover	30	0.04	0.01	0.03	0.00
H' _{Cover}	Shannon diversity index (H') of cover across 6 canopy strata	10	1.35	0.01	1.39	0.00
Edge	Edge at intersection of forest (> 2 m canopy height) and gap (≤ 2 m maximum canopy height), calculated as total edge/ellipse area	2	0.14	0.01	0.15	0.00
Gap _{prop}	Gap (≤ 2 m maximum canopy height) area, as proportion of ellipse	2	0.22	0.01	0.28	0.00
Gap _{size}	Mean gap size across ellipse	2	50.02	7.06	105.61	13.10
Edge:Area	Ratio of total gap edge to total gap area within the ellipse	2	0.86	0.03	0.75	0.01

canopy height and cover (Kramer et al. 2016a), and derived metrics such as a Shannon diversity index of cover across 5 height strata to describe canopy complexity (Table 1). Although we desired to explore the components of shrubs, downed woody debris, and herbaceous layers, MVP LiDAR data in the 0–2-m height strata suffered from signal degradation in areas of dense upper canopy, such as those found in owl core areas. We therefore excluded the 0–2-m height strata from analyses except when the maximum canopy height was <2 m.

An advantage of aerial LiDAR is exceptional spatial resolution; base LiDAR data for the MVP area has a 1-m pixel size with sub-meter accuracy. We did not extract LiDAR variables directly from 1-m raster cells that overlapped an owl use location; given the mean telemetry distance error of 68.5 m, extraction of a LiDAR value at an estimated location had potential to introduce substantial spatial error and misinterpretation. For this reason, we calculated LiDAR metrics across the entire error ellipse of owl locations, thus describing the overall habitat conditions within the ellipse. Similarly, for random points that approximated available foraging habitat, we used the mean telemetry error to create a 68.5-m radius circle around each random point, and calculated LiDAR metrics across the entire circle. Our choice of an aggregation method was likely more robust than alternatives, although still susceptible to spatial autocorrelation of neighboring pixels and smoothing of spatial heterogeneity, which would be more pronounced for dissimilar than similar pixel values (Gotway and Young 2002).

We considered owl and random locations to be within treatment if the location fell within a treatment polygon in the MVP map, or within the 5-m error buffer of the treatment polygon boundary. Additionally, we visited all owl locations within or near treatment areas during daytime hours to ground-truth the treatment status indicated by the map. We did not consider ground-truthed owl locations 5.0–68.5 m from a treatment boundary to be within treatment because it was unclear if the animals were associated with the treatment, the area adjacent to treatment, or the treatment edge; our dataset included 31 such locations. To minimize complications of this uncertainty, we avoided statistical methods requiring a categorical response of owl locations within treatment.

Home Range Estimation and Fuels Treatment Composition

We estimated spotted owl home ranges using fixed kernel density estimator methods and 100% minimum convex polygons (MCPs). Following Williams et al. (2011), we used the MCP method strictly for comparison purposes because it is the only home range size metric included in all previous California spotted owl home range studies.

We chose fixed kernel density estimators as the home range model for this dataset because adaptive kernel estimators tend to undersmooth data at outer contour levels and overemphasize outliers (Seaman et al. 1999). To objectively assess the choice of estimator, we tested the fit of the fixed

kernel density estimator against the fit of the adaptive-kernel density estimator by applying information-theoretic model selection using the relative Kullback-Leibler (KL) distance in Animal Space Use 1.2 (Horne and Garton 2006). The relative KL distances supported fixed kernel density estimators as an appropriate choice for this dataset. We chose the likelihood-cross-validation (CVh) smoothing parameter to calculate bandwidth for fixed kernel estimators. We calculated breeding season home ranges for owls with a minimum of 30 locations, following Seaman et al. (1999), and used owl locations with 95% confidence ellipses ≤ 1.5 ha for home range derivation.

We used a simplified resource selection function (Manly et al. 2002) to evaluate the fuels treatment composition of owl home ranges relative to the study area. The area contained within the 95% fixed kernel volume contour defined spotted owl home range use area, whereas the study area described the available area. We quantified fuels treatments for each owl's home range by overlaying the 95% fixed kernel contour with the MVP map.

We compared the proportion of fuels treatments in each home range with the total proportion available in the study area using resource selection ratios (w'_i). We estimated selection ratios, variances, and confidence limits, following Design II Sampling Protocol A in Manly et al. (2002). We used Bonferroni-corrected 90% confidence limits to define whether use of each treatment type was disproportionately abundant ($w'_i > 1$) or absent ($w'_i < 1$) in owl home ranges compared to its availability on the landscape.

Owl Use of Treatment Areas: Foraging Locations

To explore owl habitat selection within the home range, we developed *a priori* models comparing owl use locations and randomly generated locations (available locations), and evaluated these models using mixed-model logistic regression (Keating and Cherry 2004), Akaike's Information Criterion corrected for small sample sizes (AIC_c), and Akaike weights (w_i ; Burnham and Anderson 2002). We used GIS to create 5 times as many random points as owl locations within each owl's 95% home range contour and used these randomly generated points to approximate the available habitat within the home range (Johnson et al. 2006). We modeled owl identity as a random effect and all other variables as fixed effects. Because our study area is the only instance that we know of within the range of the California spotted owl to have overlapping areas of LiDAR and telemetry, and we were interested in forest structural characteristics that may be key components of owl foraging habitat and altered during fuels reduction, our analysis was exploratory and contained 68 *a priori* models.

We used a step-wise approach to build our model set. The first set of models compared distance to the owl's site center (nest tree, or primary roost for non-nesting owls), physiographic features, study year, and a null model (Table S1, available online in Supporting Information). Because spotted owls are central-place foragers, the distance to site center metric assumes that owls will not travel more than necessary to forage, and land cover types near the nest or

roost will have greater probability of use simply as a result of minimizing distance traveled (Rosenberg and McKelvey 1999, Glenn et al. 2004, Irwin et al. 2007). Given spotted owls preference for mature forest (Gutiérrez et al. 1995), we anticipated that the prevalence of large trees (>76 cm dbh) in steep, north-facing slopes in the study area would result in owl selection for steep or north-facing slopes. We did not include elevation in models because owl home ranges in our study area contained similar elevations. We included year as a nuisance variable, anticipating possible differences between the first year of study, which was an average reproductive year, and the second year of study, which was an exceptionally poor reproductive year. We predicted that owls would forage more widely and explore novel areas during the second study year, without the need to return regularly to a nest. Finally, we included a model of owl identity as a null model because of variation in owl home ranges.

Our second step of model selection compared LiDAR-derived forest structural metrics (Tables 1 and S1). To narrow down a large list of potential LiDAR metrics, we selected forest variables that were important to spotted owl nesting and foraging habitat in prior studies.

Throughout their range, spotted owls have been documented to prefer mature forest with large-diameter trees for nesting and roosting (Bias and Gutiérrez 1992, Verner et al. 1992, Moen and Gutiérrez 1997), including late seral forests interspersed with alternate forest types and edges (Franklin et al. 2000). Large-diameter trees are important to spotted owl foraging habitat, perhaps because of their relevance to an important prey species, Humboldt's flying squirrel (Carey et al. 1992, Waters and Zabel 1995, Meyer et al. 2007). We estimated the presence of large trees using 2 methods: proportion of large trees within the ellipse, a simple measure of the presence of large trees in any configuration, and large tree density, a measure sensitive to clustering of large trees.

Following Kramer et al. (2016b) and North et al. (1999), we estimated the proportion of large trees by first calculating the maximum canopy height across the landscape in 1×1 -m pixels and distributing the maximum heights into 6 classes: 0 to 2, >2 to 8, >8 to 16, >16 to 32, >32 to 48, and >48 m. We predicted that owls would preferentially select for higher proportions of 32–48-m trees (class 5), considered nesting habitat, and 16–32-m trees (class 4), which are often considered suitable foraging habitat (Verner et al. 1992). We were unable to include the tallest size class, >48 m, because of its rarity within the study area (0.3% of all LiDAR-derived pixels).

Tree size, as measured by tree diameter, is not directly estimated by LiDAR and is typically inferred using individual tree segmentation algorithms or statistical modeling (García-Feced et al. 2011, Jakubowski et al. 2013). Tree segmentation algorithms require extensive tree stem maps as training data, and can be prone to decreased accuracy when stems are close to each other, such as areas of dense canopy cover (Kaartinen et al. 2012). Following Kramer et al. (2016a), we opted for a regression approach to estimate the density of large trees (>76 cm dbh) as trees/ha,

using an algorithm created from MVP data that could also be easily adapted to other studies. To estimate large tree density, we used the equation:

$$\sqrt{\frac{Trees}{ha}} = 2.37 + 0.786 \left(\sqrt{CHM32} \right) - 0.909 (\log(VAR) + 1), \quad (1)$$

where CHM32 is the proportion of area with >32 m maximum canopy height, an equivalent for trees >76 cm dbh, and VAR is the variance of point heights above 2 m (Kramer et al. 2016a). This large tree density model had a cross-validation error of less than a single tree, and an adjusted R^2 value of 0.77 for the MVP area, which is comparable to other tree segmentation and statistical modeling methods. We predicted that spotted owls would preferentially forage in areas with high density of large trees.

Spotted owl management guidelines regularly divide canopy cover into 2 activity-based functional categories: high (>70%) cover, considered to be optimal nesting habitat, and medium (40–70%) cover, considered to be suitable foraging habitat. Given the importance of high canopy cover areas to spotted owls in recent studies (Tempel et al. 2014, 2015; North et al. 2017a), we calculated the proportion of high (>70%) canopy area within each ellipse. We chose a 30-m pixel size for this calculation, based on Program Fusion guidelines (McGaughey 2012). We estimated canopy cover using 900 1-m $\times$ 1-m cells, and calculated percent cover area as the number of cells within the 900-cell grid that were considered canopy (min. height ≥ 2 m) divided by the total number of cells (900). Given the importance of cover at height strata created by large trees (North et al. 2017a), we also estimated the cover contribution of co-dominant and large trees by repeating the above method and using minimum canopy heights of 16 m and 32 m.

We included the proportion of high (>70%) canopy cover in models because of its importance to survival, reproduction, and site occupancy in prior spotted owl studies (Franklin et al. 2000, Blakesley et al. 2005, Seamans and Gutiérrez 2007, Tempel et al. 2014). Further, we included the proportion of medium (40–70%) canopy cover in models because management guidelines define medium canopy cover as suitable foraging habitat based on the findings of early foraging studies (Call et al. 1992, Zabel et al. 1992). Additionally, Williams et al. (2011) described spotted owl preference for areas of both high and medium canopy cover, particularly in mature forests, for foraging. We estimated medium (40–70%) and high (>70%) cover at 3 height strata: ≥ 2 m to represent the overall canopy, ≥ 16 m to address cover contribution of co-dominant trees, and ≥ 32 m for cover created by large trees.

We predicted that owl foraging would positively correlate with both high (>70%) and medium (40–70%) canopy cover classes, regardless of the minimum canopy height used in cover calculations. Further, we predicted owl selection of high and medium cover would follow 1 of 2 possible trends: linear, in which areas with greater proportions of high or medium canopy cover are used preferentially; and quadratic,

in which the likelihood of owls selecting an area for foraging increases to a maximum probability at an ideal contribution of high or medium cover, then either declines as the proportion of the cover class increases, or holds at a threshold. Our model set thus included linear and quadratic trends for medium and high cover categories. We did not create candidate models containing both high and medium cover classes because the classes are mutually exclusive by definition and thus correlated.

To estimate vertical canopy complexity, we generated a Shannon diversity index (Equation 2) for canopy cover. Following North et al. (1999) and Kramer et al. (2016b), we divided the vertical canopy into 5 horizontal bands at >2 to 8-m, >8 to 16-m, >16 to 32-m, >32 to 48-m, and >48-m height strata, and estimated LiDAR-derived canopy cover within each band. We then calculated the Shannon diversity index (H') for cover across the telemetry error ellipse as

$$H' = - \sum_{i=1}^S P_i \ln P_i \quad (2)$$

where S is the number of horizontal canopy strata (5) and P_i is the mean canopy cover for each strata within the ellipse. We predicted that owls would prefer foraging areas with greater vertical structure or denser canopy throughout the vertical stand, which would correspond to lower diversity values.

We were interested in exploring owl foraging preference for forest gaps and edges, given their importance to owl survivorship and reproductive fitness (Franklin et al. 2000), and their foraging preferences (Williams et al. 2011). We defined a gap in this study as any area, 2-m $\times$ 2-m pixel or greater, in which the maximum canopy height is ≤ 2 m; a 4-m² pixel size was the smallest resolution available to us because of computational limitations. We defined edge as the hard edge between forest (>2-m canopy height) and gap (≤ 2 -m canopy height). We predicted that owls would prefer areas with intermediate proportions of gaps and edges, where increases of small-mammal abundance at early seral forest edges balance with protective cover of mature forest (Zabel et al. 1995, Ward et al. 1998, Franklin et al. 2000). We also anticipated that owls would prefer smaller gaps, represented in the data as small mean gap size because smaller gap size offers increased protection from predators and more contiguous surrounding forest for movement. Lastly, we predicted that owls would prefer gaps with maximum edge per exposed area, to increase the availability of forest edge preferred by small mammals without compromising protective cover from predators.

We modeled each of the LiDAR variables above, as stand-alone models. In addition, we created simple additive models containing 2 or 3 variables in the general configuration of large trees + cover + gaps or edge (Table S1).

Our third step of model selection explored associations of owl foraging locations with fuels treatments, alone and additively with the top models from the first 2 modeling steps (Table S1). Although mechanical thin treatments were distributed throughout the study area, understory thin and underburn treatments were not; understory thins were implemented only

in the southern half of the study area and underburns were only conducted in the northern half. To preserve power, we pooled all fuels treatment types together. Given the presence of mechanical thin treatments in all owl home ranges, we were able to specifically address mechanically thinned treatments. We predicted that owl use of an area for foraging would decline as the proportion of mechanical thin or total treated area increased. We also considered that above a certain threshold of treatment area, owls would move elsewhere to forage, and included a quadratic trend of mechanical thin and fuels treatments in the model set.

We searched for any correlation of variables prior to running all models and excluded models that would contain collinear components. We used the pROC package in Program R to estimate an area under the receiver operating characteristic (ROC) curve, an assessment of the goodness of fit of the top model(s); we defined the top model(s) as that with the lowest AIC_c value or within 2 AIC_c of the lowest value. Given the small sample sizes typical of radio-telemetry studies and our study, our last modeling step was to test the robustness and sensitivity of our modeling results to influential observations by removing one individual at a time from the dataset and re-evaluating all models using the same methods as described above.

RESULTS

We tracked 10 spotted owls (6 females, 4 males) during the study; we tracked 6 owls continuously throughout the first and second post-treatment years. We radio-marked 8 owls (3 males, 5 females) in 2007, including both members of 2 pairs. We found 2 of these birds deceased the following winter: a male was depredated and necropsy results for a female indicated nematode parasitism. We radio-marked 2 additional owls in 2008, bringing the sample size again to 8 owls: 3 males and 5 females, including 2 pairs. One female moved outside of the study area during the study period and was excluded from analyses. We collected 446 nocturnal use locations, with 4 of 236 locations (1.7%) occurring within fuels treatments in 2007, and 32 of 210 locations (15.2%) occurring within fuels treatments in 2008.

Home Range Size and Placement

We estimated home ranges for 9 owls using 30–60 foraging locations per bird (Seaman et al. 1999). Home ranges estimated with the 95% fixed kernel estimator averaged $2,494 \pm 405.1$ ha during 2007 and $3,386 \pm 625.6$ ha during 2008. Average MCP home range sizes for this study were $1,281 \pm 208.4$ ha and $2,026 \pm 336.2$ ha for 2007 and 2008, respectively.

Of the 3 treatment types, owl home ranges contained primarily mechanical thin areas ($\bar{x} = 271 \pm 60.2$ ha, $n = 9$), which were composed of DFPZs ($\bar{x} = 234 \pm 51.8$ ha, $n = 9$) and group selections ($\bar{x} = 36.8 \pm 8.8$ ha, $n = 9$). The amount of each treatment type within home ranges varied widely among owls, especially for underburn ($\bar{x} = 236 \pm 70.6$ ha, $n = 4$), and understory thin ($\bar{x} = 222 \pm 70.1$ ha, $n = 5$), which were not available within all owl home ranges. Spotted owl home ranges contained an average of $17.1 \pm 3.3\%$ ($n = 9$) total fuels treatments (Table 2). Selection ratios (w'_i)

Table 2. Proportion of area treated and resource selection function for 4 fuels treatment types in 9 spotted owl home ranges and overall study area, Meadow Valley Project area, northern Sierra Nevada, California, USA, 2007–2008.

	Study area	Owl $\bar{x}$	w_i^a	SE(w_i)	Bonferroni confidence limits	
					Lower	Upper
DFPZ ^b	0.07	0.08	1.018	0.176	0.598	1.438
Group selection	0.01	0.01	1.043	0.199	0.566	1.520
Understory thin	0.06	0.04	0.663	0.347	0.000	1.495
Underburn	0.03	0.03	1.125	0.638	0.000	2.652
All treatments	0.17	0.16	0.914	0.189	0.462	1.366

^a Selection ratio.

^b Defensible Fuel Profile Zone.

suggested that proportions of treated areas within owl home ranges were similar to proportions of treatments available on the landscape (Table 2). All 90% Bonferroni confidence intervals for fuels treatments overlapped 1, indicating no difference between the composition of fuels treatments within home ranges and that available within the study area.

Owl Use of Treatment Areas: Foraging Locations

At the foraging-location scale, individual owl use of fuels treatments varied widely, and independently of the percentage of the home range that had been treated. Across all birds and both study years, 36 owl locations (8%) were within fuels treatments; all fuels treatment categories were used by an owl on at least 1 occasion. Locations within fuels treatments comprised 3–13% of the nocturnal use locations for 4 owls and 4 owls were never located within treatments (Fig. 2A). One male (P58) accounted for 15 (42%) locations within fuels treatment; this male foraged in an area that had been treated by prescribed underburn 1–7 years prior to site occupancy, and 29% of the owl's home range was within fuels treatments (14% mechanical thin, 15% underburn). This home range was unique in the amount of underburned forest it contained, and unfortunately there was not a comparable home range within the study area to further clarify possible trends related to underburned forest. We observed spotted owls foraging in mechanical thin on 14 occasions; across all owls, a mean of $3.15 \pm 1.2\%$ ($n = 9$) of owl foraging locations

occurred in mechanical thin. When calculated as a proportion of the error ellipse, the mean proportion of mechanical thin at owl locations was $5.5 \pm 1.0\%$ ($n = 446$), compared with $9.9 \pm 0.5\%$ ($n = 2,100$) for random locations (Fig. 3). Similarly, the mean proportion of all fuels treatments at owl locations was also lower ($\bar{x} = 11.0 \pm 1.4\%$, $n = 446$) than at random locations ($\bar{x} = 15.2 \pm 0.7\%$, $n = 2,100$).

The top model for owl foraging locations in a post-treatment landscape included negative correlations with mechanical thin, high ($>70\%$) canopy cover in the ≥ 32 -m height strata, proportion of gaps, and distance to the owl's site center, and a marginally positive correlation with slope (Table 3). Two competitive models were very similar to the top model, and differed only in their consideration of fuels treatments: a model that did not include a treatment effect (model 2, Table 3) ranked 0.47 AIC_c below, and a model with a weak positive relationship of fuels treatments (model 3, Table 3) ranked 2.40 AIC_c below the top model (Burnham and Anderson 2002). The goodness-of-fit test (area under the ROC curve) suggested that the 3 top models were all a reasonably good fit to the data (area under the ROC = 0.76, 0.75, and 0.77 for models 1, 2, and 3, respectively).

Our top model was susceptible to influential observations. When we singly removed from the dataset any of 2 individual owls containing larger proportions of mechanical thin in

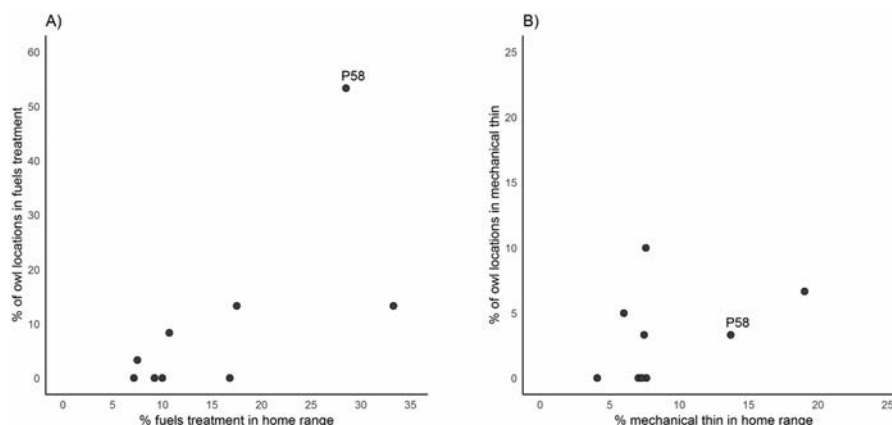


Figure 2. Percentage of spotted owl foraging locations within fuels treatments compared with availability of fuels treatments within each individual owl breeding season home range, in the Meadow Valley Project area, northern Sierra Nevada, California, USA, 2007–2008. We show this relationship for total combined fuels treatments (A), mechanical thin treatments (B), and an individual owl (P58) who accounted for 42% of all owl foraging locations within treatment.

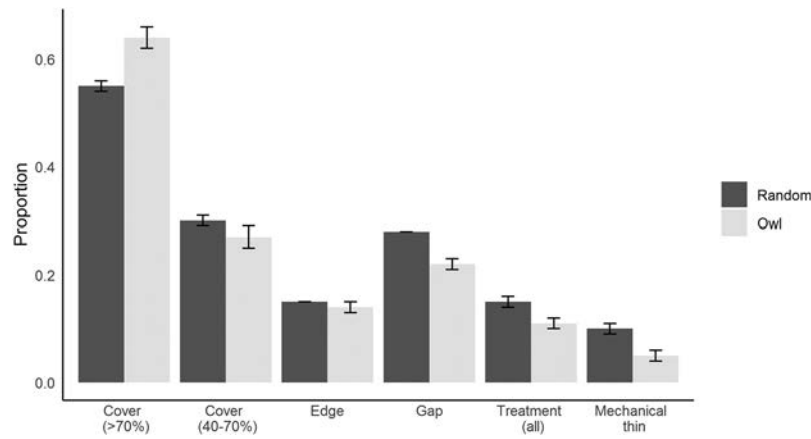


Figure 3. Means and standard errors for habitat variables at spotted owl foraging locations and random locations within owl home ranges, in the Meadow Valley Project area, northern Sierra Nevada, California, USA, 2007–2008.

their home range (Fig. 2B), the top model became model 2, which included the same covariates as the top model except it did not include a mechanical thin covariate (Table 3). Although removal of each of these owls changed the ranking of the 2 top models, model 1 remained within 1.1 AIC_c of model 2, β -parameters for model coefficients remained relatively unchanged to those for model 1 with all owls included, and the area under the ROC curve remained unchanged at 0.76, suggesting that the contribution of mechanical thin to our top model was minimal and susceptible to home range variation. The removal of each of the other owls from the dataset did not change the model ranking, β -parameters, or area under the ROC curve by any amount sufficient to alter model ranking or interpretation.

Increases in the proportion of gaps in the landscape corresponded with declining probabilities of spotted owl foraging (Table 4; Fig. 4A). The mean gap size for random locations was more than double that of owl foraging locations (Table 1), but this was not explanatory in top models (Table S1). Despite large differences in mean gap size, the

proportion of edge was similar between owl and random locations (Table 1), and edge did not rank highly in model sets (Table S1).

Spotted owls foraged in a variety of canopy complexities (Table 1). The top model described declining probability of spotted owl foraging with increasing high canopy cover above 32 m (Fig. 4D), although confidence intervals overlap zero, indicating large variation among individuals (Table 4). Although high canopy cover above 32 m, restricted to areas of the landscape with large trees, was a component of top models, large tree density and proportions of large trees were not explanatory (Tables 3 and S1).

Owl foraging locations contained greater proportions of high (>70%) overall canopy cover than random locations (Table 1); however, this difference did not rank highly in candidate models as a linear or quadratic trend (Table S1). Medium cover, typically considered suitable foraging habitat, did not rank competitively in candidate models when calculated as overall cover (>2 m min. canopy height), cover of co-dominant trees (≥ 16 m min. canopy height), or as

Table 3. Models that best explained spotted owl foraging habitat selection in a landscape with fuels treatments, Meadow Valley Project area, northern Sierra Nevada, California, USA, 2007–2008. We present all models within 100 corrected Akaike's Information Criterion (AIC_c) points of the top model.

Model		K^a	AIC_c^b	ΔAIC_c^c	w_i^d	Cum. Wt. ^e
1	$Gap_{prop}^f + Cover_{>70\%, 32m}^g + Distance_{core}^h + Slope + MechThin^i$	7	1,688.67	0.00	0.478	0.478
2	$Gap_{prop} + Cover_{>70\%, 32m} + Distance_{core} + Slope$	6	1,689.14	0.47	0.378	0.856
3	$Gap_{prop} + Cover_{>70\%, 32m} + Distance_{core} + Slope + Treatment_{All}^j$	7	1,691.08	2.40	0.144	1.000
4	$Gap_{prop} + Cover_{>70\%, 32m} + MechThin$	5	1,765.05	76.38	0.000	1.000
5	$Gap_{prop} + Cover_{>70\%, 32m}$	4	1,767.55	78.88	0.000	1.000
6	$Gap_{prop} + Cover_{>70\%, 32m} + Treatment_{All}$	5	1,769.09	80.42	0.000	1.000

^a Number of model parameters.

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

^c Difference in AIC_c values between the model and the best model.

^d Akaike weight.

^e Cumulative model weight.

^f Proportion of gap (≤ 2 m maximum canopy height).

^g Proportion of >70% cover at >32-m height strata.

^h Distance to site center.

ⁱ Proportion of mechanical thin.

^j Proportion of fuels treatment (all).

Table 4. Akaike weights (w_i), β -coefficients, standard error, lower and upper 95% confidence intervals, and P -values for models that best described spotted owl foraging in a treated landscape, Meadow Valley Project Area, Sierra Nevada, California, USA, 2007–2008.

Variable	Coefficient	SE	CI _{low}	CI _{high}	P
Model 1 ($w_i = 0.478$)					
Gaps (proportion)	−2.68	0.36	−3.39	−1.97	<0.001
Proportion of >70% cover at >32-m height strata	−2.50	4.35	−11.02	6.02	0.565
Distance from site center	−0.69	0.09	−0.86	−0.51	<0.001
Slope	0.01	0.01	0.00	0.03	0.042
Mechanical thin (proportion)	−0.43	0.28	−0.99	0.12	0.124
Model 2 ($w_i = 0.378$)					
Gaps (proportion)	−2.79	0.36	−3.49	−2.08	<0.001
Proportion of >70% cover at >32-m height strata	−2.33	4.36	−10.87	6.21	0.593
Distance from site center	−0.69	0.09	−0.86	−0.51	<0.001
Slope	0.02	0.01	0.00	0.03	0.017
Model 3 ($w_i = 0.144$)					
Gaps (proportion)	−2.81	0.37	−3.54	−2.08	<0.001
Proportion of >70% cover at >32-m height strata	−2.29	4.34	−10.81	6.22	0.597
Distance from site center	−0.69	0.09	−0.87	−0.51	<0.001
Slope	0.02	0.01	0.00	0.03	0.016
Proportion of fuels treatment (all)	0.06	0.22	−0.38	0.50	0.774

cover contribution of large trees (≥ 32 m min. canopy height; Table S1).

Owl foraging locations in our study were closer ($\bar{x} = 1,839 \pm 81$ m, $n = 446$) to the site center than expected at random ($\bar{x} = 2,366 \pm 34$ m, $n = 2,100$). Our top model similarly reflected a declining probability of owl foraging with increasing distance (Table 4; Fig. 4B). Owl foraging locations occurred in areas with slightly steeper slopes than anticipated at random (Table 1), which was also reflected in the top model as a mildly positive trend (Table 4; Fig. 4C).

DISCUSSION

The Meadow Valley Project presented a unique opportunity to investigate spotted owl foraging patterns and short-term response to full implementation of a landscape-scale fuels reduction project. At the landscape scale, spotted owl home ranges contained fuels treatments in relative proportion to their prevalence in the landscape (Table 2). Bonferroni confidence limits for the resource selection function varied from 0 to 2.65, suggesting that a larger sample size would be needed to clarify landscape trends regarding fuels treatment types (e.g., mechanical thin vs. underburn) (Fig. 5).

At the foraging location scale, probability of use declined with increasing distance from the owl's core area, as expected for a central-place forager (Rosenberg and McKelvey 1999). Further, probability of use for owl foraging was negatively related to the proportion of gaps (canopy height < 2 m) in the ellipse, and edge was not a component in competitive models. We had anticipated that gaps and edge would be features in model results, given their importance in previous findings for California spotted owl habitat use (Irwin et al. 2007, Bond et al. 2009, Williams et al. 2011, Eyes et al. 2017) and northern spotted owl habitat use (Zabel et al. 1995, Ward et al. 1998, Comfort et al. 2016). In our study, the proportion of gaps was the most important vegetation covariate, with owl foraging locations having an average gap proportion of 22%. We did not find evidence to support our hypothesis of a positive association with intermediate

proportions of gap but rather found a negative relationship of owl foraging with increasing gap proportion. Prior studies have reported positive correlations of spotted owl annual survival and reproductive output with mature forest edge, hypothesizing that the intersection of late seral forest and areas of shrubs and saplings may be important for prey species associated with early seral habitat, such as woodrats (*Neotoma* spp.), pocket gophers (*Thomomys* spp.) and deer mice (*Peromyscus* spp.; Franklin et al. 2000, Olson et al. 2004, Dugger et al. 2005, Tempel 2014). Our definition of edge as the intersection of forest (≥ 2 m canopy height) and open gaps (< 2 m maximum canopy height) at fine spatial resolution may not have been as biologically meaningful for the owl as intersections among coarsely defined vegetation classes, such as intersections of shrub patches with mature forest (Williams et al. 2011) or owl habitat with non-habitat (Franklin et al. 2000). The importance of edge to owl foraging may depend on the type of edge (hard vs. soft), land cover type, scale of patch sizes, disturbance type, and ecological context (Bond et al. 2009, Comfort et al. 2016, Eyes et al. 2017).

Fuels treatments typically incorporate a reduction of canopy cover to or near 40%, a reduction of understory density, and increased tree spacing as design features to modify fire behavior. The proportion of fuels treatment, calculated as both proportion of mechanical thin and as a combined area of all treatments, was lower at owl foraging locations versus random locations (Fig. 3), although owls exhibited considerable individual variation (Fig. 2). Although our top model included the proportion of mechanical thin as a weak negative effect, it was sensitive to influential observations; the exclusion of either of 2 owls (P58, D72) resulted in a top model that did not contain a fuels treatment covariate. A competitive model 2.40 AIC_c below the top model also contained a fuels treatment covariate, structured as all treatment types pooled together. This third-ranked model was also sensitive to influential observations; removal of owl P58 from the dataset changed the marginally positive fuels treatment effect (Table 4) to a negative, non-significant

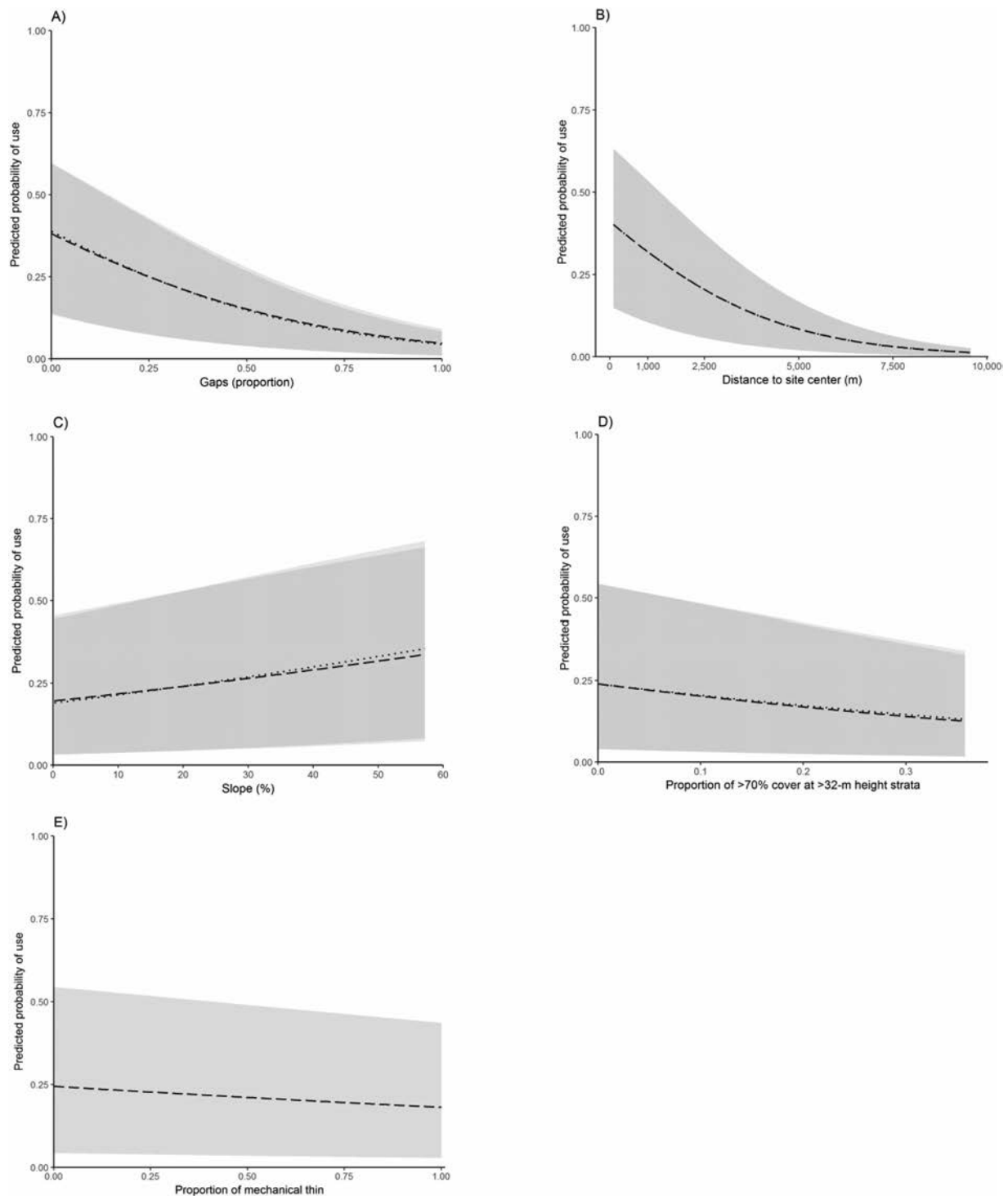


Figure 4. Predicted spotted owl foraging probabilities and 95% confidence intervals, derived from the 2 models of best fit in the Meadow Valley Project area, Sierra Nevada, California, USA, 2007–2008. We present probabilities derived from model 1 (gap + cover + distance + slope + mechanical thin) as a long-dashed line, and probabilities derived from model 2 (gap + cover + distance + slope) as a dotted line, for the following: proportion of gap (≤ 2 -m maximum canopy height) within the ellipse (A), distance from the location to the owl's site center (B), percent slope (C), proportion of ellipse that is $>70\%$ cover at a minimum canopy height of >32 m (D), and proportion of mechanical thin within the ellipse (E).

effect, illustrating variation in owl home ranges. Of note, 53% of owl P58's locations were located within fuels treatment, predominantly in areas of underburn, a treatment type with limited or no availability to other owls in the study area. Although a single observation, this merits mention in

the context of recent studies that have reported California spotted owls to forage in patches that experienced low and moderate severity wildfire (Bond et al. 2016, Jones et al. 2016, Eyes et al. 2017). Thus, we believe the instability of our top models that include fuels treatment covariates are a result

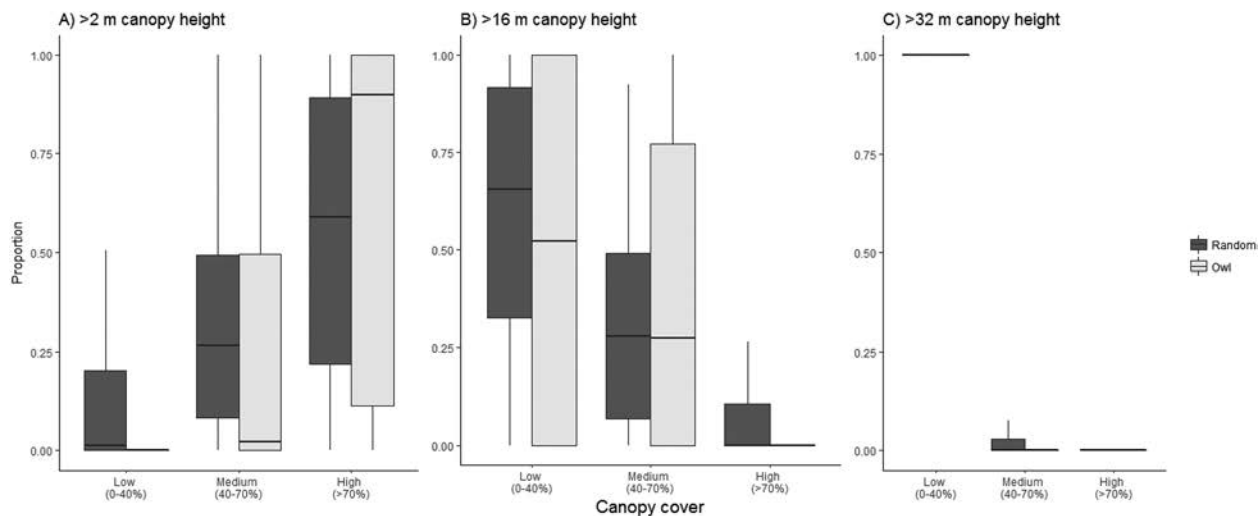


Figure 5. Comparison of canopy cover categories for spotted owl use locations and random locations within owl home ranges in a treated landscape in the Meadow Valley Project area, northern Sierra Nevada, California, USA, 2007–2008. We calculated cover as the proportion of forested 1-m pixels above a minimum canopy height of 2 m, representing overall canopy cover (A), 16 m, representing cover of co-dominant and dominant trees (B), and 32 m, describing cover of large trees (C). We show upper ($Q_{75\%}$) and lower ($Q_{25\%}$) quartiles as box extents and the median as the central horizontal line; vertical lines show the maximum and minimum values, excluding outliers which are defined as beyond $1.5 \times (Q_{75\%} - Q_{25\%})$ of the quartiles.

in part of our small sample size and the individual variation we observed across owls. Variation in foraging patterns may be characteristic for California spotted owls given differences among individuals, and prey and habitat availability across territories (Williams et al. 2011, Irwin et al. 2015).

Overall high (>70%) and medium (40–70%) canopy cover were not features of top models (Table S1), and >70% cover >32 m canopy height appeared as a non-significant negative trend in top models. These results are unexpected given a number of studies linking spotted owl site selection to areas of higher canopy cover (Franklin et al. 2000, Blakesley et al. 2005, Tempel et al. 2014), and a study in which California spotted owls selected for canopy closure more than for large tree sizes (Zabel et al. 1992). The differences in canopy cover results between our study and other studies may be in part derived from alternate mapping methods; earlier studies have used vegetation inventory plots, aerial photographs, or orthophotoquads to estimate canopy cover. Additionally, we analyzed canopy cover as a single attribute, whereas other studies have nested canopy cover within a combination metric that described canopy cover and tree stand size together as a unified covariate.

We found that the proportion of gaps and distance from the owl's site center were the strongest predictors of foraging locations for our study. The variation we observed in owl use of fuels treatments may be in part related to treatment effects on the proportion of gaps. A *post hoc* examination found that within owl home ranges, random locations in mechanically thinned forest contained greater proportions of gaps ($\bar{x} = 0.41 \pm 0.01$, $n = 205$) than found at this study's owl foraging locations ($\bar{x} = 0.22 \pm 0.01$, $n = 413$).

Mechanical thin treatments, including DFPZs and group selections, are characterized by a reduction of understory components such as large woody debris, shrub, and herbaceous cover: habitat elements important to small

mammals, particularly woodrats (Lee and Tietje 2005, Innes et al. 2007) and Humboldt's flying squirrels (Lehmkuhl et al. 2006), key California spotted owl prey species (Verner et al. 1992). Zabel et al. (1995) and Ward et al. (1998) both concluded that woodrats provided an energetic benefit to spotted owls over other prey species, and that owls selected foraging sites where woodrats were abundant. In a study that spatially overlaps our study area, presence of woodrat houses was influenced by the presence of black oak, steep slopes, and logs >30 cm mean dbh (Innes et al. 2007), all features that are rare in DFPZs and group selections.

Humboldt's flying squirrels prefer forests containing numerous large live trees, snags, well-developed understories, and many large logs on the ground (Lehmkuhl et al. 2006, Manning et al. 2012); these conditions are typically not maintained in a mechanical thin. Waters and Zabel (1995) reported low densities of flying squirrels in post-treatment stands, and Meyer et al. (2007) suggested that mechanical thinning may reduce the microhabitat suitability for flying squirrels for several years post-treatment. Holloway et al. (2012) reported low flying squirrel abundance in treatments that resulted in evenly spaced trees, which is a fire management feature of DFPZs. Sollmann et al. (2016) reported reduced densities of flying squirrels within fuels treatments and a corresponding shift in flying squirrel spatial distributions, out of fuels treatments and into unharvested areas of greater canopy closure, such that pre- and post-treatment densities were similar across the larger combined treatment and surrounding area. These results suggest that treatment effects on key spotted owl prey species should be considered at scales beyond the immediate treated patches.

We were not able to assess post-treatment alterations to several habitat attributes important to small-mammal abundance, including downed woody debris, snags, shrub, and herbaceous cover, because of degradation of the 0–2-m

band of the LiDAR signal in areas of complex canopy. Further, we were unable to draw definitive conclusions of understory thin and underburn treatment types because of sample size limitations. The active selection of post-understory burn selection of 1 individual on this study suggests further research may be warranted to investigate whether there may be positive benefits to owl foraging habitat from prescribed fire that are not realized from solely mechanical treatments.

Results from our study provide insight into the short-term response of spotted owls to the implementation of a landscape fuels treatment strategy. Inferences from our study should be interpreted with the understanding that we conducted an observational study susceptible to uncontrolled factors. For example, treated areas may have lacked foraging suitability before treatments were installed because of prey abundance or spatial location on the landscape. Our study was representative of the challenges of a passive adaptive management framework (Kendall 2001), in which the timing and spatial location of treatments were mandated by management objectives and thus precluded a controlled experiment. This is not an unusual circumstance on USFS lands where contracted treatments can be implemented within 5-year windows based on logistical, financial, and other operational factors. Given the broad importance of understanding how landscape forest and fuels restoration strategies affect California spotted owls and other species of concern in the Sierra Nevada, we believe that a reduction of barriers to implementing more rigorous study designs would strengthen research inferences to address these important information needs.

Our study focused on California spotted owl foraging response to fuels treatments in the immediate 2 years following implementation. Associations among owls and fuels treatments are likely to change over time as vegetation matures, and exploring patterns over longer time periods may be useful for a more comprehensive understanding of the effects of fuels treatments. In this study, the fine-resolution habitat data offered by LiDAR imagery was informative for modeling California spotted owl foraging habitat. We encourage further use and development of LiDAR vegetation data because the structural information it offers may be better suited than coarse-resolution vegetation data to address management and conservation concerns, particularly at spatial scales relevant to California spotted owls, project planning, and forest restoration.

MANAGEMENT IMPLICATIONS

As dry western forests continue to experience intensification in wildfire size and severity, a critical ecosystem management focus is forest resilience to wildfires that are outside of historical precedent. Modification of forest fuels and vegetation, implemented as fuels treatments, are likely to remain a frequently used tool to modify fire behavior and restore ecological resilience in fire-adapted forests. Current forest management guidelines emphasize structural heterogeneity, including the introduction of gaps. Our findings suggest that moderate to high proportions of gaps may

reduce the probability of spotted owl foraging, which creates conflicting implications for mechanically treated areas. We suggest consideration of gap proportions within the range associated with higher owl foraging probability until additional information becomes available. Acknowledging the prevalence of fuels treatments in current forest management, we encourage further investigation of effects on California spotted owl habitat use to broaden our initial findings. Increased availability of LiDAR vegetation data coupled with recent advances in satellite geospatial-tagging technology hold promise for further understanding of the effects of fuels treatments and forest restoration approaches on California spotted owls and their habitat.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Short Communication

Stable isotopes reveal unexpected relationships between fire history and the diet of Spotted Owls

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Although the effects of shifting fire regimes on bird populations have been recognized as important to ecology and conservation, the consequences of fire for trophic interactions of avian species – and raptors in particular – remain relatively unknown. Here, we found that within national parks with long-standing (40+ years) fire management programmes, California Spotted Owls *Strix occidentalis occidentalis* consumed predominantly Woodrats *Neotoma* spp. and Pocket Gophers *Thomomys* spp.; however, in contrast to our predictions, when their territories experienced more extensive and frequent fire, Spotted Owls consumed proportionally more Flying Squirrels *Glaucomys oregonensis*. We hypothesize this finding could have been driven by either changes to prey abundance following fires (e.g. increases in flying squirrels) or changes to prey availability (e.g. shifts in forest structure or flying squirrel spatial distribution that increased predation upon them by owls). Our work thus demonstrates that fire may have unexpected consequences for the trophic interactions of raptor species and provides valuable information for the conservation of Spotted Owls in fire-prone forest landscapes.

Keywords: fire ecology, mixing models, Sierra Nevada, *Strix occidentalis occidentalis*, trophic interactions.

The size, severity and frequency of wildfires are changing in some ecosystems owing to anthropogenic land use, fire suppression and climate change (Westerling 2016). A rich body of literature shows diverse relationships between fire and the demography, distribution and behaviour of avian taxa (e.g. Hutto & Patterson 2016). The effects of fire on avian populations are diverse. High-severity fire can be beneficial to populations of some species (e.g. Western Wood-Pewee *Contopus sordidulus*) but detrimental to others (e.g. Ash-throated Flycatcher *Myiarchus cinerascens*; Fontaine & Kennedy 2012). Understanding how avian species respond to fire is thus integral to the effective conservation of bird populations. Yet, the degree to which fire shapes the trophic interactions of avian populations – for raptors in particular – remains relatively unknown (but see Sahores & Trejo 2004). Given that trophic interactions can drive raptor demography (Martin 2008), prey dynamics (Korpimäki *et al.* 2002) and ecosystem processes (Terborgh *et al.* 2001), further research on the relationships between raptor diet and fire is warranted.

Here, we studied the relationships between fire history and trophic interactions of a territorial raptor, the California Spotted Owl *Strix occidentalis occidentalis* (hereafter 'Spotted Owl'). We conducted our research in the Sierra Nevada, CA, USA, where the potential impact of fire on Spotted Owl populations has garnered considerable attention in recent decades (Ganey *et al.* 2017) as larger and more severe fires have increased in frequency (Safford & Stevens 2017, Stevens *et al.* 2017). Whereas a number of studies have found that Spotted Owls are able to survive, reproduce and forage successfully in landscapes that experience predominately low-severity fire (e.g. Bond *et al.* 2002, Roberts *et al.* 2011), others have shown that Spotted Owls do not persist within extensive severely burned areas (e.g. Jones *et al.* 2016). However, it remains unknown whether and to what degree trophic interactions might mediate population responses to fire (Ganey *et al.* 2014).

We used stable isotopes to test the hypothesis that fire affects Spotted Owl consumption of Flying Squirrels *Glaucomys oregonensis* vs. Woodrats *Neotoma* spp. and Pocket Gophers *Thomomys* spp. Because Woodrats and Pocket Gophers are associated with younger, shrubby habitat and meadows, respectively, fire of all severities may generate suitable habitat for these species by promoting patches of early seral conditions (Roberts *et al.* 2015). Conversely, although lower-severity fire may have limited impacts on Flying Squirrel populations, they are likely to be negatively affected by high-severity fire because it mainly disturbs closed-canopy forests,

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where Flying Squirrels primarily reside (Pyare & Longland 2002, Meyer *et al.* 2005a, Roberts *et al.* 2015). Thus, we predicted that greater prevalence, area and diversity of fire within Spotted Owl territories would act to shift owl diet towards Woodrats and Pocket Gophers and away from Flying Squirrels. Given that the relative consumption of these prey groups may be an important driver of Spotted Owl population status (Hobart *et al.* 2019), improving our understanding of how fire affects diet may offer insights into how changing fire regimes could affect Spotted Owl populations and conservation efforts.

METHODS

We studied Spotted Owls in Yosemite, Sequoia and Kings Canyon National Parks of the central and southern Sierra Nevada (Fig. 1), where historical fire regimes are heterogeneous and dominated by lower-severity fire with small patches of high-severity fire. Although fire suppression began around the turn of the century, the National Park Service (NPS) began fire restoration programmes in the 1960s (Sequoia–Kings Canyon) and 1970s (Yosemite; van Wagtenonk 2009). Since that time, the NPS has used both prescribed and managed wildland fires to reduce fuel accumulation resulting from fire suppression and restore historical forest and burn-severity heterogeneity (Eyes *et al.* 2017).

In April and May of 2017 and 2018 we captured 41 owls (17 females, 24 males) at 31 territories using established methods (Franklin *et al.* 1996) to affix GPS tags and sample feathers for isotopic analyses. Because feather is an inert tissue that reflects the diet for the period it was synthesized (Hobson & Clark 1992) and Spotted Owls moult body feathers during the breeding season (Forsman 1981), our samples reflected the diet for the current breeding season. We also opportunistically collected regurgitated Spotted Owl pellets for prey isotopic signatures (30 Pocket Gophers, 35 Woodrats, 35 Flying Squirrels). All animal research was approved by the University of Wisconsin institutional animal care and use committee and permission was granted by the necessary state and federal agencies.

For owls with GPS data ($n = 25$ owls from 23 territories), we used nightly locations to quantify 95% kernel density estimate (KDE) territory polygons. For owls without GPS data ($n = 16$ owls from 13 territories), we defined territories as circular buffers (1.92 km radius) centred on nests or roosts with areas equal to the mean area of KDE polygons for owls with GPS data. Quantifying conditions within territories approximated by buffers has previously proven effective for both occupancy (e.g. Jones *et al.* 2016) and diet-based (e.g. Hobart *et al.* 2019) research. Within owl territories (either KDE polygons or circular buffers), we quantified fire history based on two data sources over four overlapping time steps: 5-

year (2012–16), 10-year (2007–16), 20-year (1997–2016) and 33-year steps (1984–2016; see Table S1 for a summarized description of each variable). Our first data source was CAL FIRE's Fire and Resource Assessment Program (FRAP; <https://frap.fire.ca.gov/mapping/gis-data/>), from which we downloaded perimeter data for fires over 10 acres in size (the minimum fire size monitored by FRAP). For each time step, we calculated the number and area of wildfires and prescribed fires that overlapped each owl territory. Our second data source was the Monitoring Trends in Burn Severity (MTBS; <https://www.mtbs.gov/>) programme, from which we downloaded fire severity information (low: <25% overstorey mortality; moderate: 25–75% overstorey mortality; and high: >75% overstorey mortality) for fires larger than 1000 acres (Eidenshink *et al.* 2007). We calculated each severity class by time step, resulting in 12 time-step burn-severity categories. If a single location burned more than once, the calculated area was cumulative and included all fires. For each owl territory we calculated (i) the proportional area in each time-step burn-severity, (ii) the Shannon diversity index of fire severity within a burned area and (iii) the Shannon diversity index of fire severity within a burned area in addition to unburned area (identical to i, except including unburned as a fourth category). All spatial analyses were performed using ArcMap 10.5.1 (ESRI, Redlands, CA, USA).

For isotopic analysis, 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 0.5 N HCl for ≥48 h to remove 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. 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 analyser and a high-temperature conversion elemental analyser. Results were expressed as parts per mil (‰) ratios relative to the international standards Vienna Pee Dee Belemnite (C) and atmospheric nitrogen (N).

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 had adequately sampled prey and applied appropriate trophic discrimination factors. To estimate proportional Spotted

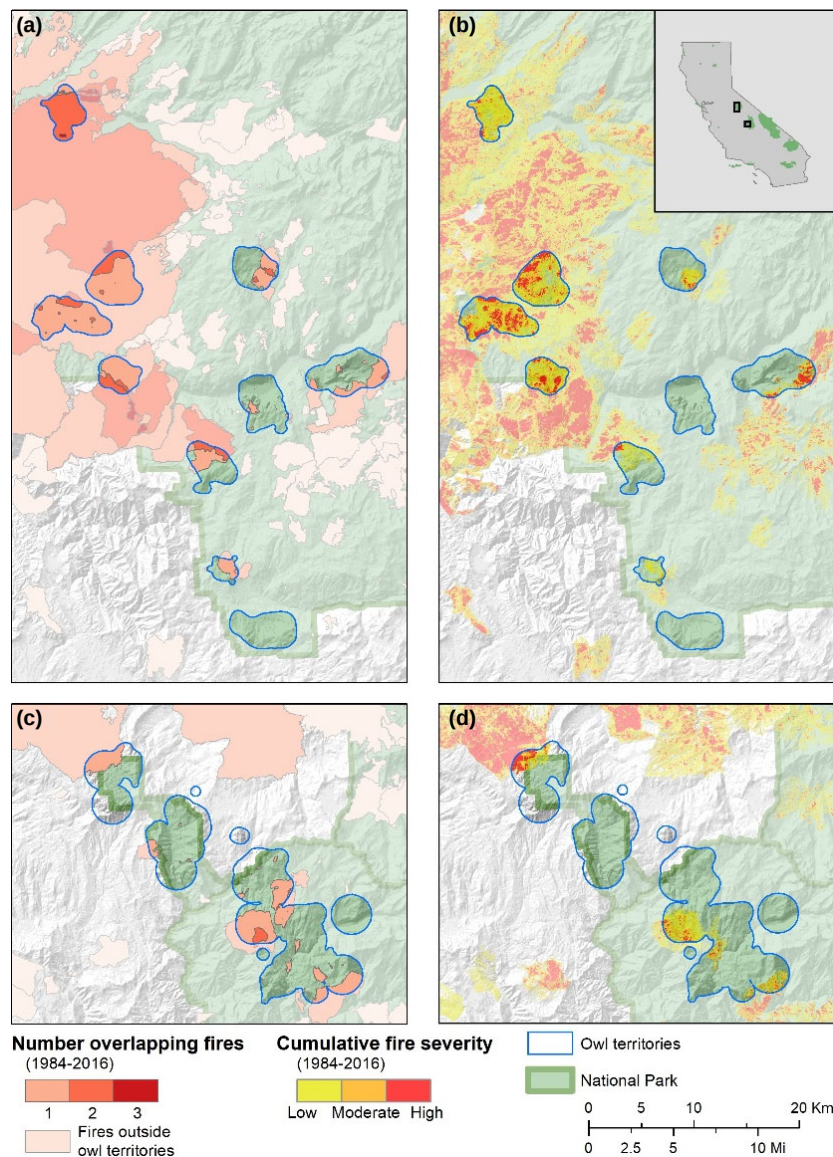


Figure 1. Map of the study areas in Yosemite (a, b) and Sequoia and Kings Canyon (c, d) National Parks, showing the distribution of fire perimeters and perimeter overlap (a, c) and cumulative fire severity (b, d) from all fires that burned between 1984 and 2016.

Owl diet, we employed Bayesian mixing models using the package MixSIAR, which quantifies the contribution of sources (prey) to mixtures (predators) while allowing for the incorporation of covariates, priors and flexible error structures (we point interested readers to Stock *et al.* 2018 for a comprehensive overview of model formulation and assumptions). We specified generalist ('un-informative') priors and ran three Markov chains (length = 300 000; burn-in = 200 000; thinning rate = 100), yielding an effective sample size of 3000 (calculated using the R package 'coda'; Plummer *et al.*

2006). We specified process $\times$ residual error structure for all models (Stock *et al.* 2018). We considered Gelman–Rubin diagnostic ($\hat{R}$) values <1.05 to indicate model convergence. Although the diet of male and female owls differed ($\sim 10\%$ proportional difference), such variability was modest enough that we chose to include both sexes in mixing models. We were, however, precluded from including sex as a categorical independent variable by model structure limitations. We included 14 MTBS-based and 16 FRAP-based fire variables in a set of MixSIAR models where each model had

one continuous covariate (Table 1; see Stock *et al.* 2018 for model-fitting details). We used leave-one-out (LOO) cross-validation to rank the relative predictive capability of FRAP and MTBS variables and considered models ranked above a null model (i.e. no covariate included) to be plausible descriptions of Spotted Owl diet (i.e. 'supported'). We did not include owl territory as a random effect because models with a random effect for territory did not converge and, in this context, the isotopic signatures of a pair of owls occupying the same territory can be assumed to be independent (see Appendix S1 for details).

RESULTS

Among 41 Spotted Owls residing at 31 territories within national parks, Woodrats and Pocket Gophers (mean $\pm$ sd: 0.76 ± 0.037) contributed more to owl diet than did Flying Squirrels (mean $\pm$ sd: 0.24 ± 0.037 ; values obtained from the top model, see below). Yet, isotopic mixing models suggested consistent relationships between fire and Spotted Owl diet: all supported models (Table 1) indicated that fire was positively related to proportional consumption of Flying Squirrels by owls (Fig. 2, Figs S1 and S2). The highest-ranked MTBS-based variables were the proportion of an owl territory that burned at moderate severity over 10- and 20-year windows ($w = 0.17$ and 0.15 , respectively; Fig. 2a; Table 1). Additionally, the proportions of high-severity fire over 10-, 20- and 33-year windows – which were highly correlated with moderate-severity fire (Table S2) – were also relatively highly supported (Table 1). The number of wildfires that occurred within an owl territory over a 10-year window (between 2007 and 2016) was the most supported FRAP-based fire variable ($w = 0.60$; Fig. 2b; Table 1; see Table S3 for variable correlations). Credible intervals (95%) for the slope terms of the top MTBS- and FRAP-based fire covariates suggested that the relationships between these fire history variables and Spotted Owl diet were significant (0.058–0.44 and 0.14–0.81, respectively).

DISCUSSION

Stable isotopes revealed consistent relationships between fire history and Spotted Owl diet in national parks with restored fire regimes. Although Woodrats and Pocket Gophers were the predominant prey, Spotted Owls consumed an increasing proportion of Flying Squirrels when their territories experienced more extensive and frequent fire. This result was opposite to our *a priori* predictions and, indeed, could be considered unexpected given previous work suggesting that partially restored fire regimes in national parks increase Woodrat abundance (Roberts *et al.* 2015). However, because isotopic

Table 1. Relative ranking of the predictive performance of fire variables, grouped by variable type.

	LOO	Δ LOO	Weight
MTBS variables			
Moderate severity (10 years)	104.9	0.0	0.17
Moderate severity (20 years)	105.2	0.3	0.15
High severity (10 years)	105.3	0.4	0.14
High severity (20 years)	105.4	0.5	0.14
High severity (33 years)	105.6	0.7	0.12
Fire diversity (3 classes)	106.7	1.8	0.07
Moderate severity (33 years)	107.4	2.5	0.05
High severity (5 years)	107.8	2.9	0.04
Fire diversity (4 classes)	108.1	3.2	0.04
Moderate severity (5 years)	108.2	3.3	0.03
Null	109.0	4.1	0.02
Low severity (10 years)	110.1	5.2	0.01
Low severity (20 years)	110.4	5.5	0.01
Low severity (5 years)	112.6	7.7	0.00
Low severity (33 years)	113.1	8.2	0.00
FRAP variables			
# wildfire (10 years)	102.8	0.0	0.60
# wildfire (5 years)	105.3	2.5	0.17
# wildfire (20 years)	107.3	4.5	0.06
Null	109.0	6.2	0.03
# wildfire (33 years)	109.2	6.4	0.02
Wildfire area (10 years)	109.7	6.9	0.02
Wildfire area (20 years)	109.8	7.0	0.02
Prescribed fire area (20 years)	110.4	7.6	0.01
Prescribed fire area (33 years)	110.4	7.6	0.01
# prescribed fire (5 years)	110.9	8.1	0.01
Prescribed fire area (5 years)	111.0	8.2	0.01
Prescribed fire area (10 years)	111.6	8.8	0.01
Wildfire area (5 years)	111.6	8.8	0.01
# prescribed fire (20 years)	111.7	8.9	0.01
# prescribed fire (33 years)	111.8	9.0	0.01
# prescribed fire (10 years)	112.6	9.8	0.00
Wildfire area (33 years)	112.8	10.0	0.00

'LOO' denotes leave-one-out cross-validation value and Δ LOO denotes the difference in LOO value between a given variable and the top variable of a group.

mixing models estimate proportional consumption, the positive association observed between fire and Flying Squirrels could have been driven by increased consumption of Flying Squirrels with a smaller increase (or no change) in Woodrat and Pocket Gopher consumption. It is also important to recognize that fire-associated changes in the proportional consumption of the two prey groups could have occurred because of shifts in accessibility (e.g. reduced search times) independent of changes in the abundance of either prey group. Below we explore potential ecological mechanisms that may have driven the observed results, discuss implications for Spotted Owl conservation, and provide directions for future research.

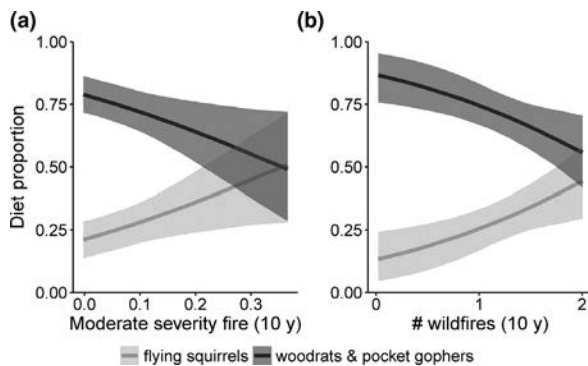


Figure 2. Relationships between California Spotted Owl diet and (a) the proportion of moderate-severity fire within owl territories in the last 10 years; and (b) the number of wildfires within owl territories in the last 10 years.

Because moderate-severity fires tend to affect ground cover more than the upper canopy (Sugihara *et al.* 2006) it is possible that terrestrial and fossorial (i.e. burrowing) mammals are more adversely affected by fire of this severity than are arboreal species, particularly over shorter time scales. Among the principal prey of Spotted Owls, Flying Squirrels are largely arboreal, Woodrats are semi-arboreal but use stick middens on the ground for shelter and nesting, and Pocket Gophers are fossorial within meadows (Williams *et al.* 1992). Thus, Woodrat and Pocket Gopher populations may decline following moderate-severity fires that consume middens and meadows, respectively. Yet, the Bushy-Tailed Woodrat *N. cinerea* – the predominant *Neotoma* species in our study area – relies more on rocky features (e.g. talus) than do other *Neotoma* species and may thus be somewhat buffered from negative impacts of fires (Williams *et al.* 1992). We suggest that further detailed research is necessary to understand how fire-mediated changes to forest structure affect Spotted Owl prey species (and Woodrats in particular) in these national parks.

It is also plausible that increased hypogeous fungal productivity in previously burned forests benefits mycophagous Flying Squirrels more than herbivorous Woodrats and Pocket Gophers. Fire can stimulate the growth of some hypogeous fungi (Johnson 1995), which could provide valuable food resources to Flying Squirrels, thus increasing their population densities. Indeed, the consumption of hypogeous fungi by a mycophagous marsupial increased following experimental fires (Taylor 1991, Johnson 1995). Yet, others have found that fire causes short-term decreases in both hypogeous fungal biomass and the consumption of fungus by small mammals (Johnson *et al.* 2001, Meyer *et al.* 2005b). Thus, relationships among fire, fungus and predator–prey interactions may be context-dependent and will probably be best quantified with targeted research.

Finally, fire-mediated changes in Spotted Owl prey availability could have led to increased consumption of Flying Squirrels. Following experimental mechanical fuel reduction treatments in the Sierra Nevada, Flying Squirrels appeared to shift their distribution from treated to untreated forest patches (Sollmann *et al.* 2016). If densities of Flying Squirrels also increase in unburnt forest patches following a nearby fire, owls may consume relatively more Flying Squirrels within territories highly affected by fire because increased densities could make Flying Squirrels a more optimal prey (Pyke *et al.* 1977). Alternatively, burning of midcanopy tree cover may increase the efficiency with which Spotted Owls detect Flying Squirrels, by reducing structural occlusion (i.e. by increasing visibility), as suggested by Wilson (2010). Thus, multiple avenues exist by which fire may alter prey availability and subsequently shift the relative importance of Flying Squirrels versus Woodrats and Pocket Gophers.

Although we could not directly attribute our results to any single mechanism discussed above, our research has important implications for owl ecology and conservation. Using identical isotopic methods, Hobart *et al.* (2019) found that increased proportional consumption of Flying Squirrels was associated with negative consequences for Spotted Owls and that owls relied relatively less on Flying Squirrels in national parks (where fire regimes are restored) than in national forests (where fires are suppressed). Hobart *et al.* (2019) thus speculate that restored fire regimes in national parks may increase the consumption of Woodrats and Pocket Gophers by owls, leading to fitness and demographic benefits. Indeed, restored fire regimes are a defining ecological characteristic of the national parks studied here (Table S4) – where Spotted Owl populations are stable (Sequoia–Kings NP), are relatively high-density (Yosemite NP) and are not adversely affected by most fires (Roberts *et al.* 2011, Tempel *et al.* 2017). Our current findings thus appear somewhat at odds with previous research and it remains unclear how the increased consumption of Flying Squirrels following fires affects Spotted Owl populations. We suggest that heterogeneous fire may increase the consumption of Flying Squirrels as well as Woodrats and Pocket Gophers by Spotted Owls, but that consumption of Flying Squirrels increases the most, perhaps via one or more of the mechanisms discussed above. If true, restored fire regimes may increase the biomass and diversity of owl prey species – both of which are associated with heightened individual fitness (Steenhof *et al.* 1997).

Several research avenues may improve the understanding of relationships between fire and Spotted Owl trophic interactions. Although we could not include prey availability information here, considering small mammal abundance and distribution may elucidate mechanistic insights into how fire alters prey selection

by Spotted Owls. Moreover, coupling prey availability information with high-resolution movement and diet data would allow researchers to identify when and where Spotted Owls capture different prey species. In addition, ground-based vegetation assessments are likely to be critical to elucidate mechanisms linking fire and owl diet, as fire history did not appear to be strongly related to a suite of remote-sensed forest characteristics in our study area (Table S5). Finally, an important limitation of our current study is that it was carried out exclusively in national parks, which are unique with respect to their restored fire regimes. Within fire-suppressed landscapes (e.g. national forests) – where fires tend to be more homogeneous and severe (Steel *et al.* 2015) – relationships between Spotted Owl diet and fire history may take a different form. Future research with expanded data and geographical scopes may be critical in resolving uncertainty surrounding the effects of fire on Spotted Owls (Ganey *et al.* 2017). Moreover, because the Spotted Owl is a model species in landscape and population ecology (Noon & Franklin 2002), such endeavours are likely to have implications for raptors and forest-dependent species elsewhere.

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DATA AVAILABILITY STATEMENT

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. On owl pairs and the independence of isotopic data.

Figure S1. Modelled relationships between Spotted Owl proportional diet and MTBS-based fire variables that were ranked above a null model (excluding the top-ranked variable; Fig. 1a).

Figure S2. Modelled relationships between Spotted Owl proportional diet and FRAP-based fire variables that were ranked above a null model (excluding the top-ranked variable; Fig. 1b).

Table S1. A brief description of all MTBS- and FRAP-based fire variables. All fire variables were calculated within Spotted Owl territories (see main text for the designation of owl territories).

Table S2. Matrix of Pearson's correlation coefficients for all pairwise combinations of the MTBS-derived fire variables used here.

Table S3. Matrix of Pearson's correlation coefficients for all pairwise combinations of the FRAP-derived fire variables used here.

Table S4. Mean and standard deviation (in parentheses) of fire history variables calculated within spotted owl territories. 'SKC' denotes Sequoia-Kings Canyon NP; 'YOS' denotes Yosemite NP.

Table S5. Pearson correlation coefficients between fire history variables and forest structure variables within the owl territories studied here.



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Forest ecosystem restoration: Initial response of spotted owls to partial harvesting

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ABSTRACT

Conservation planning for spotted owls (*Strix occidentalis*) hinges upon retaining late-successional and old-growth forests. This strategy is to be supplemented over time by creating structural conditions found in such forests using innovative silviculture in less well-developed forests. Recent research indicates that spotted owls often hunt for prey or may nest in relatively young or mid-seral forest stands that were thinned or partially harvested in previous decades, but little information has been available to evaluate short-term direct responses (<5 year) by spotted owls to such practices. We used selection ratios to compare the frequency of nocturnal use by radio-tagged northern spotted owls (*S.o. caurina*) and California spotted owls (*S.o. occidentalis*) ≤ 2 years before and ≤ 2 years after 150 forest stands were thinned or partially harvested within 1200 m of nest sites of 19 owl home ranges in 5 study areas in western Oregon and northern California. We used logistic regression to investigate habitat and environmental factors that distinguished between 89 stands that were used and 115 stands that were not found used by radio-tagged owls for up to 2 years after treatment via a broad range of partial-harvest or thinning prescriptions within 2400 m of nest sites. Before harvest, radio-tagged owls generally used stands scheduled for harvest treatment in proportions significantly less than availability. After harvesting, selection ratios increased ($n = 4$), remained the same ($n = 4$), or decreased ($n = 2$) among 10 owl pairs for which we acquired sufficient telemetry data both before and after harvesting. Across all owls and all post-harvest conditions, the overall selection ratio increased after harvesting, suggesting that many of the harvests were benign or may have resulted in improved habitat. The probability of use of thinned or partially-harvested stands increased with harvest-unit size, decreased with distance from nest sites, and varied with the intensity of harvest and among forest types as represented by study areas. We found only limited evidence for a positive effect of retained basal area of large trees (≥ 66 cm diameter at breast height [dbh]), probably because many treated stands contained no such large trees prior to harvest. We found a quadratic relationship with retained basal area of mid-story conifers (10–65 cm dbh), such that harvested stands that contained 25–35 m²/ha basal area of such mid-story trees were more likely to be used, holding other factors constant at their means. We also found evidence for a positive influence of proximity to riparian zones on probability of use of harvested stands. Although we did not obtain information on prey abundance or foraging efficiency, our study suggests that judicious applications of partial-harvest forestry, primarily commercial thinning, have the potential to improve foraging habitats for spotted owls.

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Federal land management agencies endeavor to restore ecological functions, resilience and late-seral and old-growth structural conditions in many western forests. Doing so may require active management (Carey, 2003a,b), such as thinning in young and

mid-seral stands (e.g., Chan et al., 2006; Shatford et al., 2009; Ares et al., 2010) or novel modifications of forest regeneration methods. Indeed, numerous management experiments are currently exploring various silvicultural prescriptions that may hasten conversion of young, even-aged stands to multi-layered, uneven-aged conditions. Thinning has been proposed to reduce risk of uncharacteristically large, intense wildfires in dry, fire-prone

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forests (e.g., Graham et al., 2004; Gaines et al., 2010; Lehmkuhl et al., 2015). Private timber companies and some state forest managers conduct partial harvests for purposes of regenerating new stands and thin young stands as a means of increasing the rate of wood and fiber production and for recovering economic value of anticipated tree mortality (Omule, 1988).

Proposals for such active forest management within areas occupied by spotted owls continue to stir vigorous debate among forest managers, ecologists, regulatory agencies, and various stakeholders. This seems especially true for northern spotted owls, which are listed as threatened under the U.S. Endangered Species Act of 1973, including management of both dry, fire-prone forests (Irwin and Thomas, 2002; Hanson et al., 2009; Spies et al., 2010) and mesic forests (Wilson and Forsman, 2012). Empirical research is needed to identify and evaluate silvicultural prescriptions that may exert neutral or positive influences on spotted owls yet support broader forest ecosystem management goals.

Spotted owls nest and roost primarily in patches of mature and old-growth forests (Thomas et al., 1990; Verner et al., 1992), and often hunt for prey across a wider range of stand structural conditions (Forsman et al., 1984; Verner et al., 1992; Williams et al., 2011), including young and mid-seral stands that contain undergrowth plants and vegetative structures associated with their prey (Irwin et al., 2000). Based on these observations and studies that found northern spotted owls nesting successfully in stands that were partially harvested in previous decades (e.g., Forsman et al., 1984), Thomas et al. (1990) recommended adaptive management experiments to evaluate novel silvicultural prescriptions that might retain or restore the vegetative conditions and structures that are believed to promote fitness among northern spotted owls. Accordingly, the Northwest Forest Plan (USFS, 1994) identified 10 adaptive management areas where such management experiments could be implemented to test silvicultural prescriptions that may benefit northern spotted owls, as well as other late-successional forest associated wildlife. Similarly, the latest federal recovery plan for the northern spotted owl included options for forest managers to contribute to conservation via thinning (USFWS, 2011). Such active management is supported by additional observations of both the California and northern subspecies of spotted owls nesting or foraging preferentially in forests that were thinned or partially harvested in the past (e.g., Zabel et al., 1992; Buchanan et al., 1995; Lee and Irwin, 2005; Irwin et al., 2007, 2012), particularly during the non-nesting season (Irwin et al., 2013).

Thinning may affect spotted owls positively by increasing herbs and shrubs expected to influence the owl's small mammal prey base (e.g., Carey et al., 1999; Ransome and Sullivan, 2004; Dodson et al., 2008; Lindh, 2008). For example, Ransome and Sullivan (2004) demonstrated that populations of northern flying squirrels (*Glaucomys sabrinus*), the primary prey for spotted owls in many areas (Forsman et al., 2004), respond positively to increases in food supplies. Sullivan et al. (2013) found that northern flying squirrel densities 12–14 years after large-scale applications of pre-commercial thinning in young lodgepole pine (*Pinus contorta*) forests in British Columbia were similar to those in old-growth stands. Thinning in young and mid-seral forest stands has been documented to maintain or increase many populations of small mammals (Wilson and Carey, 2000; Ransome and Sullivan, 2002; Suzuki and Hayes, 2003; Gomez et al., 2005; Klenner and Sullivan, 2009; Zwolak, 2009; Verschuyt et al., 2011), many of which are nocturnal and comprise part of the owl's prey base. However, relatively intensive silvicultural treatments such as seed-tree harvests that are followed by prescribed burning may reduce production of sporocarps of hypogeous fungi (Carey, 2003a; Waters et al., 1994; Meyer et al., 2005). Hypogeous sporocarps (truffles) are important food sources for northern flying squirrel. Moreover, densities of northern flying squirrel

populations may decline over the short term after commercial thinning (Carey and Wilson, 2001; Carey, 2003a; Wilson and Forsman, 2012). Finally, Manning et al. (2012) suggested that northern flying squirrel populations may remain depressed over the long term, although that study appeared weak in terms of trapping regime and squirrel data (Sullivan et al., 2013) and no studies have evaluated the extent to which spotted owls themselves may contribute to squirrel declines in thinned stands via heavy predation.

Population performance of predatory birds is expected to be influenced by the distribution, abundance, availability (or vulnerability) and diversity of their food supplies (Newton, 1979), which for spotted owls includes small mammals, all of which are likely to be affected by vegetation changes after thinning or partial harvesting. Unfortunately, there is a dearth of published information that quantifies direct responses of spotted owls immediately after thinning or partial harvesting, before vegetation has responded. Such information could inform forest restoration efforts, assist in relative risk assessments for fuel reduction programs, and provide additional opportunities for private companies to contribute to conservation of spotted owls.

To our knowledge, no study has published direct before- vs. after responses by spotted owls to thinning and partial harvesting. The only published empirical study that reported direct short-term responses to thinning was a case study of one male northern spotted owl that used stands in proportions less than availability after thinning in northwestern Oregon (Meiman et al., 2003). No pre-harvest data on stand use were available and the thinning prescription was not reported. To be sure, there have been attempts at indirectly evaluating the post-treatment effects of thinning and partial harvesting on spotted owls. For example, Tempel et al. (2014) modeled the effects of broad combinations of 16 silvicultural treatments on California spotted owl demographic rates. They concluded there was a negative association between owl reproduction and area of “medium-intensity” timber harvests within 400-ha sample circles. They also concluded that, when implemented in forests with $\geq 70\%$ canopy cover, medium-intensity harvests were likely to reduce owl survival and territory occupancy. In that study, medium-intensity harvests included a combination of 6 silvicultural treatments such as various selection harvests, hazardous fuels reductions, fuel breaks and commercial thinning, which the authors suggested were collectively characteristic of proposed fuel treatments. However, close inspection of the models indicates that the effect of the medium-intensity harvest covariate was weak, did not contribute to model deviance and should have been excluded, based upon guidance provided by Arnold (2010). Also, by using broad categories, the Tempel et al. (2014) study did not specifically evaluate the influence of variation in retained habitat structures that are influenced by intentional management.

Zabel et al. (1992) recommended that researchers measure continuous fine-scale structural details for evaluating responses by spotted owls to modifications of forest habitats. Indeed, spotted owls are capable of identifying and intensively using small patches within what otherwise would be classified and mapped as homogeneous stands or seral stages based on characteristics of predominant overstory trees (Buchanan et al., 1995; Carey and Peeler, 1995; Irwin et al., 2000, 2007). Irwin et al. (2012) found that such measures as basal area and tree density are important influences on habitat selection by spotted owls, and are more useful than broad categories for crafting potentially useful silvicultural prescriptions.

Therefore, we evaluated initial responses by spotted owls to various thinning and partial-harvest treatments by incorporating fine-scale measures of habitat structures. We made four primary predictions based upon previous research: (1) owls would use

harvested patches equally or more often than before harvesting; (2) forest type, as a proxy for presumed predominant prey, would influence the probability of use by spotted owls of harvested stands; (3) size and location of silvicultural treatment relative to nesting sites and proximity to riparian zones would affect the probability of use after harvesting; and (4) intensity of harvest as measured by retained basal area and retained basal areas of large trees (≥ 66 cm dbh) would affect post-harvest use by owls.

1. Study areas

We evaluated short-term responses to forest thinning operations and partial harvesting within territories occupied by northern and California spotted owls in 5 study areas in western Oregon and California. Three study areas occurred within Mixed Conifer (*Abies concolor*) and Red fir (*A. magnifica*) Zones (Franklin and Dyness, 1981; Sawyer, 2007) of the Sierra Nevada near Chico, California (Irwin et al., 2007) and the southern Cascades Mountains near Yreka, California, and Klamath Falls, Oregon (Irwin et al., 2012). The Yreka and Klamath Falls study areas included mixtures of federal and private timberlands. The Chico study area mostly included private timberlands and was occupied by California spotted owls. A few locations in Western Hemlock Zone forests were thinned near Springfield, Oregon, in a private-federal mix comprised mostly of young and mid-seral Douglas-fir (*Pseudotsuga menziesii*) forests <80 year of age (Irwin et al., 2000). The fifth study area was near Ft. Bragg, California, within the Coast Redwood Zone and included a mix of private and state-owned forests.

Mixed-coniferous forest vegetation common to the Chico, Yreka, and Klamath Falls study areas included Douglas-fir, Ponderosa pine (*P. ponderosa*), white fir (*A. concolor*), incense cedar (*Libocedrus decurrens*), and occasional sugar pine (*P. lambertiana*), with local variation in frequency. California red fir (*A. magnifica*) or Shasta red fir (*A. m. var shastensis*) occurred at higher elevations. Hardwoods included tanoak (*Lithocarpus densiflorus*), canyon live oak (*Quercus chrysolepis*), California black oak (*Q. kelloggii*), Pacific madrone (*Arbutus menziesii*) and bigleaf maple (*Acer macrophyllum*). Frequent understory species included Pacific yew (*Taxus brevifolia*), Pacific dogwood (*Cornus nutallii*), California nutmeg (*Torreya californica*), and sclerophyllous shrubs such as buckbrush (*Ceanothus* spp.) and manzanitas (*Arctostaphylos* spp.). Predominant trees in the Springfield study area included Douglas-fir, western hemlock (*Tsuga heterophylla*), and western redcedar (*Thuja plicata*). Common hardwoods included Pacific dogwood, bigleaf maple, red alder (*Alnus rubra*), and Pacific yew. Undergrowth plants included swordfern (*Polystichum munitum*), salal (*Gaultheria shallon*), vine maple (*A. circinatum*), and Oregon grape (*Berberis nervosa*). Vegetation in the Ft. Bragg study area was dominated primarily by coast redwood (*Sequoia sempervirens*) and Douglas-fir forests. Understory hardwood vegetation consisted primarily of tanoak, red alder, Pacific madrone, California laurel (*Umbellularia californica*), and bigleaf maple (Diller and Thome, 1999).

The abundance of common prey items likely varied widely among these study areas, and woodrats (*Neotoma* spp.), deer mice (*Peromyscus maniculatus*), red tree voles (*Arborimus longicaudus*), and northern flying squirrels are expected to be important (Zabel et al., 1995; Forsman et al., 2004). Pocket gophers (*Thomomys* spp.) are locally important (Munton et al., 2002). Woodrats and northern flying squirrels most likely co-dominated owl diets in the Mixed Conifer areas, woodrats predominated in Coast Redwood study areas (Ward et al., 1998), while northern flying squirrels likely were most prominent in owl diets in the Douglas-fir zone (Forsman et al., 2004). During our study, northern barred owls (*Strix varia*), a major competitor for prey and nest sites

(USFWS, 2011; Wiens et al., 2014; Yackulic et al., 2014), were abundant only in the Douglas-fir study area near Springfield, Oregon at an approximate ratio of 3 barred owl pairs per spotted owl pair. During our studies, we were aware of two locations with barred owls in the Klamath Falls study area, one location with a pair in the Ft. Bragg study area and none in the Chico study area.

To reveal promising silvicultural approaches that may benefit spotted owls, it is important to apply designs that permit examination of forest-structural variation among silvicultural treatments using continuous variables rather than categories that collapse variation. Therefore, it is important to define and measure the range of variation among silvicultural treatments. Thinning is defined as a collection of intermediate cuttings designed to reduce densities of immature trees for the purpose of controlling tree species composition, stimulating the health and growth of remaining trees and increasing the total yield of woody material from stands (Smith et al., 1997; Helms, 1998; Powell, 2013). To some observers, removal of large-diameter, mature overstory trees while retaining younger trees constitutes “thinning”, but such treatments are properly labeled overwood removals (Powell, 2013), which did not occur during our study. Partial harvesting in our study areas involved two primary silvicultural systems designed to cause natural regeneration of new, usually even-aged stands of shade-intolerant trees by retaining variable densities of well-distributed mature trees. By definition, the seed-tree method retains ≥ 15 mature trees/ha that produce seed for a new stand, whereas the shelterwood method removes overstory trees in a series of harvests that eventually retain ≥ 30 seed trees/ha (Powell, 2013). Both methods were applied in parts of our study areas to produce natural regeneration. The shelterwood method can favor either shade-tolerant or shade-intolerant tree species. After regeneration occurs, the seed trees under the latter two silvicultural systems may be removed or retained, depending upon management objectives. Selection harvesting is defined as a partial-harvest silvicultural treatment designed to establish and maintain uneven-aged stands, usually comprised of shade-tolerant trees, by removing individual trees or groups of trees. Selection harvests were initiated in the Coast Redwood study area during our study but were not used widely. In addition, sanitation treatments involving chemical control of tanoak were practiced in the Coast Redwood study area. Salvage harvesting was used in a few stands within the three Mixed Conifer study areas to remove trees that were dead or in imminent danger of being killed by insects, diseases or wildfire.

2. Methods

We used a combination of quasi-experimental and observational approaches, similar to Seamans and Gutiérrez (2007), in which we included both retrospective observations and before-vs. after manipulative experiments in landscapes that contained relatively high proportions of managed forests. We employed a repeated- or multiple study-area approach (Johnson, 2002) with staggered-entry date, in which data collected from each study area were acquired under the same objectives using the same methods and employing mostly the same field crews. This approach provides greater confidence in generality of findings than single studies because the same methods are applied to address the same questions under widely differing environmental conditions. This approach allowed data to be combined in analyses in which we statistically controlled for the confounding effect of differences in size of treatments. We also statistically tested the assumption that California and northern spotted owls could be combined because they respond similarly to forest structural conditions (e.g., Thomas et al., 1990; Verner et al., 1992).

We developed a set of criteria to select owl-pair territories and silvicultural treatments for inclusion in the study. First, we asked cooperating private landowners and state and federal agencies to identify areas with pairs of spotted owls that occupied territories within which thinning or partial harvesting had been scheduled for circa 10% or more of the forests within 1200 m of nest sites, an area encompassing ~450 ha. We assumed that such amounts of treatment would be sufficient to induce a detectable short-term response because 60–80% of an owl pair's annual use occurs within such areas (Carey et al., 1992; Irwin et al., 2012). Second, we restricted our evaluation of the associated owl responses to silvicultural treatments that were ≤ 2400 m of owl nest sites. We did so because we expected such an analysis unit (~1800 ha) would encompass 90% of an owl-pair's annual use patterns; also, it was similar to the analysis unit in Dugger et al. (2005). Decisions on silvicultural prescriptions, dates of implementation, area treated and location of harvests were made by forest managers based upon local conditions and company or agency objectives after consultation with regulatory agencies. We had no way of identifying adequate controls with similar habitat conditions or specifying replicate treatments, so we present before- vs. after comparisons and describe owl responses to post-harvest conditions. We were unable to acquire pre-harvest forest inventory information for most of the owl home ranges where harvests occurred, but we did acquire pre-harvest information on total basal area from collaborating forest managers. Collaborators also provided detailed post-harvest forest inventory data for some owl-occupied areas; in the others our field crews sampled post-harvest conditions (Bell and Dilworth, 2007; Irwin et al., 2012).

After applying our design criteria, we were able to evaluate spotted owl responses to a wide range of silvicultural treatments: approximately 30% of 216 stands were modified via preparatory seed-cuts in seed-tree or shelterwood prescriptions that resulted in retained basal areas < 20 m²/ha, 50% were commercial thinnings in young and intermediate-aged forests that had 20–40 m²/ha of retained basal area, and 20% were lightly-thinned or were sanitation treatments in stands that retained > 40 m²/ha of basal area. The latter treatments and the shelterwood and seed-tree harvests occurred within mature or older forests that probably qualified as nesting and roosting habitat. Some of the larger harvest units overlapped multiple owl home ranges.

We captured and radio-tagged spotted owls using standard procedures (Forsman, 1983, and sought to map the locations of each owl 1–3 times per week at night for ≤ 2 years before and ≤ 2 years after silvicultural treatments, allowing us to compare frequency of use of stands before and after harvest to provide a reasonably large, temporally independent sample (Guterman et al., 1991). We rotated the order of tracking of each bird weekly to create a range in sampling times for each bird. We obtained transmitter signals using hand-held 3-element Yagi directional antennae (Wildlife Materials, Inc., Carbondale, IL or Telonics, Mesa, AZ). We triangulated positions of owls from 3 azimuths recorded within 10–15 min from geo-referenced receiving stations along access roads, using methods similar to Glenn et al. (2004). Coordinates of receiving stations and telemetry locations were stored in a database using LOAS software (Ecological Software Solutions, LLC, Tallahassee, FL, USA). Extensive road systems helped mitigate many of the well-known radio-tracking problems by allowing field personnel to acquire most signals < 400 m from owls. We mapped azimuths of transmitter signals in the field on 1:24,000 topographic maps. If a mapped triangulation polygon was > 2 ha, we discarded it and recorded another sample. In previous reports that included many of the radio-tagged owls included herein (e.g., Irwin et al., 2007, 2013), we noted that the average distance of estimated locations to the true geo-referenced transmitter locations was

84 m (SE = 16 m), with a median value of 56 m, and 94% of the triangulations resulted in error polygons < 1.0 ha. We presumed that nocturnal activities primarily involved foraging, although other behaviors such as territorial interactions occur at night.

We used selection ratios (Manly et al., 2002) as an initial evaluation of the overall collection of partial harvests and thinning to compare the frequency of use of stands before vs. after partial harvesting and thinning, combining telemetry data for males and females at each site as:

$$w_i = o_i / \hat{e}_i$$

where w_i is the average selection ratio for a given owl-pair home range i , expressed as the ratio of observed number of telemetry points recorded within all harvested units, o_i , to the number of telemetry points expected based upon the proportion of area treated within 450 ha, $\hat{e}_i$. We calculated an overall selection ratio for each entire sample (i.e., before and after) because it will usually have less bias and a smaller variance than averaging ratios across individual samples (Manly et al., 2002: 47). We assumed that a minimum effective sample size was 40 telemetry points. An overall selection ratio with 95% confidence interval > 1.0 indicates positive selection for pre- or post-harvest patches within home ranges, a selection ratio with 95% confidence interval < 1.0 indicates avoidance, and a ratio with confidence interval that overlaps 1.0 indicates neutrality. We used a Chi-square test, corrected for continuity, to compare the difference between overall selection ratios before vs. after harvest. As a confirmatory check, we conducted a Chi-square contingency test.

Predatory birds are expected to respond to forest structures (Janes, 1985), and we summarized the structural differences among partial harvesting and thinning treatments using inventory data collected after harvesting. We identified variables for model building based upon previous research that examined habitat structural factors and abiotic influences. For example, Irwin et al. (2007, 2012) found that basal area by size class was a stronger influence on habitat selection by spotted owls than tree densities by size class. Therefore, we expected that variation in short-term responses by spotted owls to thinning and partial-harvesting would be most related to retained basal area in various size classes. Earlier reviews (Thomas et al., 1990; Verner et al., 1992) identified the importance of vertical layering to both subspecies, so we estimated retained basal area of mid-story trees, which we defined as trees 10–65 cm in diameter at breast height (dbh). These reviews and numerous studies identified the importance of large (and old) trees (summarized in USFWS, 2011), so we estimated the basal area of large-diameter trees, which we defined as trees ≥ 66 cm dbh. We also used basal area because it is easy to estimate, is commonly used by foresters, and is recommended over canopy cover by emphasizing large, uncommon trees that are important to wildlife (Cade, 1997), including spotted owls (Irwin et al., 2012) and their prey (Carey and Peeler, 1995). Because Irwin et al. (2012) found high variation within and among stands in our study areas, we did not include data on coarse woody debris or snags, although such structures are expected to influence foraging use by spotted owls. We used study-area indicator variables as proxies for the dominant forest type and associated prey base, as well as potential differences between northern and California spotted owls. For example, we expected that northern spotted owls in the Coast Redwood region and California spotted owls in the Sierra Nevada range would respond differently to harvesting because of the greater proportion of woodrats (*Neotoma* spp.) vs. northern flying squirrels (*G. sabrinus*) in owl diets. We also expected that planimetric (map-based) factors would be associated with spotted owl use of harvested areas, including the size and location of harvest treatment relative to areas of expected intensive use near nest sites

(e.g., Meyer et al., 1998; Rosenberg and McKelvey, 1999) and proximity to streamside or riparian zones (Carey and Peeler, 1995).

We used logistic regression to sort the differences in spotted owl responses to structural habitat features retained after various silvicultural treatments and to evaluate the above-described abiotic factors that may influence the probability of use of individual harvested stands within 2400 m of nest sites. We included harvest-unit area as an offset term in logistic regressions, because larger units would be anticipated to have a greater probability of being used than small units. The use of harvest-unit size as an offset reflects the assumption that if owls use harvested areas randomly, the relative use in a harvest unit should be proportional to its size and the probability of use is adjusted accordingly. We included owl pair (or home range) as a random effect term to account for potential correlation within owl pairs. We used model selection procedures, including AIC, corrected for small samples (Burnham and Anderson, 2002), and excluding non-informative parameters following Arnold (2010) to identify a parsimonious set of factors that accounted for the most variation in probability of use of harvested stands. Proportions were arc-sine square root transformed to approximate normal distributions.

We proceeded in stages and limited the number of models examined, following Irwin et al. (2007, 2012) in which we first identified the best model that included planimetric factors, to which we sequentially added habitat covariates associated with the harvests and study area. Also based upon previous work (Irwin et al., 2007, 2012), we included a few interaction terms: distance to nest site $\times$ size of harvested stands; distance to nest site $\times$ total retained basal area (and also retained basal area of trees >66 cm dbh); and total retained basal area (and also basal area of trees ≥ 66 cm dbh) $\times$ proportion of harvest unit within 100 m of riparian zones. We used Chico as the reference indicator to determine if California spotted owls responded differently from northern spotted owls. We included an interaction term between retained basal area and study area because of the potential for dusky-footed woodrats (which dominate owl diets in some areas) to respond differently to thinning vs. regeneration harvesting in the Coast Redwood study area (Hamm and Diller, 2009). We also compared models that included quadratic and pseudo-threshold ($\log_e$) terms for total retained basal area, basal area of mid-story trees and basal area of trees ≥ 66 cm dbh, harvest unit size and proportion of harvest unit <100 m from streams. We constructed and evaluated 35 models using this process.

3. Results

We obtained data for 262 stands that received varying silvicultural treatments within 19 spotted owl home ranges. All but 2 of the 19 home ranges were occupied by pairs of owls. We did not locate radio-tagged spotted owls within 115 of these harvest units (43.8%), either before or after harvesting. Of the 262 treated stands, 216 were within 2400 m of spotted owl nest sites and 150 were within 1200 m of nest sites. We relocated individual radio-tagged spotted owls in 12 of 46 harvested stands beyond 2400 m from nest sites; these stands were excluded from analyses. All but one of these were in the Klamath Falls study area.

We located radio-tagged owls in 29 stands that were used $\geq$ one time before but not after harvesting and in 50 harvested stands that were used after treatment but not before harvesting. Before harvesting occurred, we mapped 336 of 2,507 telemetry points within harvest units (13.4%); after harvesting, 745 of 4326 telemetry points were mapped within harvest units (17.2%). Treated units ranged from 2 to 242 ha in area. We did not observe site abandonment (breeding dispersal) during our study.

We located radio-tagged spotted owls in 89 of the 216 harvested stands that occurred within 2400 m of nest sites. The 89 used stands included 61 treated stands that were used 1–4 times; 17 harvested stands that were used 5–10 times; 5 harvested stands that were used 11–20 times each, and 6 harvested stands that were used >20 times each. A pair of spotted owls in the Klamath study area used one harvested unit 93 times. The median distance from owl nests was 612 m for harvested stands that were used by owls and 924 m for harvested stands that were not used during the period of study. **In harvested stands that were used, harvests occurred as close as 13 m from nests,** whereas the minimum distance for harvest units that were not used was 78 m. Patterns of the distribution of use before and after harvests for all 19 home ranges are shown in Fig. 1. We observed high frequencies of use of some harvested units in all study areas (e.g., Fig. 1A, H, J, K, L, N, and R). However, there was a great range of variability, as frequent use (>10 locations) occurred in a unit with retained basal area of 15 m²/ha at the John's site in Klamath Falls (Fig. 1G), one with retained 25 m²/ha in a unit at the Hells site in the Yreka study area (Fig. 1L), one with 33 m²/ha in the Big River site at Ft. Bragg (Fig. 1N), and one lightly treated unit with 45 m²/ha at Springfield (Fig. 1B).

We were unable to acquire sufficient telemetry data before harvesting occurred in three home ranges (Buck, Fig. 1C; E. Miner, Fig. 1E; and Miner, Fig. 1H) and we obtained very few telemetry locations after harvesting at Pederson (Fig. 1I). We excluded data from these four home ranges for analyses of selection ratios of before vs. after use but included the first 3 in logistic regressions of used vs. unused harvest units.

3.1. Relative use of stands before and after harvesting

After excluding data from the 4 owl home ranges with little or no before- or after-harvest telemetry data, and restricting the data to 1200-m radius sampling units, the remaining 15 owl home ranges met our original criteria of having approximately 10% or more of the 450-ha sampling area harvested (Table 1), and **harvested areas ranged from 8 to 58% of 450-ha sampling areas.** Prior to harvesting, the average basal area ranged from 21.1 m²/ha to 65.4 m²/ha, whereas retained basal area after harvesting varied from 4.7 m²/ha to 40.4 m²/ha. We found a wide range of selection ratios for the 150 harvested stands that occurred within 1200 m of nest sites before harvests occurred (0.00–2.99) as well as after harvests occurred (0.28–1.77). We obtained no telemetry data before harvesting in 3 stands within 1200 m of the Horse nest site (Table 1) and no telemetry data after harvest at 1 treated stand within 1200 m of the Tops nest site, so we excluded those 2 home ranges before estimating the overall selection ratios. Telemetry data acquired before harvesting was limited at 3 other sites (Drury, Edge, and Johns) in Table 1. After harvesting, selection ratios appeared to increase for 4 owl pairs, remained essentially the same for 4 pairs, and decreased for 2 pairs among owl pairs for which we acquired sufficient telemetry data both before and after harvesting. The overall selection ratio for 13 owl home ranges across all 146 harvested stands before harvest was 0.794, with a 95% Bonferroni confidence interval of 0.043. Thus, **radio-tagged owls generally used stands scheduled for harvest less frequently than expected based upon availability (i.e., “avoided”) within 450-ha areas. The overall selection ratio after harvesting was 0.990, with a 95% Bonferroni confidence interval of 0.025, indicating stands were used in proportion to availability after harvest.** The two overall selection ratios differed ($Z = 20.0$, $P < 0.001$, indicating that radio-tagged owls generally increased their use of stands after stands were thinned or partially harvested. A simple contingency analysis of before vs. after harvest led to the same result. The large amount of variation was likely associated with

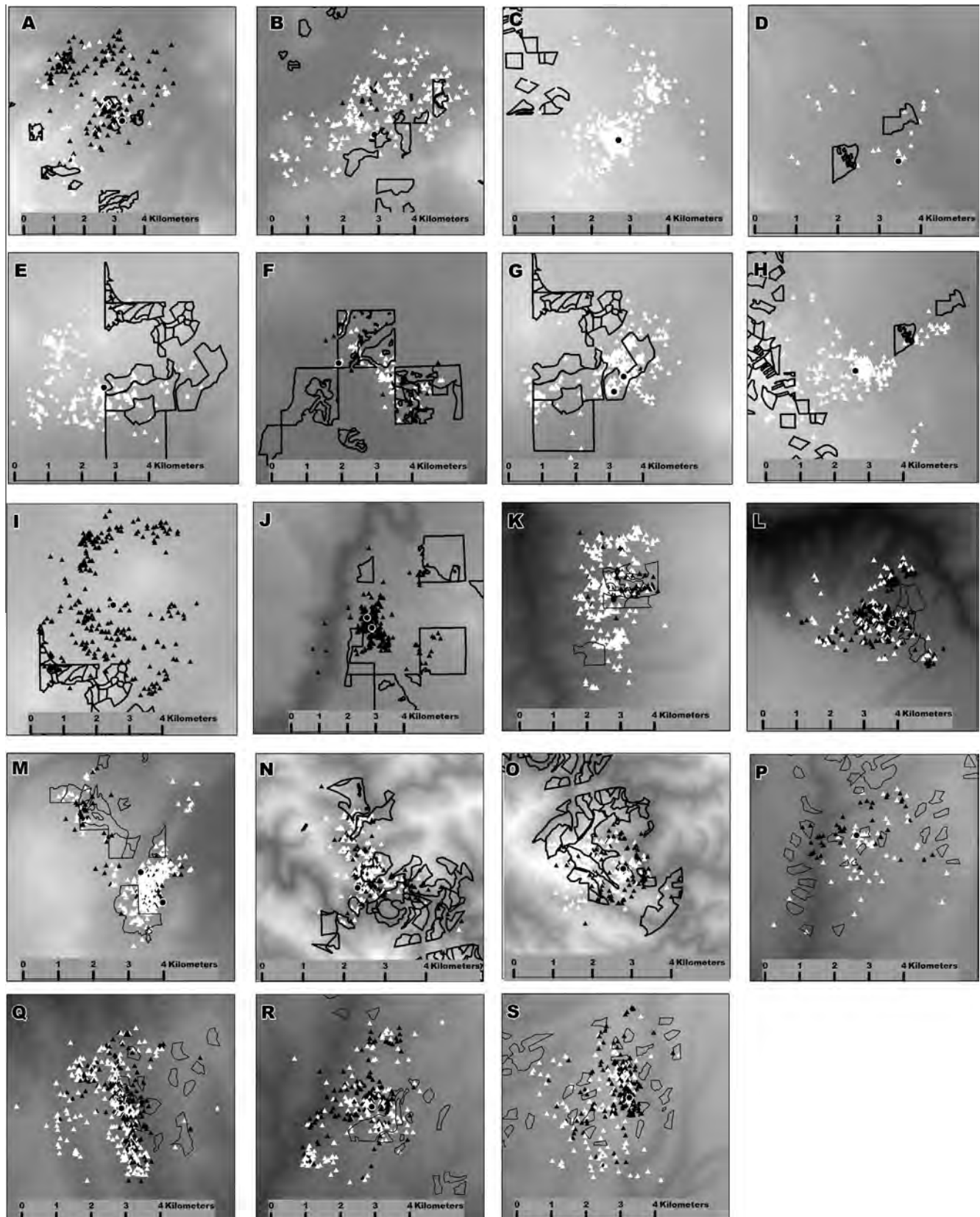


Fig. 1. Maps of telemetry points recorded within 2400 m of nest sites for radio-tagged spotted owls before (solid triangles) and after (white triangles) thinning or partial-harvesting (dark lines) within five study areas: Springfield, Oregon, including Anthony (A) and Drury (B) home ranges; Klamath Falls, Oregon, including Buck (C), Edge (D), E. Miner (E), Horse (F), Johns (G), Miner (H), Pederson (I), and Tops (J) home ranges; Yreka, California, including Hegro (K), Hells (L), and Rock (M) home ranges; Ft. Bragg, California, including B. River (N) and Camp (O) home ranges; and Chico, California, including Butte (P), Cold (Q), Powell (R), and Skip (S) home ranges. Nest sites are depicted as solid dots. Telemetry points and harvest units beyond 2400 m from nest sites generally were not included.

Table 1

Observed and expected frequencies of use of timber-harvest units by radio-tagged spotted owls and selection ratios^a for harvest units before and after harvesting within 1200 m (450 ha) of nest sites in five study areas in western Oregon and northern California, USA.

Study area	Proportion of 450 ha	Before harvest					After harvest				
Site		Basal area ^b	Obs. ^c	Expected ^d	Selection ratio	No. points	Basal area ^b	Obs. ^c	Expected ^d	Selection ratio	No. points
<i>Springfield</i>											
Anthony	0.133	48.0	10	9.0	1.11	68	36.4	8	7.8	1.03	58
Drury	0.144	55.0	0	1.6	0.00	11	40.4	16	12.0	1.33	83
<i>Klamath</i>											
Edge	0.440	50.0	2	0.9	2.22	2	25.7	25	14.1	1.77	32
Johns	0.583	65.4	1	7.0	0.14	12	37.4	142	122.9	1.15	211
Horse	0.514	51.4	0	0.0	0.00	0	35.0	59	102.3	0.58	199
Tops	0.078	21.1	3	7.2	0.42	92	14.1	0	0.0	0.00	0
<i>Yreka</i>											
Hegro	0.089	36.2	13	23.0	0.56	259	25.7	4	7.6	0.53	85
Hells	0.229	37.6	43	14.4	2.99	63	32.7	47	41.9	1.65	183
Rock	0.180	28.0	3	10.8	0.28	60	18.7	21	75.4	0.28	419
<i>Ft. Bragg</i>											
Big River	0.461	40.1	22	89.4	0.25	194	22.0	88	80.2	1.10	174
Camp	0.426	27.9	40	56.2	0.71	109	19.9	69	69.4	0.99	163
<i>Chico</i>											
Butte	0.093	45.0	6	4.4	1.36	47	20.0	9	5.2	1.73	56
Cold	0.100	41.8	47	21.4	1.92	214	4.7	23	21.5	1.07	215
Skip	0.112	53.7	9	15.6	0.58	140	7.5	6	9.9	0.61	89
Powell	0.256	44.1	27	27.3	0.99	107	24.2	32	27.0	1.19	105
TOTALS ^a			226	288.2	0.763	1378		549	597.2	0.92	2072

^a Excluding data from Horse and Tops, which could not be compared for before vs. after data; the overall selection ratio for Before is 223/281 = 0.794; the overall selection ratio for After is 490/494.9 = 0.990.

^b Average basal area within harvest units, m²/ha.

^c Number of telemetry points observed within stands before or after harvest.

^d Number of telemetry points expected, estimated by multiplying proportion of 1200-m analysis units by number of telemetry points.

differences among silvicultural prescriptions in relation to treatment size, location, and environmental factors, which we evaluate in the next section.

3.2. Habitat conditions in used vs. unused treated stands

We obtained data for 204 harvested stands within 2400 m of nest sites in 18 owl home ranges for evaluating factors influencing the probability of use after silvicultural treatment. Results for the top 6 models are shown in Table 2. The top-ranked model, if judged by the lowest AIC score, accounted for >80% of the model weights and the top 3 competing models accounted for >95% of the model weights. These models differed only in the form of measure (untransformed vs. log_e transform) for proportion of harvest unit <100 m from streams and the relative importance of basal area of large-diameter trees. The probability of use of harvested stands decreased with distance from nest sites and increased with the

proportion of stands within 100 m of streams. We found weak evidence for a positive effect of retained basal area of large-diameter trees, as an 85% confidence interval for the coefficient overlapped 0.0. We found strong evidence for a quadratic effect of basal area of mid-story conifers, which was maximized at 25–35 m²/ha when all other covariates were held constant at their means. The probability of use of harvested stands also differed among study areas. Using Chico (and California spotted owls) as the reference study-area indicator, we found that harvested units at Yreka were less likely to be used than those in Chico and Klamath Falls, which did not differ from each other, and we found relatively greater probability of use of harvested sites at Springfield and Ft. Bragg.

4. Discussion

Our study is the first to quantify before- versus after responses by a relatively large sample of spotted owls to active forestry that

Table 2

Coefficients and AIC^a values for habitat and environmental covariates in top logistic regression models of the probability of use of partially-harvested or thinned stands within 2400 m of nest sites of spotted owls in western Oregon and northern California, USA.

Covariate	Model 1	Model 2	Model 3	Model 4	Model 5	Model 6
Nest distance (m)	−1.13e−3	−1.06e−3	−1.00e−3	−1.86e−3	−1.03e−3	−1.05e−3
Mid-story (m ² /ha)	1.62e−1	1.63e−1	9.37e−1	1.45e−1	9.44e−2	8.47e−2
Mid-story ²	−4.19e−3	−4.14e−3	−2.72e−3	−3.85e−3	−2.73e−3	−2.60e−3
Large tree (m ² /ha)	2.41e−2		5.82e−2		5.11e−2	
Large tree * Nestdist.					5.53e−6	
RMZ proportion ^b						3.49e−1
Log _e (RMZ prop.)	3.86e−1	3.50e−1		4.40e−1		
Yreka area	−1.04	−1.10		−0.47		
Springfield area	1.52	1.80		1.99		
Ft. Bragg area	1.33	1.45		1.83		
AIC _c	32245.37	32246.98	32251.82	32253.53	32253.91	32254.76
AIC weight	0.808	0.127	0.032	0.014	0.011	0.007

^a Akaike information criterion, corrected for small sample sizes.

^b Proportion of harvest unit <100 m from streams.

included a large number of thinning and partial harvesting treatments across a variety of forest types. We did not observe site abandonment, despite treatments that comprised up to 58% of 450-ha areas surrounding nests sites. Our data supported the hypothesis that spotted owls would use thinned or partially-harvested stands equally or more often than before harvesting. In overall comparisons, spotted owls used stands scheduled for harvest significantly less than expected on the basis of availability before harvest. After silvicultural treatment, spotted owls increased overall use of the same stands, and used them collectively in proportion to availability. Many of the stands planned for harvest evidently were too dense and owls hunted in them relatively infrequently before harvesting. Yet, nearly 50% of the harvested units within owl home ranges were not found to be used by owls up to 2 years before or after harvesting, and many others were used only a few times. Thus, the majority of harvests essentially had no detectable effects on the associated spotted owls. We attribute this largely to planned avoidance through pre-harvest guidance by regulatory agencies that minimized active or intensive forestry in close proximity to nest sites or within nesting and roosting habitat.

As expected, we found no reason to believe that northern spotted owls and California spotted owls differed in response to thinning or partial harvests. We did find differences among study areas that seemed attributable to forest type as a proxy for expected prey base: the probability of use of harvested stands by spotted owls was greater in Douglas-fir forests at Springfield and in Coast Redwood forests at Ft. Bragg in comparison to mixed-coniferous forests at the other 3 study areas. These differences might be associated with the observation that harvested stands at Springfield and Ft. Bragg contained greater basal area of large-diameter trees (15.6 and 10.6 m²/ha) than those in the Yreka and Chico study areas (0.8 and 2.0 m²/ha). However, harvested stands at Klamath Falls averaged 10.3 m²/ha of basal area in large-diameter trees, and models without a study area effect were not strongly supported. Use of harvested stands at Ft. Bragg accords with other studies (e.g., Hamm and Diller, 2009) that suggest that young Coast Redwood forests are more productive of prey in general, particularly for dusky-footed woodrats (*N. fuscipes*). The observations for Springfield could be related to low sample sizes. There, only two owl home ranges received silvicultural treatments, and one heavily-used harvested stand (Fig. 1B) was a lightly-thinned unit that encompassed an unharvested riparian zone that may have provided a supply of bushy-tailed woodrats (*N. cinerea*) (Carey et al., 1992). Thinned stands in this study area also may have provided an increased supply of deer mice (*P. maniculatus*) (Suzuki and Hayes, 2003), or the harvesting may have resulted in increased vulnerability of northern flying squirrels and red tree voles. Without complementary information on the relative abundance and availability of prey populations, especially at the landscape level, we cannot generalize widely from the greater probability of use by owls of some, but not all, harvested stands at Springfield.

As we predicted, size, location, and intensity of treatment influenced the probability of use of stands post-harvest. The relative probability of use of harvested stands by spotted owls increased with area treated, increased with decreasing distance from nest sites, and increased with the proportion of harvest-unit area ≤100 m of streams and associated riparian management zones. The use of harvested stands may also have been influenced by juxtaposition with habitats expected to be used frequently, such as edges of brushy-stage clearcuts in the case of Coast Redwood stands or in unharvested late-successional stands, but we did not map those categorical features. Proximity to streams likely was important because associated riparian zones are protected, and probably provided important sources of prey (Carey and Peeler, 1995).

The intensity of harvest exerted a strong effect on probability of use of harvested units. We found a quadratic effect of mid-story basal area in which the highest likelihood of foraging use post-harvest occurred in stands with retained basal area of 25–35 m²/ha, holding other factors constant at their mean values. This implies that the probability of use decreased in stands with significantly greater or lesser retained basal area: stands evidently can be too dense or too open, similar to conclusions regarding longer-term effects of partial harvesting in Irwin et al. (2012). This and information in Irwin et al. (2013) suggests that the most-intensive partial harvests in nesting and roosting habitat were used less frequently. Also, our information suggests that the retained mid-story trees probably facilitated successful acquisition of prey by providing perch sites from which owls hunted and possibly increased foraging efficiency via increased access to prey. Contrary to our prediction, basal area of retained large trees ≥65 cm dbh exerted only a weak statistical effect across all treated stands and was not an important factor influencing use of harvested stands. The weak effect seems related to the wide range of availability of such large trees across our samples, and many young and intermediate-aged stands that were commercially thinned contained no large trees. Telemetry error might have influenced the observed use of small harvest units, although resolution of our telemetry system was sufficient because of an extensive road system.

5. Management implications

The advisability of silvicultural applications in areas occupied by spotted owls has had both proponents and challengers. Proponents, cognizant of successes over the long term, know that large-diameter trees, which provide important habitat for arboreal prey, can be produced faster when grown in low densities (Curtis and Marshall, 1986). Challengers, aware of past failures in which harvest volume became the short-term objective rather than wildlife habitat, recommend avoiding any silvicultural intervention in all stands older than 50 years of age that are in reserved areas (FEMAT, 1993: 12). On the other hand, the latest Recovery Plan for the northern spotted owl (USFWS, 2011) indicates that limited pre-commercial and commercial thinning are allowable in areas otherwise reserved from regeneration harvests. Yet, even that suggestion appeared to be countermanded by the Critical Habitat Rule (USFWS, 2012: 271), a regulatory document which argued that thinning which removes young, shade-intolerant conifers to reduce competition with larger legacy conifers is expected to result in a substantial decrease in canopy cover and a subsequent degradation in habitat quality. This latter view holds that high levels of canopy cover contribute heavily to providing quality habitat (Tempel et al., 2014). Perhaps accordingly, recent recommendations for fuel reductions in fire-prone landscapes suggest to conduct silvicultural experiments within foraging habitat while avoiding such active management within nesting and roosting habitat within spotted owl home ranges (Gaines et al., 2010; Lehmkuhl et al., 2015).

Given information presented herein and previous research (Carey and Peeler, 1995; Fiedler and Cully, 1995; Carey, 2003a,b; Irwin et al., 2004, 2013; Sullivan et al., 2013), we suggest managers consider a modified view in which judicious applications of silvicultural practices, primarily commercial thinning, are likely to improve the values of low-quality foraging habitat for spotted owls in the short run. This would include young and intermediate forests with dense canopy cover but without large trees, multiple canopy layers and canopy gaps that typify nesting and roosting habitat. Moreover, recent publications suggest that habitat quality of treated areas may further improve over time (Irwin et al., 2007,

2012) as conifers increase radial growth and undergrowth shrubs and herbs, important to the owl's prey, respond to increased light, growing space, soil nutrients and moisture. Below, we present suggestions and important caveats for managers to consider for the forest zones included in our research.

5.1. Douglas-fir/Western Hemlock Zone

There are several million hectares of second-growth Douglas-fir forests in the Pacific Northwest (DeBell and Curtis, 1993; Hayes et al., 1997) that may be too dense for successful acquisition of prey by spotted owls, although prey may be relatively abundant (Rosenberg and Anthony, 1992; Manning et al., 2012) and spotted owls may be present if patches of older forest, large nesting structures, large snags, coarse woody debris, and undergrowth shrubs are present (Irwin et al., 2000). Such young and intermediate forests generally do not contain multiple canopy layers, but commercial thinning of 30–50 year-old stands to 30–40 m²/ha can lead to establishment of Douglas-fir and western hemlock in the understories (Shatford et al., 2009). However, repeated and/or heavy selective removal of western hemlock may be required to establish Douglas-fir in the mid-story (Wilson and Puettmann, 2007).

Some species of small mammals increase in abundance following thinning in Douglas-fir dominated stands (Klenner and Sullivan, 2009). For example, reproductive performance of deer mice, increased shortly after thinning to basal areas of 16–31 m²/ha (Suzuki and Hayes, 2003), which includes the range for which we found greatest probability of use of harvested stands by owls. Thinning and retaining large legacy trees in young Douglas-fir/western hemlock forests should contribute to spotted owl foraging habitat until forest crowns close and crowd out the undergrowth vegetation (Carey and Harrington, 2001).

The thinned units that were used the most by northern spotted owls in our Douglas-fir study area were in close proximity to riparian zones, which may have contained bushy-tailed woodrats (Carey et al., 1992). Thus, our study supports the supposition by Carey and Peeler (1995) that thinning in close proximity to stream-side zones should benefit northern spotted owls. Yet, we do not know if the initial increases in use that we observed will be anything more than transient. Thinning produces a transient response in canopy closure because Douglas-fir has rapid lateral growth of 2–3% per year (Bailey and Tappeiner, 1998).

Therefore, the biggest technical challenge to implementing ecologically-motivated silviculture in young and mid-successional Douglas-fir/western hemlock forests within spotted owl home ranges may lie in scheduling harvests over time and space to promote increased short-term foraging opportunities for owls while providing inter-connected refugia that sustain populations of northern flying squirrels and red tree voles over the longer term. Wilson and Forsman (2012) provided suggestions for future manipulative research that may result in opportunities to develop an occluding mid-story layer of shade-tolerant conifers that could integrate habitat needs for flying squirrels, red tree voles, and northern spotted owls over the longer term at the landscape level.

5.2. Mixed Conifer Forests

There may be more latitude and need for managing young or intermediate Mixed Coniferous forests on behalf of spotted owls, where woodrats are anticipated to be more important in owl diets and/or where uncharacteristic wildfires may threaten habitat sustainability. We observed the greatest probability of foraging use of harvested stands occurred in those with 25–35 m²/ha of retained mid-story basal area, particularly in association with streamside zones. Such harvests might be conducted under a silvicultural prescription that calls for thinning from below or individual tree

selection that involves small openings (e.g., <5 ha) and retains trees in an irregular distribution that includes some occluding patches of smaller-diameter trees in a size-class distribution akin to that suggested by Fiedler and Cully (1995) for Mexican spotted owls (*S. lucida*). Retaining early-seral dominants such as Douglas-fir and sugar pine (*P. lambertiana*), including scattered old remnants, should be management goals. More intensive partial harvests such as shelterwood or seed-tree preparatory harvests seem likely to result in negative effects on spotted owls, except in areas known to be used by owls in winter (Irwin et al., 2013).

Reducing fuel loads via thinning small (13–19 cm dbh) understory trees may improve foraging spotted owl habitat in the short term. We also recommend lowest management intensity in drainage bottoms adjacent to streamside zones, increasing to mid-slope, and highest near ridgetops (North et al., 2009; Stine et al., 2014).

5.3. Coast Redwood Forests

Relatively heavy thinning should improve young and intermediate forests as winter foraging habitat for northern spotted owls in the Coast Redwood zone. Use of silviculturally-treated stands by spotted owls for winter foraging may be facilitated by retaining conifer basal area of 9–18 m²/ha (Irwin et al., 2013), along with purposeful production of a heavy shrub layer that includes shrubs such as whiteleaf manzanita (*A. manzanita*) and blueblossom (*C. thursiflorus*) and hardwoods such as Pacific madrone, bigleaf maple, and tanoak.

5.4. Summary

Acknowledging our study should be considered a first-approximation, we believe the results support judicious thinning and/or modified partial harvesting as tools for forest managers to improve extant low-quality foraging habitat for spotted owls. The information also informs planning for owl-occupied landscapes that are more resilient to uncharacteristic wildfires and perhaps to climate change. In Douglas-fir/western hemlock forests, much greater care must be taken in applying intermediate silvicultural practices in areas where spotted owls and other predators may significantly deplete populations of northern flying squirrels and red tree voles. In such areas, it will be challenging to sustain continuous and heterogeneous sources of prey without retaining large snags, large amounts of coarse woody debris, undergrowth shrubs and hardwoods. In all areas, nesting and roosting habitat must be protected because spotted owls may abandon territories if significant and intense harvesting occurs within close proximity of their nest trees. There is little information regarding the size of area surrounding nest trees that must be protected, although McComb et al. (2002) found nest cores of northern spotted owls in Douglas-fir forests were 28 ha and Irwin et al. (2012) found that large-diameter trees affected foraging within an area of 50 ha surrounding nest sites. Finally, northern barred owls could confound efforts to integrate forest ecosystem management with conservation of spotted owls. In areas with extensive young forests that are proposed for intermediate silviculture, long-term research and monitoring are needed to track responses of populations and distributions of spotted owl and barred owls, and to estimate rates of prey biomass acquisition by owls, as well as to monitor prey population dynamics across a landscape mix of managed and unmanaged stand conditions.

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Pyrodiversity and biodiversity: A history, synthesis, and outlook

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Abstract

Aim: Pyrodiversity is the spatial or temporal variability in fire effects across a landscape. Multiple ecological hypotheses, when applied to the context of post-fire systems, suggest that high pyrodiversity will lead to high biodiversity. This resultant “pyrodiversity–biodiversity” hypothesis has grown popular but has received mixed support by recent empirical research. In this paper, we sought to review the existing pyrodiversity literature, appraise support for the pyrodiversity–biodiversity hypothesis, examine potential mechanisms underlying the hypothesis and identify outstanding questions about pyrodiversity and future research needs.

Location: Global terrestrial ecosystems.

Methods: We performed a systematic literature review of research related to pyrodiversity and the pyrodiversity–biodiversity hypothesis. We also examined how two individual species with distinct relationships with fire (spotted owl *Strix occidentalis* and black-backed woodpecker *Picoides arcticus*) respond to pyrodiversity as case studies to illustrate underlying mechanisms.

Results: We identified 41 tests of the pyrodiversity–biodiversity hypothesis reported from 33 studies; 18 (44%) presented evidence in support of the pyrodiversity–biodiversity hypothesis, while 23 (56%) did not. Our literature review suggested that support for the pyrodiversity–biodiversity hypothesis varies considerably with no consistent patterns across taxonomic groups and ecosystem types. Studies examining the pyrodiversity–biodiversity hypothesis often define pyrodiversity in different ways, examine effects at different scales and are conducted in ecosystems with different natural fire regimes, baseline levels of biodiversity, and evolutionary histories. We suggest these factors independently and jointly have led to widely varying support for the pyrodiversity–biodiversity hypothesis.

Main Conclusions: Clarifying the pyrodiversity–biodiversity hypothesis will be facilitated by stronger development of the different potential mechanisms underlying pyrodiversity–biodiversity relationships, which can be aided by examining how individual species respond to pyrodiversity. Future research would benefit from a closer examination of the role of scale (e.g. scale dependence) in pyrodiversity–biodiversity relationships, standardization of pyrodiversity metrics, broad-scale mapping of pyrodiversity, and macroecological study of pyrodiversity–biodiversity relationships.

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KEYWORDS

ecological mechanisms, fire management, fire mosaic, megafires, pyrodiversity, pyrodiversity–biodiversity hypothesis, scale

1 | A CONCEPTUAL HISTORY AND EVOLUTION OF PYRODIVERSITY

Pyrodiversity describes the degree of variation in post-fire landscape characteristics within or among fires. While at its core pyrodiversity is a technical descriptor of the properties of burned areas, its conceptual roots are biological and tightly linked to community ecology, niche theory and biodiversity conservation. The term was formally introduced by Martin and Sapsis (1992), who described pyrodiversity as an agent of biodiversity, whereby “pyrodiversity begets biodiversity.” The authors hypothesized that the degree of variation contained within different dimensions of a fire regime, such as fire return interval, seasonality, size or intensity, will result in an associated mosaic of successional stages and structure that would define the breadth of niche space for different species to occupy. Thus, pyrodiversity is a composite characteristic of a fire regime: certain fire regimes will have higher or lower pyrodiversity, which will in turn lead to higher or lower biodiversity, respectively.

A central concern in the contemporary pyrodiversity literature is that a variety of anthropogenic factors may be decreasing pyrodiversity across landscapes, potentially leading to biodiversity losses. Indeed, a central element of Martin and Sapsis’ work was pointing out that pyrodiversity was likely decreasing because of recent human activities—in particular, the loss of indigenous fire, which had created or sustained pyrodiversity. Supporting this claim, there is now widespread historical and contemporary evidence of people promoting pyrodiversity across large landscapes (Bird et al., 2008; Taylor et al., 2016; Trauernicht et al., 2015), which is likely to influence how contemporary biotic communities respond to pyrodiversity. Whether real or hypothesized, temporal trends in pyrodiversity have the potential to reshape biodiversity patterns across ecosystems.

Yet, complicating our study of such trends is that there is no single operational definition of pyrodiversity. Martin and Sapsis’ proposition nearly three decades ago provided a strong conceptual foundation for the study of the pyrodiversity–biodiversity hypothesis, but their original definition of pyrodiversity was broad and operationally vague. How could pyrodiversity be measured and the pyrodiversity–biodiversity hypothesis be tested in practice? Since its conceptual introduction, pyrodiversity has been defined in many ways by researchers attempting to test the pyrodiversity–biodiversity hypothesis—each describing a different dimension or “axis of variability” in fire regime characteristics (Appendix 1). In addition, pyrodiversity is etymologically related to other concepts in fire ecology (Box 1), and so, the pyrodiversity–biodiversity hypothesis has—in essence—also been tested under other names (e.g. “patch-mosaic burning hypothesis”).

What constitutes a test of the pyrodiversity–biodiversity hypothesis? Most attempts to define pyrodiversity involve selecting a single fire dimension, such as fire age, and quantifying the spatial variation in that characteristic within each sampling unit (e.g. Taylor et al., 2012). The variability in that characteristic for each sampling unit can then be linked to species diversity within that sampling unit, enabling an explicit test of the hypothesis that increased pyrodiversity correlates with increased biodiversity (typically alpha diversity, but also see studies examining pyrodiversity relationships with beta diversity, e.g. Farnsworth et al., 2014; Leavesley & Cary, 2013; McGranahan et al., 2018; Pastro et al., 2011). Yet, the broad original definition of pyrodiversity has led to some relatively permissive interpretations of the concept, as well as confusion regarding what exactly does, and does not, constitute a study of pyrodiversity and a test of the pyrodiversity–biodiversity hypothesis. In our view, a test of the pyrodiversity–biodiversity hypothesis should meet a defined set of criteria (Box 2). While there exists a vast literature on how fire and fire regimes affect various aspects of biodiversity (e.g. how fire frequency influences plant richness)—and other recent syntheses have focused on these broad questions (Kelly et al., 2020)—relatively few studies explicitly examine the pyrodiversity–biodiversity hypothesis (Box 2).

The lack of a single definition of pyrodiversity has also led to considerable innovation in how pyrodiversity can be measured. Some researchers have explored empirical support for the pyrodiversity–biodiversity hypothesis using multiple independent measures of pyrodiversity (e.g. Farnsworth et al., 2014), while others have developed integrated multi-axis metrics of pyrodiversity (e.g. Ponisio et al., 2016; Steel et al., 2021). More recently, technological advances have permitted an expansion of how pyrodiversity can be defined, particularly incorporating fine-scale heterogeneity. For example, remote sensing tools such as Landsat allow researchers to define pyrodiversity as the variability in burn severity in forest systems (e.g. variation in tree basal area or canopy mortality) following fire in each sampling area (e.g. Tingley et al., 2016). In an interesting deviation from traditional inquiry, Bowman et al. (2016) defined pyrodiversity as “the coupling of biodiversity and fire regimes in food webs” focusing on trophic feedbacks and critiquing “simple, one-way statistical linkages between biodiversity surrogates and fire regimes...” that have characterized pyrodiversity–biodiversity research to date. Bowman et al. (2016)’s renewed focus on mechanism and ecosystem processes that shape and underly the pyrodiversity–biodiversity relationship is useful, and we discuss below the importance of future research focusing on mechanisms. The variety of approaches for defining and quantifying pyrodiversity have their own strengths and weaknesses, but each is also consistent with the breadth of Martin and Sapsis’ pyrodiversity–biodiversity hypothesis. In the absence of any critical evaluation of different metrics, there has been no

BOX 1 Pyrodiversity and related ecological concepts

The term pyrodiversity is related to several other ecological concepts. All of the below concepts are themes in landscape ecology and relate in some way to the measurement of variability but have subtly different histories of use and interpretations. Here, we define several of these concepts and describe how they are intertwined with pyrodiversity.

Patch-mosaic burning is a fire management approach originally applied in some South African national parks (e.g. Kruger and Pilanesberg) in the early 1990s (Van Wilgen et al., 1998). Application of the approach has since expanded and is more or less synonymous with the term pyrodiversity. The goal of patch-mosaic burning was to establish a mosaic of vegetation structural types through prescribed burning that would allow “efficient means of conserving biodiversity” (Van Wilgen et al., 1998). Under this fire management paradigm, prescribed burns are initiated at random locations throughout the project area and allowed to burn out by themselves until an established quota of burned area is reached. The result is a heterogeneous mosaic of burn conditions that vary in extent, seasonality and other characteristics. The emergence of the patch-mosaic burning paradigm paralleled the broader cultural shift away from equilibrium thinking to recognizing the importance of non-equilibrium processes in ecology (Parr & Brockett, 1999; Pickett & White, 1985). Related concepts/terminology include vegetation mosaic, fire mosaic and successional mosaic.

Mixed-severity fire is a term commonly used to describe fires that contain a broad gradient of post-fire tree basal area or canopy mortality (i.e. severity) with some mixture of low-, moderate- and high-severity effects. Mixed-severity fire is most commonly defined as containing between 20% and 70% tree mortality (or “high-severity fire”) across a fire area (Agee, 1993) although some definitions include an even broader range (e.g. 5%–70%). Such fires could almost certainly be characterized as containing a relatively high degree of pyrodiversity in most circumstances, although the spatial pattern of burn severity and the scale at which pyrodiversity is summarized may influence this generalization. Many fire regimes, particularly those in western North America, have widely been characterized as having mixed-severity fire regimes (e.g. DellaSala & Hanson, 2015). However, Collins et al., (2017) pointed out that the term mixed-severity fire is so broad that it carries little meaning, because nearly all forest fires experience between 20% and 70% high-severity fire, and moreover, this definition ignores the role of spatial patterns of burn severity. Pyrodiversity may face a similar issue related to how it is defined and interpreted (e.g. at what point is a fire, or a landscape, considered “pyrodiverse”) and reinforces the need to consider how pyrodiversity and associated ecological effects may vary as a function of scale.

Fire regime is the typical frequency, size, seasonality, intensity, pattern and other attributes of burned areas that have been typical for a given ecosystem over a long period of time (Agee, 1993; Gill, 1975; Kilgore, 1981). Different ecosystems are characterized by different fire regimes because of broad-scale variation in climate, vegetation type and ignition frequency (Pyne et al., 1996). Pyrodiversity thus might be considered one component of fire regimes (which itself is comprised of one or more components), where fire regimes are characterized by a typical (or range of) within- or among-fire pyrodiversity. For example, frequent-fire regimes in seasonally dry forests might be characterized by relatively high pyrodiversity (i.e. they contain a more dynamic mosaic of successional stages). In contrast, infrequent-fire regimes in more mesic and high-elevation forest types might be characterized by relatively low pyrodiversity (i.e. having larger, more homogeneous fires and even-aged forest conditions). However, this dichotomy depends in part on the spatial and temporal scales being used to characterize fire regimes. Martin and Sapsis (1992) noted that fire suppression has altered fire regimes and has thereby likely reduced pyrodiversity (i.e. made fires more homogeneous), particularly at larger spatial scales, in some systems such as parts of the Pacific Northwest of the United States. Indeed, recent empirical work has confirmed that fires in California, USA, are increasingly becoming more homogeneously severe (Stevens et al., 2017; Steel et al., 2018).

The intermediate disturbance hypothesis (IDH) posits that too much or too little disturbance will favour lower species richness, but moderate levels of disturbance will maximize species richness (Connell, 1978; Karr & Freemark, 1985). For example, if disturbances that reset successional dynamics are very frequent, the community will be dominated by a smaller number of *r*-selected dispersal-adapted species and colonizers. If disturbances are too infrequent, late-successional characteristics will dominate and the community will be characterized by a smaller number of *K*-selected species and old-growth specialists. However, if disturbances are moderately frequent, the community will represent a highly dynamic mixture of *r*- and *K*-selected species that will lead to higher species richness. Fire regimes characterized by higher pyrodiversity may reflect “intermediate” levels of disturbance because low pyrodiversity could reflect either too much or too little disturbance, depending on how pyrodiversity is quantified. Thus, there is a natural connection between the IDH and the pyrodiversity–biodiversity hypothesis. Like pyrodiversity, the IDH is likely to show high sensitivity to the spatial and temporal scales at which disturbance is quantified.

Natural range of variability (NRV), also called historical range of variability (HRV), describes the range of ecological conditions that are typical of a given ecosystem or region, often prior to widespread modification by Western human society. Fire regime is thus an approach for characterizing the NRV of fire in a system. Because pyrodiversity is a metric that characterizes variation in fire conditions, there is therefore a natural linkage between these two concepts: historical patterns of pyrodiversity characterized

BOX 1 (Continued)

one axis of the natural range of variability in fire characteristics. NRV is often invoked in ecosystem restoration, where it is used to guide management and restoration targets to approximate historical and ecologically appropriate landscape conditions (Safford & Stevens, 2017; Swanson et al., 1994).

Patchiness is a concept with roots in landscape ecology that describes the degree of variability in discrete land cover or habitat classes (e.g. vegetation types) in a landscape. Patchiness can be formally quantified in a wide variety of ways, including patch density (number of patches of a given type), mean patch size, patch richness (number of different patch types) or other metrics that characterize patches in terms of their shape (e.g. fractal dimension, perimeter-to-area ratio). Fires can be characterized in terms of their patchiness (e.g. size or shape of different burn severity classes or fire age classes), and thus, there might be some predictable relationships between patchiness and pyrodiversity. For example, landscapes with high patch richness (e.g. many different burn severity or fire age classes) would be more pyrodiverse. Some studies investigating ecological effects of pyrodiversity used fire “patchiness” as a synonym for pyrodiversity (e.g. Lawes et al., 2015; McGranahan et al., 2018; Menges & Quintana-Ascencio, 2004). Patches of different fire severities or ages also imply the existence of edges between patch types, and pyrodiversity characterized at finer spatial scales will be higher at these interfaces between patches than within a given patch.

single “correct” or “best” way to define pyrodiversity, and different researchers have unsurprisingly defined pyrodiversity in different ways according to the objectives and ecological context of their studies.

One consequence of the wide variety of approaches for quantifying pyrodiversity is that different researchers have seldom asked the same question of the pyrodiversity–biodiversity hypothesis. Directly comparing support for the hypothesis among studies that apply different operational definitions of pyrodiversity might seem questionable, because the lack of a consistent definition may make broad generalizations and synthesis across studies challenging. However, this variability may also hold unexpected benefits because different approaches for quantifying pyrodiversity may allow researchers to test different ecological mechanisms underlying the pyrodiversity–biodiversity hypothesis. Among studies, pyrodiversity is not only quantified in different ways, and tests applied to different taxa in different ecosystems, but it is also quantified at different spatial and temporal scales. As is the case for all ecological phenomena (Levin, 1992; Wiens, 1989), pyrodiversity–biodiversity relationships are likely to be scale-dependent. Thus, the scale (e.g. spatial grain or extent, or temporal window) selected by the researcher will influence whether the hypothesis is supported because different scales may test different mechanisms and may be more or less relevant for different taxa.

Here, we attempt to summarize and synthesize the existing state of knowledge on the pyrodiversity–biodiversity hypothesis, provide clarity on proposed mechanisms, and search for any consistent rules or results. Additionally, we present case studies of two focal species of conservation concern in western North America for which emerging research is demonstrating that pyrodiversity plays a role in the species’ ecology, providing intriguing evidence for underappreciated mechanisms that could underlie the pyrodiversity–biodiversity hypothesis. We then identify major unanswered questions and identify research gaps in the study of pyrodiversity and the pyrodiversity–biodiversity hypothesis. In sum, we conclude that, while much

research has been conducted on pyrodiversity, rich opportunities remain to rapidly advance pyrodiversity research in the era of megafires.

2 | SYNTHESIS OF EXISTING TESTS OF THE PYRODIVERSITY–BIODIVERSITY HYPOTHESIS

We performed a systematic literature review of pyrodiversity research via Web of Science using the workflow outlined in Grames et al. (2019) and the associated R package litsearchr version 1.0.0. First, we conducted a naive search using the search string (“pyrodiversity” AND “biodiversity”) across three databases: Biological Abstracts, BIOSIS Citation Index and Zoological Record. Then, we used the litsearchr package to consolidate and de-duplicate records from the naive search results and build a keyword co-occurrence network to capture themes related to, but not included in, our original search string. We manually reviewed keywords and generated an expanded Boolean search for a refined literature review. The final search string was ((pyrodivers* OR “fire* mosaic*” OR “burn* pattern*” OR “mosaic* burn*” OR “patch* mosaic*” OR “pyrodivers* landscap*”) AND (biodivers* OR “beta* divers*” OR “communiti* composit*” OR “speci* composit*” OR “speci* divers*” OR “speci* rich*” OR “alpha* divers*” OR “communiti* divers*” OR “disturb* hypothesi*” OR “intermedi* disturb*”). We conducted this refined search across the three above-mentioned databases and assembled a final de-duplicated database on 5 October 2020.

Here, we summarize the results of the literature search. The search returned 176 results, 95 of which we determined to be relevant to the present paper (other studies were largely unrelated to fire and biodiversity). In addition, we searched through references of two recent fire-related review papers (He et al., 2019; Kelly et al., 2017) to identify papers that our literature search might have missed; this yielded an additional three papers that clearly examined

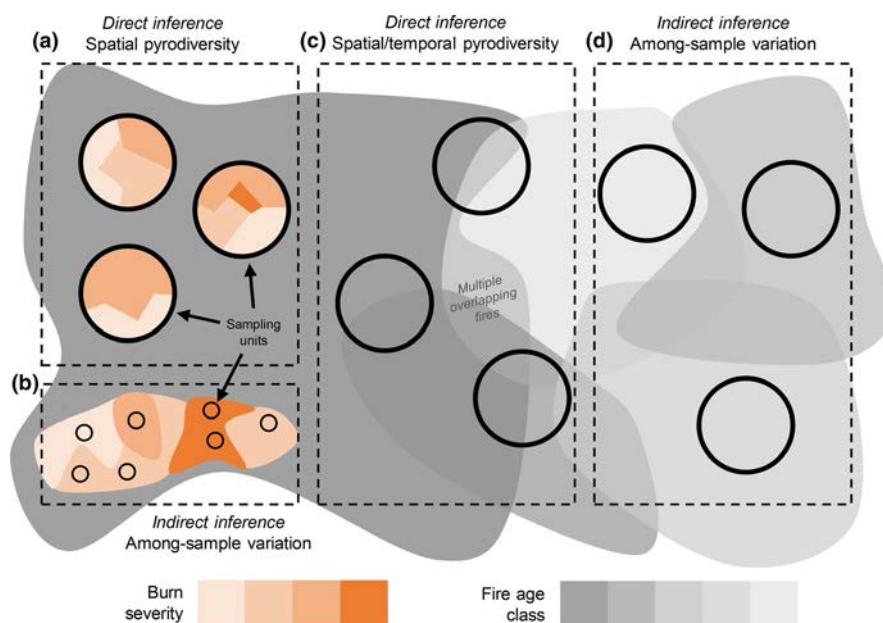
BOX 2 Testing the pyrodiversity–biodiversity hypothesis

Pyrodiversity was originally conceived as an inherently spatio-temporal concept. Martin and Sapsis (1992) described pyrodiversity as “variety in interval between fires, seasonality, dimensions, and fire characteristics, producing biological diversity at the micro-site, stand, and landscape level.” This broad (and somewhat vague) definition has led to a proliferation of approaches for testing the pyrodiversity–biodiversity hypothesis in practice. Yet, in our view, simply examining how biodiversity responds to a chosen element of a fire regime does not provide the required elements for a direct test of the pyrodiversity–biodiversity hypothesis.

We propose that a direct test of the pyrodiversity–biodiversity hypothesis should include a metric of variation (e.g. coefficient of variation, Shannon diversity index) to be quantified on a fire characteristic (e.g. fire age, burn severity) *within* spatially replicated sampling units or a buffered area surrounding each sampling unit (insets a and c below). Variation should occur *within* sampling units, not strictly *among* sampling units. The *within*-sample variation in fire characteristics (i.e. pyrodiversity) is then linked to a *within*-sample measure of biodiversity (e.g. alpha diversity), and standard procedures such as regression or other models can be used to determine whether a linear or nonlinear relationship between the two variables exists (e.g. Tingley, et al., 2016).

The pyrodiversity–biodiversity hypothesis is sometimes examined in indirect ways as well. This situation often arises when variation in fire characteristics (e.g. time since fire, fire severity) occur *among* sampling units (see insets b and d below), and variation in species richness or community composition is then linked to *among*-sample variation in fire characteristics. Often, studies taking this approach will then infer that because different species are associated with different fire characteristics, it follows that landscape variation in these characteristics will support higher biodiversity (e.g. Taillie et al., 2018). We refer to this situation as an indirect inference about the pyrodiversity–biodiversity hypothesis. Indirect approaches may also go one step further by using optimization analyses of among-sample variation to more formally assess combinations of fire characteristics expected to promote biodiversity (e.g. Kelly et al., 2015).

Individual studies testing the pyrodiversity–biodiversity hypothesis may quantify either *spatial* or *temporal* components of pyrodiversity, or a combination of both (see below figure). Spatial pyrodiversity is the spatial variation in a fire characteristic (e.g. burn severity) within a sampling unit (see inset a). Temporal pyrodiversity is the spatial variation in a temporal fire characteristic (e.g. fire age/successional stage) within a sample unit (see inset c), which we note is inherently spatio-temporal. If no variation occurs within sampling units (insets b and d), then pyrodiversity has not been measured and a direct test of the pyrodiversity–biodiversity hypothesis is not possible. For example, sampling in inset b would simply yield a test of how biodiversity responds to burn severity, and inset d would test how biodiversity was affected by time since fire; neither would be considered a direct test of the pyrodiversity–biodiversity hypothesis.



the pyrodiversity–biodiversity hypothesis. We reviewed all 98 papers and noted the publication date, geographic location, ecosystem type, taxa studied, whether a test of the pyrodiversity–biodiversity

hypothesis appeared to have been performed and whether support for the hypothesis was inferred by the authors, how pyrodiversity was defined or conceptualized, and other key points and conclusions

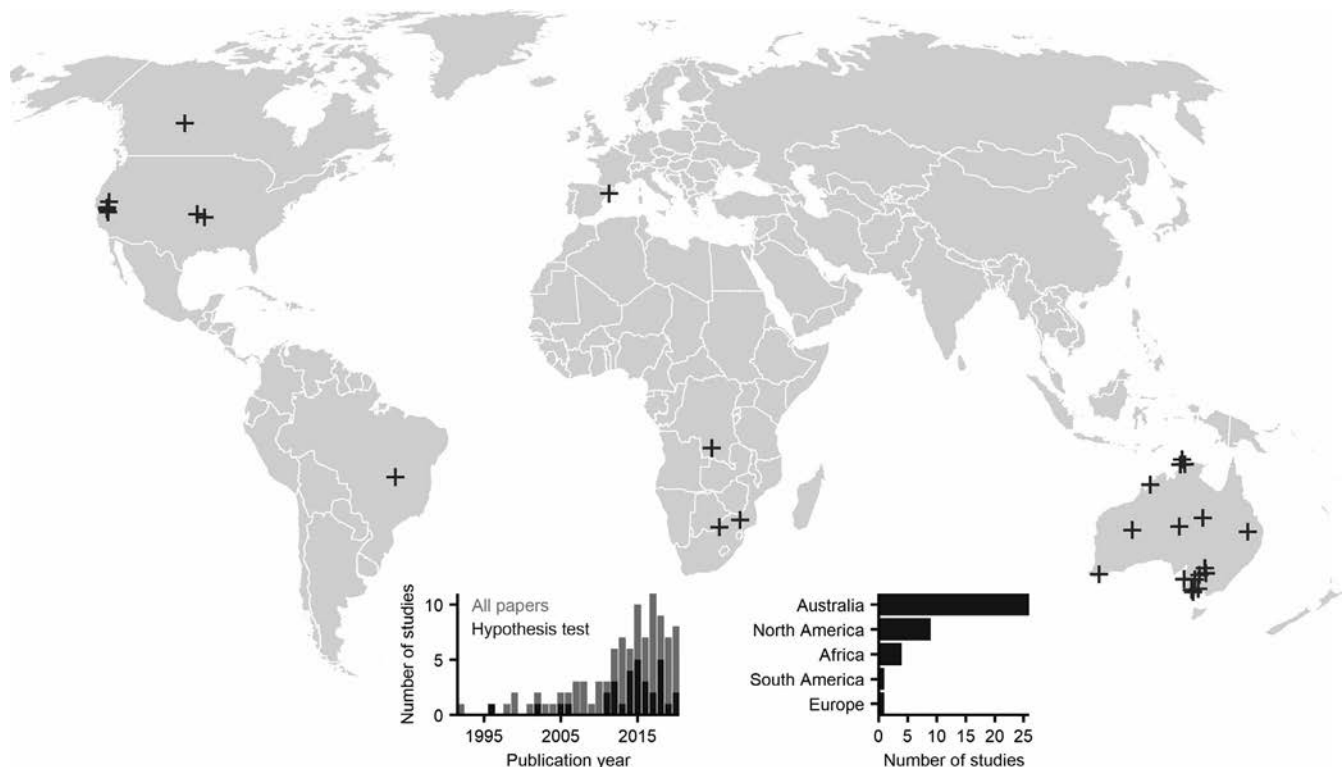


FIGURE 1 Global distribution of pyrodiversity–biodiversity research. Each grey “+” represents the approximate spatial location of studies that tested the pyrodiversity–biodiversity hypothesis (or, for broader-scale studies, the “+” shows the approximate geographic centre of the study area). The inset bar graph on the left shows trends in pyrodiversity-related research over the period 1992–2020; dark grey bars represent studies that tested the pyrodiversity–biodiversity hypothesis, while light grey bars show the total number of relevant studies from our literature search. The inset bar graph on the right shows the number of studies per continent. Our literature search did not reveal existing pyrodiversity–biodiversity research in Asia (there are no wildfires in Antarctica)

reached by the authors. Thirty-three studies appeared to have performed a test of the pyrodiversity–biodiversity hypothesis, and five of those studies reported effects across more than one broad taxonomic group (for a total of 41 study–taxa combinations that we treat as independent units) (see Appendix 1). We identified a distinction between *direct* and *indirect* inferences about the pyrodiversity–biodiversity hypothesis, which relates to whether the selected fire characteristic varied *within* or *among* sampling units, respectively (Box 2, Appendix 1).

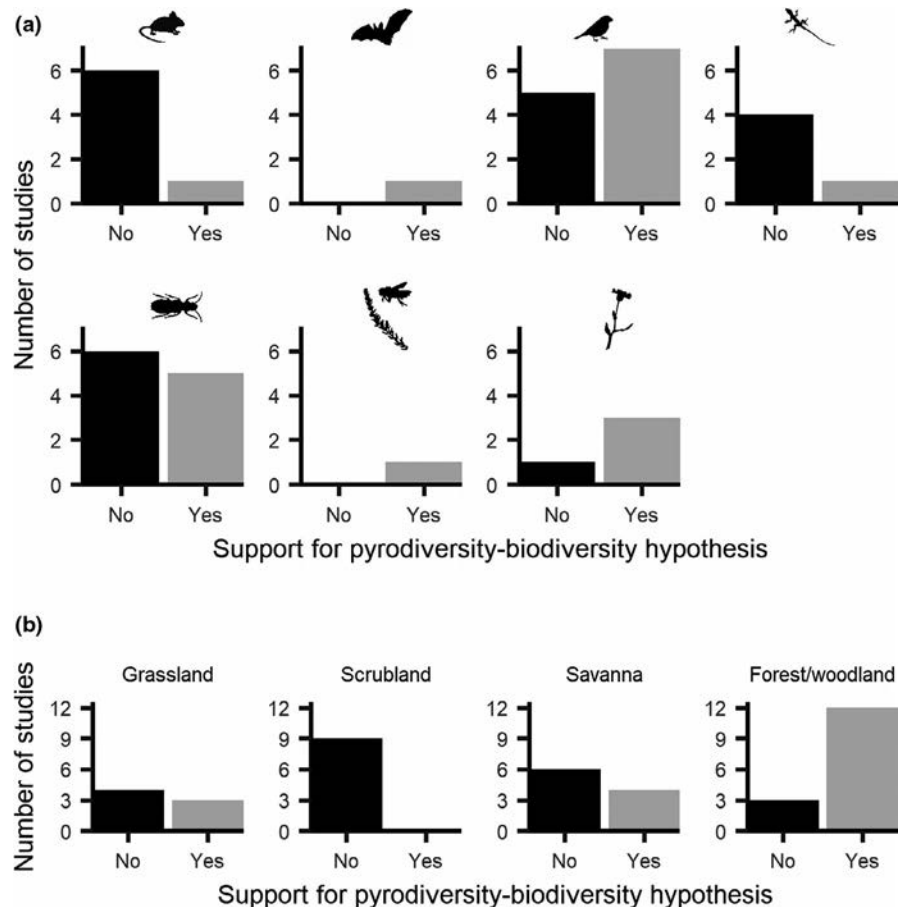
Because of high variability in study design and how pyrodiversity was defined, we did not feel there was enough consistent information to compute standardized effect sizes in a meta-analytic framework. Therefore, effects from studies were tallied using a simplified “vote-counting” approach (Bushman, 1994). Vote-counting approaches have noted shortcomings, including but not limited to failing to account for sample and effect sizes. Moreover, tallying of studies in the “vote-counting” approach may be more likely to mask different kinds of pyrodiversity–biodiversity relationships, such as nonlinear (or “hump-shaped”) relationships (e.g., Steel et al., 2021). We acknowledge these caveats and point out that here our aim is to provide a broad summary of the pyrodiversity–biodiversity literature, with a focus on support for positive associations between pyrodiversity and biodiversity. However, there are many ways that spatio-temporal variation in fire regimes can shape biodiversity.

As further evidence accumulates and studies of pyrodiversity–biodiversity relationships become more standardized (see “Synthesis and research gaps,” as well as Box 2), additional types of evidence synthesis may be possible.

Studies examining the pyrodiversity–biodiversity hypothesis have been conducted on four continents with the majority of studies occurring in Australia (26 studies), followed by North America (9), Africa (4), South America (1) and Europe (1) (Figure 1). We observed a recent increase in research on the pyrodiversity–biodiversity hypothesis, with an initial increase beginning in 2006 (perhaps motivated by the seminal work by Parr & Andersen in 2006 that popularized and critiqued the hypothesis) followed by a rise in tests of the hypothesis after 2011 (Figure 1). The pyrodiversity–biodiversity hypothesis has been examined in birds (12 studies), invertebrates (11), mammals (7), reptiles (5), plants (4), plant–pollinator interactions (1) and bats (1) (Figure 2a). These studies have occurred in grasslands (7 studies), scrub/shrublands (9), savannas (10) and forests/woodlands (15) (Figure 2b).

Our literature review suggests that support for the pyrodiversity–biodiversity hypothesis varies considerably across taxonomic groups and ecosystem types. Of the 41 tests reported from 33 studies, 18 presented evidence in support of the pyrodiversity–biodiversity hypothesis, while 23 did not indicate support for the hypothesis. All taxonomic groups containing more than one study examining the

FIGURE 2 Summary of studies examining the pyrodiversity–biodiversity hypothesis grouped by broad taxonomic group and ecosystem type. (a) Support for the pyrodiversity–biodiversity hypothesis (from top left) terrestrial mammals, bats, birds, reptiles, invertebrates, plant–pollinator interactions, and pollinators (b) Support for the pyrodiversity–biodiversity hypothesis among four broad ecosystem types



pyrodiversity–biodiversity hypothesis showed mixed support: different studies suggested support either for or against the hypothesis (Figure 2a). The same pattern of mixed support was apparent when results were grouped by ecosystem type, except for scrub/shrubland ecosystems in which all existing studies have reported no support for the pyrodiversity–biodiversity hypothesis. Therefore, it does not appear that the pyrodiversity–biodiversity hypothesis is consistently supported or not supported within particular taxonomic groups or ecosystem types, suggesting that variation in the literature may be due to other factors. Thus, we must consider what factors may influence whether the pyrodiversity–biodiversity hypothesis is supported in empirical study.

We suggest that there are at least three interacting factors that may drive variation in support for the pyrodiversity–biodiversity hypothesis among studies: mechanism, history, and scale. In this context, mechanism refers to different studies asking different questions of the pyrodiversity–biodiversity hypothesis by defining pyrodiversity in different ways (see Appendix 1). As an example, examining how species richness is affected by the diversity of fire age classes across a landscape is asking a question related inherently to temporal processes—how different species accumulate and replace one another through time across different successional stages initiated by fire (e.g. Nimmo et al., 2013). In contrast, examining how species richness is affected by diversity in burn severity is asking a question inherently about spatial processes—how species

accumulate and partition resources across space based on structural heterogeneity produced by a single fire event (e.g. Steel et al., 2019). Questions related to the pyrodiversity–biodiversity hypothesis can thus vary in terms of exploring temporal versus spatial mechanisms, but spatial and temporal processes can also interact to influence strength of a pyrodiversity–biodiversity effect (e.g. Tingley et al., 2016).

Many specific spatial and temporal mechanisms grounded in ecological theory have been proposed (He et al., 2019; Kelly et al., 2017). For example, Kelly et al. (2017) discuss several hypotheses based on ecological mechanisms that may give rise to observed pyrodiversity–biodiversity relationships, including habitat complementation (spatial variation in fire effects fulfils multiple habitat needs of an individual species), habitat heterogeneity (spatial variation in fire effects enhances multispecies coexistence through creation of diverse habitats), habitat refuge (spatial variation in fire effects produces refuges and alters predator–prey interactions) and fire season (temporal variation in fire seasonality influences fire effects and alters multispecies coexistence). Different approaches for quantifying pyrodiversity may allow the above hypotheses to be further parsed. Studies examining these mechanisms and other spatial and temporal mechanisms in different systems should not necessarily be expected to arrive at the same conclusions about the pyrodiversity–biodiversity hypothesis when quantifying pyrodiversity in different ways.

The second factor that may drive variation in support for the pyrodiversity–biodiversity hypothesis among studies is history. In this context, history refers to the evolutionary environment and ecological regimes that have characterized different systems over time, and which may constrain the development of pyrodiversity–biodiversity relationships. For example, we may not expect the pyrodiversity–biodiversity relationship to look the same in boreal forests as in temperate or tropical forests. These ecosystems vary greatly in their overall species diversity (generally increasing from boreal to temperate to tropical) (Gaston, 2000) and limiting factors that influence fire ignitions and behaviour (ranging from fuel-limited dry ecosystems to climate-limited wet ecosystems) (Krawchuk & Moritz, 2011).

Fire regimes are a significant evolutionary force in both plants and animals (Bond & Keeley, 2005; Pausas & Parr, 2018). As such, there is an interplay between fire regimes over evolutionary time and accumulation of adaptive traits by species to those fire regimes. For example, conifer species associated with frequent-fire regimes have thick bark, tall crowns and flammable litter, while species associated with infrequent-fire regimes have thin bark, shorter crowns and less flammable litter (Stevens et al., 2020). These adaptations then produce stabilizing feedbacks that reinforce the fire regime (He et al., 2019). Because fire can reset community dynamics (He et al., 2019), there may be an expectation that ecosystems with more frequent-fire and low- to moderate-severity regimes might support more opportunities for evolutionary forces to rapidly give rise to biodiversity. In contrast, infrequent-fire systems might more often be characterized by climax communities dominated by a smaller number of species, and fewer opportunities for fire-related disturbances to open evolutionary pathways. Thus, the same degree of pyrodiversity (however defined) may never be observed in frequent- versus infrequent-fire systems; even if it was, the same degree of pyrodiversity might be associated with different levels of biodiversity and thus a different expected “shape” to the pyrodiversity–biodiversity relationship (e.g., Steel et al., 2021).

The third factor that may drive variation in support for the pyrodiversity–biodiversity hypothesis among studies is scale. In this context, scale may refer to several components of a given study, but we are referring to the spatial and temporal extent and grain of the analysis and to what extent these scales relate to relevant ecological scales for the organism(s) or taxa under study. For example, pyrodiversity at larger scales (e.g. larger spatial extent and grain) may be more relevant for larger-bodied mammalian assemblages than for terrestrial invertebrates because often the scale of effect varies positively with characteristics such as body size and dispersal ability (Jackson & Fahrig, 2012). Thus, relevant spatial scales for studying pyrodiversity–biodiversity relationships might scale with body size or other traits. Larger spatial and temporal scales of measurement may also be required to capture sufficient variability to detect a pyrodiversity–biodiversity relationship in infrequent-fire systems in comparison with frequent-fire systems.

In general, our review revealed that little attention is paid to the problem of scale in the study of pyrodiversity–biodiversity

relationships, with some exceptions. For example, while studying avian communities in dry mixed-conifer forests of California, Tingley et al. (2016) explored whether support for the pyrodiversity–biodiversity relationship was scale-dependent (e.g. pyrodiversity measured at the plot level or fire level). In this case, the authors found support for this relationship at both spatial scales—although slightly stronger at the larger scale—and similar support for this relationship being time-dependent (and thus scale-dependent in the temporal sense). In general, we advocate for future research to explicitly consider a multi-scale perspective in which support for the pyrodiversity–biodiversity hypothesis is tested at multiple spatial and temporal scales when possible, avoiding assumptions about the correct scale of effect (McGarigal et al., 2016).

In addition to operating independently on apparent pyrodiversity–biodiversity relationships, these three factors are also likely to interact with one another in complex ways. Certain definitions of pyrodiversity may represent mechanisms that more naturally operate at certain spatial or temporal scales, whose relative importance could vary based on the ecological and evolutionary history of the system under study. For example, consider defining pyrodiversity as the spatial variability in burn severity (e.g. Steel et al., 2019). This definition—which provides a mechanism for how species accumulate and partition resources across space based on structural heterogeneity produced by fire—might be more relevant in systems where stronger spatial gradients in burn severity exist because of higher spatial variation in fuel conditions (e.g. fuel-limited dry forest ecosystems). Within-fire variation in burn severity inherently occurs at finer spatial scales than any among-fire measures of pyrodiversity, and therefore might be more relevant for smaller-bodied organisms because of scaling of effects with body size as discussed above. In summary, all three of these factors—mechanism, history and scale—should be considered together when designing and interpreting studies that examine the pyrodiversity–biodiversity hypothesis.

3 | MECHANISMS UNDERLYING A DIVERSE RESPONSE TO PYRODIVERSITY

The high degree of variability in studies testing diversity responses to pyrodiversity gives rise to numerous questions about the mechanisms underlying such a phenomenon and whether a pyrodiversity–biodiversity effect is real. At the same time, there is widespread evidence that environmental heterogeneity broadly drives variation in species richness (Stein et al., 2014) and that this is a consequence of heterogeneity in species' responses to environmental variation. This diversity in species' environmental affinities is the foundational mechanism proposed for why biodiversity should respond positively to pyrodiversity (He et al., 2019; Kelly & Brotons, 2017).

Although beyond the scope of our review, a large and growing literature demonstrates support for species-specific responses to the heterogeneity of habitats and conditions that exist following fire. This literature is much older than the newer phenomenon

of explicitly testing pyrodiversity–biodiversity (Figure 1) and has roots in the classic “habitat heterogeneity hypothesis” (Lack, 1969; MacArthur & Wilson, 1967; Simpson, 1949). Given how long this question has captivated ecologists, there now exists a wide variety of studies that convincingly demonstrate that species-specific responses to post-fire conditions exist, at least, in bats (Blakey, Webb, et al., 2019; Buchalski et al., 2013) and other mammals (Bliege Bird et al., 2018), birds (Hutto, 2008; Smucker et al., 2005), herptiles (Rochester et al., 2010; Russell et al., 1999), pollinators (Carbone et al., 2019) and plants (Pausas & Ribeiro, 2017). Moreover, this species-specific variation arises from how different species’ traits benefit or hinder establishment along the spectrum of post-fire environments (Blakey, Webb, et al., 2019; Pausas & Keeley, 2014; Pausas & Lavorel, 2003).

Given the preponderance of evidence that species broadly show heterogeneity in response to post-fire ecosystems and that pyrodiversity increases heterogeneity in post-fire landscapes, it is perhaps surprising that direct evidence for a pyrodiversity–biodiversity relationship is so limited and equivocal (Figure 2). In addition to the reasons discussed in the previous section, a challenge in interpreting empirical research to date is that fire is very difficult to experimentally reproduce, lending limited opportunities for mechanism testing. Until many more pyrodiversity–biodiversity studies can be replicated across landscapes, taxa and dimensions of fire variability, such phenomenological studies of species assemblages will likely remain inherently ambiguous in their overall conclusions. In addition, some species might successfully occupy landscapes across a gradient from low to high pyrodiversity but may vary greatly in their abundance across that same gradient. Therefore, there exists the possibility that studies based on presence/absence measures (i.e. species richness) could underestimate the effects of pyrodiversity on generating patterns in biodiversity.

But another approach to learning about the mechanisms underlying pyrodiversity–biodiversity is to decompose the effect from an aggregate impact on biodiversity, to a component effect on individual species. We can thus ask does pyrodiversity benefit individual species? Alternatively, does pyrodiversity harm or inhibit individual species? Depending on the frequency with which species fall into one category or another, we can assemble a bottom-up picture of how pyrodiversity impacts communities. To this end, single-species studies on pyrodiversity impacts can contribute positively to our developing understanding of its effects on biodiversity.

One way to investigate whether there are species that benefit from—or, alternatively, are hindered by—pyrodiversity is to examine species that seemingly exist at opposite ends of the spectrum of affinity for disturbance. Put another way, we should pick a “fire-reliant” species that is attracted to recent patches of severely burned habitat and compare its relationship with pyrodiversity (in this case, spatial variation in burn severity) relative to a species that is known to be intolerant of disturbance, such as an “old-growth” forest indicator. To be clear, neither type of species is expected to respond positively to pyrodiversity: the old-growth species eschews large-scale disturbance of any kind, while the fire-reliant species benefits from

recent, severe fire, but not necessarily a diversity of fire characteristics. With no strong expectations of affinity for pyrodiversity from either species, any such discovery to the opposite would effectively change our perceptions of the range of mechanisms underlying a proposed pyrodiversity–biodiversity effect.

4 | CASE STUDY OF AN “OLD-GROWTH” SPECIES, THE SPOTTED OWL

We begin this thought experiment by highlighting recent research conducted on the spotted owl (*Strix occidentalis*), a flagship “old-growth” species of far western North America. We here focus specifically on the California spotted owl (*S. o. occidentalis*), and so, hereafter reference to the “spotted owl” refers to this subspecies. The spotted owl primarily occurs in mid-elevation mixed-conifer montane forest, and many studies and syntheses have demonstrated the species’ reliance on late-seral forests characterized by large trees and a relatively closed overstorey canopy (Jones et al., 2018; North et al., 2017; Tempel et al., 2016). Conservation strategies focused on spotted owls have therefore suggested delineating large blocks of undisturbed habitat to meet the needs of the species (Verner et al., 1992). While “old-growth” conditions are considered important for supporting nesting, roosting and foraging activities, spotted owls are known to use a broader range of forest conditions for foraging (Blakey, Siegel, et al., 2019; Roberts, 2017). However, because nesting habitat is considered to be more limited in landscape availability, human and natural disturbances that significantly alter forest structure such as clear-cutting and large, severe fires have long been considered a threat to owl habitat and long-term population persistence (Peery et al., 2017; Verner et al., 1992).

Recent research has indeed shown that large, severe fires are detrimental to spotted owls and their habitat (e.g. Jones et al., 2016), but has also uncovered significant nuance in how spotted owls respond to a range of post-fire conditions and has shed light on potential mechanisms that may underlie owls’ response to pyrodiversity. Within fires, spotted owls continue to occupy and reproduce in territories that have experienced relatively high pyrodiversity—as characterized by a mixture of unburned, and low- and moderate-severity fire, with smaller patches of high-severity fire (Jones et al., 2016; Schofield et al., 2020). Over the short term, spotted owls may even continue to occupy and nest in territories that burned extensively at high-severity as long as there is sufficient residual late-seral habitat (e.g. in riparian areas) (Lee & Bond, 2015), but it is unclear how persistent these apparent neutral effects may be. Demographic analysis has suggested that although some spotted owls may continue to occupy territories that have experienced extensive severe fire, these territories show lower survival and increased recruitment rates suggesting that occupied territories within severe fire represent population “sinks” (Rockweit et al., 2017).

Studies of the movement and foraging ecology of owls that persist in burned landscapes have perhaps revealed the most about how pyrodiversity may shape spotted owl habitat. It has long been

known that spotted owls will forage in forest habitat that has experienced different burn severities and may even prefer foraging in severely burned forest (Bond et al., 2009). Two recent papers (Jones et al., 2020; Kramer et al., 2021) together suggest that a complex interplay between forest heterogeneity, pyrodiversity, and severe fire patch size may better explain how and why spotted owls use burned landscapes the way that they do. Owl use of severely burned forest appears to be mediated by severe fire patch size. In general, spotted owls select smaller patches of severely burned forest for foraging activities, avoid larger patches (Jones et al., 2020; Kramer et al., 2021) and tend to stay within 100m of “green” forest when foraging in severely burned areas (Jones et al., 2020). Both Jones et al., (2020) and Kramer et al., (2021) tested whether owls selected or avoided areas with higher pyrodiversity (in this case, defined as the Shannon diversity of burn severity classes), and the two studies reached opposite conclusions. Jones et al. (2020) provided some evidence that owls *selected* more pyrodiverse areas for foraging, while Kramer et al., (2021) suggested they *avoid* more pyrodiverse areas.

This apparent contrasting result makes more sense when overlaid on the two study landscapes: Jones et al. (2020) found that owls used more pyrodiverse areas within the context of a broadly homogeneous, fire-suppressed landscape (i.e. U.S. National Forests, a mixed-use landscape); Kramer et al., (2021) found owls avoided more pyrodiverse areas within the context of an already structurally heterogeneous landscape with a long history of managed and prescribed fire use (i.e. U.S. National Parks, a preservation-based landscape). Thus, the relative importance of pyrodiversity in creating owl foraging habitat may depend on the existing degree of surrounding landscape heterogeneity in forest structure. It is clear that spotted owls use more heterogeneous landscapes for foraging activities (Atuo et al., 2019), and in some cases (e.g. in homogeneous fire-suppressed forests), pyrodiversity may introduce some of that important variability to the benefit of spotted owls. Moreover, this observation suggests that in single-species studies, the effect of pyrodiversity on behaviour or vital rates may be related to pyrodiversity creating some minimum, or threshold level of structural diversity in otherwise homogeneous landscapes that provides required resources for the species. Thus, the effects of pyrodiversity on the ecology of single species could be highly nonlinear.

As for the driver of this pyrodiversity relationship, there is some evidence that cross-trophic interactions are the mechanism underlying spotted owls' preference for the structural heterogeneity that can be introduced through pyrodiversity. In the Sierra Nevada of California, spotted owl territories are less likely to go extinct when owls occupying those territories consume more woodrats and fewer flying squirrels (Hobart et al., 2019). Woodrats tend to be associated with open, early-seral forest, while flying squirrels tend to be associated with late-seral, closed-canopy forest (Roberts et al., 2015). Therefore, in fire-suppressed forests, pyrodiverse areas characterized by smaller patches of severely burned forest may introduce forest conditions that either recruit woodrats or increase local densities of flying squirrels (Sollmann et al., 2016), and both outcomes could improve spotted owl hunting efficiency (Hobart et al., 2021).

Pyrodiverse areas may also give owls access to “open” forest patches for hunting while maintaining concealment in surrounding green forest from predators such as great horned owls (Gutiérrez et al., 1995; Johnson, 1992).

5 | CASE STUDY OF A “FIRE-RELIANT” SPECIES, THE BLACK-BACKED WOODPECKER

As a counterexample to the spotted owl, we highlight the black-backed woodpecker (*Picoides arcticus*), a species that is emblematic of burned forests in western North America. The black-backed woodpecker occurs broadly across North America, from its southernmost range in the Sierra Nevada of California, eastward across the boreal belt to Québec and the Adirondack and White Mountains of New England and the Maritimes. Everywhere, it is associated with dense pockets of disturbed conifer trees, particularly those killed by fire (Tremblay et al., 2016). The black-backed woodpecker is frequently described as the most fire-associated species of bird in North America, possibly the world (Hutto, 2008). It is also closely associated with recent fires, often colonizing forests within the first year since burning, and declining in density 4–5 years after fire (Tingley et al., 2020). The reason for its strong post-fire affinity derives from its natural history. Black-backed woodpeckers excavate their nests preferentially in recently killed, undecayed snags (i.e. standing dead trees: Saab et al., 2009; Seavy et al., 2012). Foraging also occurs nearly exclusively on dead or dying trees, from which beetle larvae—particularly that of woodboring beetles (e.g. Cerambycidae)—are extracted. As the woodboring beetles primarily lay their eggs in the undecayed wood of recently killed trees (Powell, 2000), the primary food source, and thus the woodpecker itself, is tightly constrained to recent post-fire areas.

The literature surrounding black-backed woodpeckers' post-fire affinity describes a species that should greatly benefit from large, extensive areas of forest burned at high severity (Hutto, 2008). Nest sites are preferentially located in the highest density stands of small- to medium-sized conifer snags (Saab & Dudley, 1998; Seavy et al., 2012). Of North American woodpeckers found in the east, black-backed woodpeckers are considered the most specialized for foraging on dead wood (Nappi et al., 2015), and home range size (as a proxy for resource availability) scales inversely with the density of fire-killed snags within a home range (Tingley et al., 2014). Broadly, black-backed woodpeckers are more likely to be found closer to high-severity burned patches with high snag densities and farther from the fire perimeter (Saracco et al., 2011; Tingley et al., 2020; White et al., 2019).

Yet, new research is highlighting the potentially critical role that pyrodiversity—specifically, spatial heterogeneity in burn severity—plays in structuring the habitat use and selection of black-backed woodpeckers. A critical first observation has come from studies following recent “megafires” in California, where exceptionally large forested areas burned quickly over a matter of days, leaving large

expanses of high-severity burned forest (e.g. Coen et al., 2018). Such fires were expected to be ideal breeding grounds for black-backed woodpeckers, yet surveys found surprisingly few individuals (White et al., 2019) and models overpredicted observed abundances (Tingley, Wilkerson, et al., 2016). Tracking studies have helped clarify the reasons behind this discrepancy. In one study following black-backed woodpeckers in six fires of northern California, adult woodpeckers chose to forage in areas of medium and high burn severity, but that were proximal to low-severity or unburned forest (Stillman et al., 2019). Similarly, in the choice of nest location, black-backed woodpeckers were very unlikely to choose to build a nest in a tree that was >500 m from the closest patch of live forest (Stillman, Siegel, Wilkerson, Johnson, Howell, et al., 2019). In both cases— foraging and nest site placement—adult black-backed woodpeckers selected areas with higher heterogeneity in burn severity (i.e. greater pyrodiversity; Stillman, Siegel, Wilkerson, Johnson, Howell, et al., 2019; Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019).

The mechanism underlying this surprising pyrodiversity affinity in black-backed woodpeckers appears to be predation risk of juveniles. Tracking observations revealed that juveniles—particularly recent fledglings—equally prefer live trees to snags and spend significantly more time in low-severity and unburned forest than adults (Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019). As juvenile black-backed woodpeckers are often dependent on parents for provisioning for approximately 35 days after fledging, juveniles and adults concentrated in edge areas where live forest abutted high-severity patches with large concentrations of snags (Stillman, Siegel, Wilkerson, Johnson, & Tingley, 2019). The dangers to juvenile black-backed woodpeckers of entering the high-severity burned areas were significant—survival of that 35-day window is only 13% for fledglings in a high-severity patch, but rises to 53% for fledglings in unburned to medium-severity patches (Stillman et al., 2021). Juvenile mortality was primarily due to predation by raptors—hunters that find prey primarily through visual cues. As a result, an age-specific trade-off between predation and starvation (Houston et al., 1993) may drive a species-level habitat affinity for areas with greater pyrodiversity.

6 | SYNTHESIS AND RESEARCH GAPS

The extent to which the pyrodiversity–biodiversity hypothesis is supported depends on a variety of factors, indicating a highly context-specific phenomenon. The strength of the pyrodiversity–biodiversity relationship has been shown to vary by taxa, spatial scale, temporal scale, geographic region and biome (Figure 2). Critically, the strength of the relationship also varies by how pyrodiversity itself has been measured and defined, which widely varies in the literature. Despite more than 40 published examples to date that explicitly test the pyrodiversity–biodiversity hypothesis (Figure 2), the extreme heterogeneity in design, approach, and scale of these studies complicates evidence synthesis. Plainly, we still know far too little about how pyrodiversity impacts biodiversity in most systems in most parts of the world.

Yet, the spotted owl and black-backed woodpecker case studies present an intriguing, alternative path to gaining ecological understanding of pyrodiversity. Here are two iconic species co-occurring in western North American conifer forests that have long been seen to occupy distinct and largely non-overlapping habitats within the same landscape. As scientists dig deeper into how heterogeneity in fire impacts these two species, we learn that the “old-growth specialist” owl can benefit from diverse post-fire landscapes, while the “fire-reliant” woodpecker selects for burned forest patches that are close to living, green forest. The mechanisms underlying these two single-species pyrodiversity–biodiversity relationships seem convergent: severe fire brings a boon of resources (nesting for the woodpecker, food for both the owl and woodpecker), but severe fire also brings danger (predation risk for the woodpecker and possibly the owl, and loss of limiting nesting habitat for the owl). Consequently, a pyrodiverse forest presents sufficient areas with elevated resources that are also adjacent to locations for protection and cover. Pyrodiversity, thus, stands to facilitate the creation of patch diversity that satisfies predictions from predation foraging risk optimization theory (Brown, 1999; Brown et al., 1999).

The amalgam of mixed global support for pyrodiversity–biodiversity relationships, combined with emerging mechanism-based support within individual species, assists in clarifying the existing gaps in our composite understanding of the pyrodiversity–biodiversity hypothesis. To best move forward in testing this hypothesis, we present the following six key research gaps:

1. *Stronger development of the different potential mechanisms underlying the pyrodiversity–biodiversity relationship.* Mechanistic understanding, to date, has been weak to non-existent and was vague in the original conceptualization. Evidence suggests that multiple, non-exclusive mechanisms may impact pyrodiversity–biodiversity relationships (e.g. Kelly et al., 2017), and a stronger inferential approach in the future will result in specific studies designed to test for particular mechanisms within the composite framework.
2. *Testing for sensitivity to different pyrodiversity metrics and scale dependence.* Examining whether the pyrodiversity–biodiversity relationship is sensitive to different approaches for quantifying pyrodiversity (Appendix 1) could illuminate underlying mechanisms and help explain why some studies do not find support to the relationship. Moreover, the pyrodiversity–biodiversity relationship is likely to be scale-dependent, but general rules for such scale dependence are unknown.
3. *Standardization of metrics for pyrodiversity.* Pyrodiversity has been measured in many different ways, even when describing diversity within a single axis of fire regimes (e.g. variation in burn severity). A strong mechanism-based foundation and further empirical research (examining the relative importance of different pyrodiversity metrics; see #2 above) will help provide a foundation for the superiority of certain metrics over others, while still recognizing that definitions may require adjustments based on data availability or study objectives. Broad adoption of particular metrics

among researchers (and testing of multiple independent metrics) could aid future synthesis and meta-analysis.

4. *Bridging from species to communities.* Biodiversity responses to pyrodiversity have been measured broadly at the aggregate level—for example tallies of species richness—yet biodiversity is composed of many species, each with their own traits and preferences. With evidence that individual species may benefit from pyrodiversity, it is important to know how widespread this phenomenon is, and whether other species (and how many) show opposite responses. Analysis of functional traits and phylogeny may help build generalizable predictions of pyrodiversity–biodiversity strength that can be translated into less data-rich systems.
5. *Broad-scale spatial and temporal mapping of pyrodiversity.* Pyrodiversity has been assumed to have decreased because of human landscape modification and fire suppression (Martin & Sapsis, 1992). However, little empirical work has explored how pyrodiversity has changed through time across global ecosystems. Quantifying pyrodiversity across large (regional, global) spatial extents (e.g. Hempson et al., 2018; Steel et al., 2021), spatial scaling of pyrodiversity, and evaluating consistency of these patterns using different definitions of pyrodiversity will go a long way in understanding its fundamental ecological role across ecosystems.
6. *Macroecological studies of pyrodiversity–biodiversity relationships.* Most studies of pyrodiversity–biodiversity relationships have focused on study areas with a relatively small spatial extent. Large-scale mapping of pyrodiversity (see #5 above) will facilitate linking measures of pyrodiversity to regional, continental, or global biodiversity datasets that could facilitate a valuable macroecological perspective of pyrodiversity–biodiversity relationships.

Research that focuses on the above needs will improve our understanding of pyrodiversity and the pyrodiversity–biodiversity hypothesis. In an era of unprecedented changes to fire regimes because of climate change and past land use, a better understanding of pyrodiversity–biodiversity relationships across global ecosystems could improve forecasts of biodiversity change and bolster conservation and fire management planning. In some systems and at certain scales, a pyrodiversity paradigm may help maintain biodiversity, promote conservation of focal species with different life histories and permit flexibility and creativity in the implementation of fire management. However, the current literature does not illuminate those relevant systems and scales. Additional research and syntheses are urgently needed in this era of megafires.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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BIOSKETCHES

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APPENDIX 1

Summary of studies that examined the pyrodiversity–biodiversity hypothesis (PBH). Each row corresponds to a study–taxa combination because some studies examined support for the hypothesis across multiple taxonomic groups.

Reference	Support inferred for PBH	Direct test or indirect inference	How “pyrodiversity” was defined or conceptualized	Variation within or among sampling units	Continent	Ecosystem	Taxa
Masters (1996)	Yes	Indirect	“Fire mosaic”; variation in time since fire	Among	Australia	Grasslands	Reptiles
Stuart-Smith et al. (2002)	Yes	Direct	“Patchy mosaic”; implicit structural heterogeneity within burned plots	Within ^a	North America	Forest/woodland	Birds
Brotons et al. (2005)	Yes	Direct	Variation in habitat type composition and configuration created by fire	Within	Europe	Forest/woodland	Birds
Cook and Holt (2006)	No	Direct	“Mosaic burning”; vegetation heterogeneity	Within	North America	Grasslands	Beetles
Pastro et al. (2011)	No	Direct	Mixture of successional stages; implicit structural heterogeneity within prescribed burn plots	Within ^a	Australia	Grasslands	Plants
Pastro et al. (2011)	No	Direct	Same as above	Within ^a	Australia	Grasslands	Reptiles
Pastro et al. (2011)	No	Direct	Same as above	Within ^a	Australia	Grasslands	Mammals
Andersen and Hoffmann (2011)	No	Direct	Implicit successional heterogeneity present in frequent-fire versus long-unburned areas	Within ^a	Australia	Savanna	Ants
Langlands et al. (2012)	Yes	Indirect	Variation in post-fire ages, scale or intensity of fire	Among	Australia	Grasslands	Spiders
Davies et al. (2012)	No	Indirect	Variation in seasonality and frequency of fire	Among	Africa	Savanna	Termites
Kelly et al. (2012)	No	Direct	Shannon diversity of fire age classes	Within	Australia	Scrubland	Mammals
Taylor et al. (2012)	No	Direct	Shannon diversity index of fire age classes within sampling units	Within	Australia	Scrubland	Birds
Nimmo et al. (2013)	No	Direct	Shannon diversity index of the proportional cover of three fire age classes	Within	Australia	Scrubland	Reptiles
Maravalhas and Vasconcelos (2014)	Yes	Indirect	Variation in fire frequency and timing	Among	South America	Savanna	Ants
Andersen et al. (2014)	No	Indirect	Variation in fire frequency and seasonality	Among	Australia	Savanna	Ants
Farnsworth et al. (2014)	No	Direct	Shannon diversity index of fire age classes	Within	Australia	Scrubland	Reptiles
Sitters et al. (2014)	Yes	Direct	Variation in age class diversity and configuration	Within	Australia	Forest/woodland	Birds
Avitabile et al. (2015)	No	Direct	Shannon diversity index of fire age classes	Within	Australia	Scrubland	Termites
Cohn et al. (2015)	Yes	Direct	Number of fire age classes in a sampling unit	Within	Australia	Forest/woodlands	Plants
Radford et al. (2015)	No	Direct	Number of fire age classes in a sampling unit	Within	Australia	Savanna	Mammals
Kelly et al. (2015)	No	Indirect	Variation in time since fire; optimization of a mixture of successional stages	Among	Australia	Scrubland	Birds
Kelly et al. (2015)	No	Indirect	Same as above	Among	Australia	Scrubland	Reptiles

APPENDIX 1 (Continued)

Reference	Support inferred for PBH	Direct test or indirect inference	How "pyrodiversity" was defined or conceptualized	Variation within or among sampling units	Continent	Ecosystem	Taxa
Kelly et al. (2015)	No	Indirect	Same as above	Among	Australia	Scrubland	Mammals
Lawes et al. (2015)	No	Direct	"Patchiness"; average distance to unburned area over the sampling unit	Within	Australia	Savanna	Mammals
Burgess and Maron (2016)	No	Direct	Simpson diversity index of fire-mediated patch types	Within	Australia	Forest/woodlands	Birds
Tingley et al., (2016)	Yes	Direct	Standard deviation of continuous burn severity (per cent canopy mortality) in a sampling unit	Within	North America	Forest/woodlands	Birds
Ponísio et al. (2016)	Yes	Direct	Simpson's diversity of unique fire history classes	Within	North America	Forest/woodlands	Bees
Ponísio et al. (2016)	Yes	Direct	Same as above	Within	North America	Forest/woodlands	Flowering plants
Ponísio et al. (2016)	Yes	Direct	Same as above	Within	North America	Forest/woodlands	Plant:pollinator inxn
Prowse et al. (2017)	No	Indirect	Variation in time since fire	Among	Australia	Forest/woodlands	Birds
Brown and York (2017)	Yes	Direct	Variation in post-fire age classes and number of fires	Within	Australia	Forest/woodlands	Flies
Brown and York (2017)	Yes	Direct	Same as above	Within	Australia	Forest/woodlands	Wasps
Taillie et al. (2018)	Yes	Indirect	Variation in burn severity, time since fire and their interaction	Among	North America	Forest/woodlands	Birds
McGranahan et al. (2018)	Yes	Direct	Variation in number of patches in a sampling unit, fire return interval and burn season	Within	North America	Grasslands	Prairie plants
Davies et al. (2018)	No	Indirect	Variation in fire frequency	Among	Australia	Savanna	Mammals
Davis et al. (2018)	No	Direct	Shannon diversity index of fire age classes within sampling unit	Within	Australia	Scrubland	Termites
Beale et al. (2018)	Yes	Direct	Volume of the minimum convex hull of the four-dimensional space described by all the fires within a sampling unit	Within	Africa	Savanna	Birds
Beale et al. (2018)	Yes	Direct	Same as above	Within	Africa	Savanna	Mammals
Bliege Bird et al. (2018)	Yes	Indirect	Shannon diversity of successional stages within sampling units	Within	Australia	Scrubland	Mammals (and one species of Reptile)
Steel et al. (2019)	Yes	Direct	Heterogeneity in burn severity within a sampling unit, corrected for mean severity	Within	North America	Forest/woodlands	Bats
Docherty et al. (2020)	Yes	Direct	Multiple measures including Shannon diversity in age class, shape complexity, edge contrast index and fire frequency	Within	Africa	Savanna	Birds
Wills et al. (2020)	No	Direct	Variation in fire age class/vegetation succession	Within	Australia	Forest/woodlands	Birds

^a Study inferred pyrodiversity effects from assumed (unmeasured) heterogeneity within sampling units experiencing certain fire regimes.

Accelerated forest restoration may benefit spotted owls through landscape complementation

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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

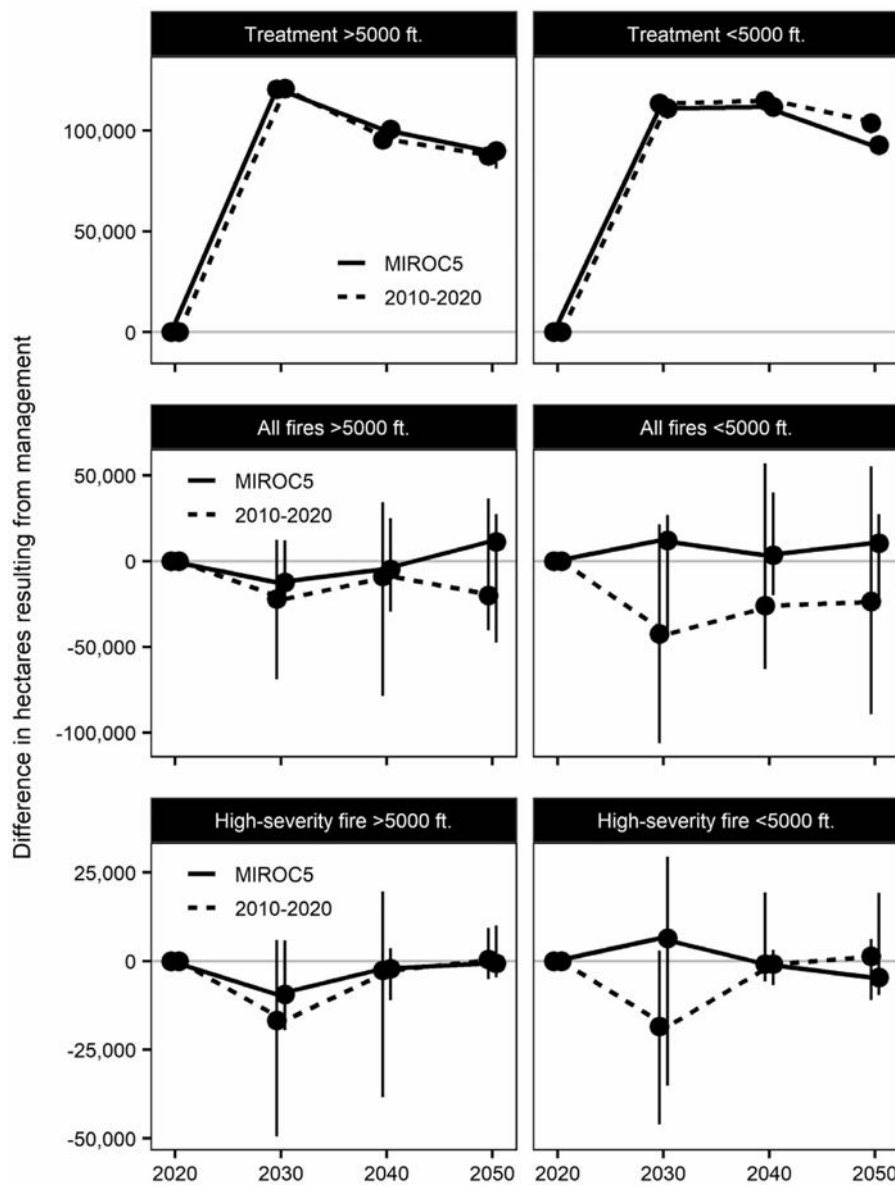


Figure 2 Predictions of future treatments (top row), fire area (middle row) and high-severity fire area (bottom row) relative to the minimal management scenario (gray horizontal line). Lines represent the difference between accelerated management and minimal management scenarios. Vertical error bars indicate the 80% prediction interval based on 10 LANDIS-II replicates, and circles represent the median value across replicates.

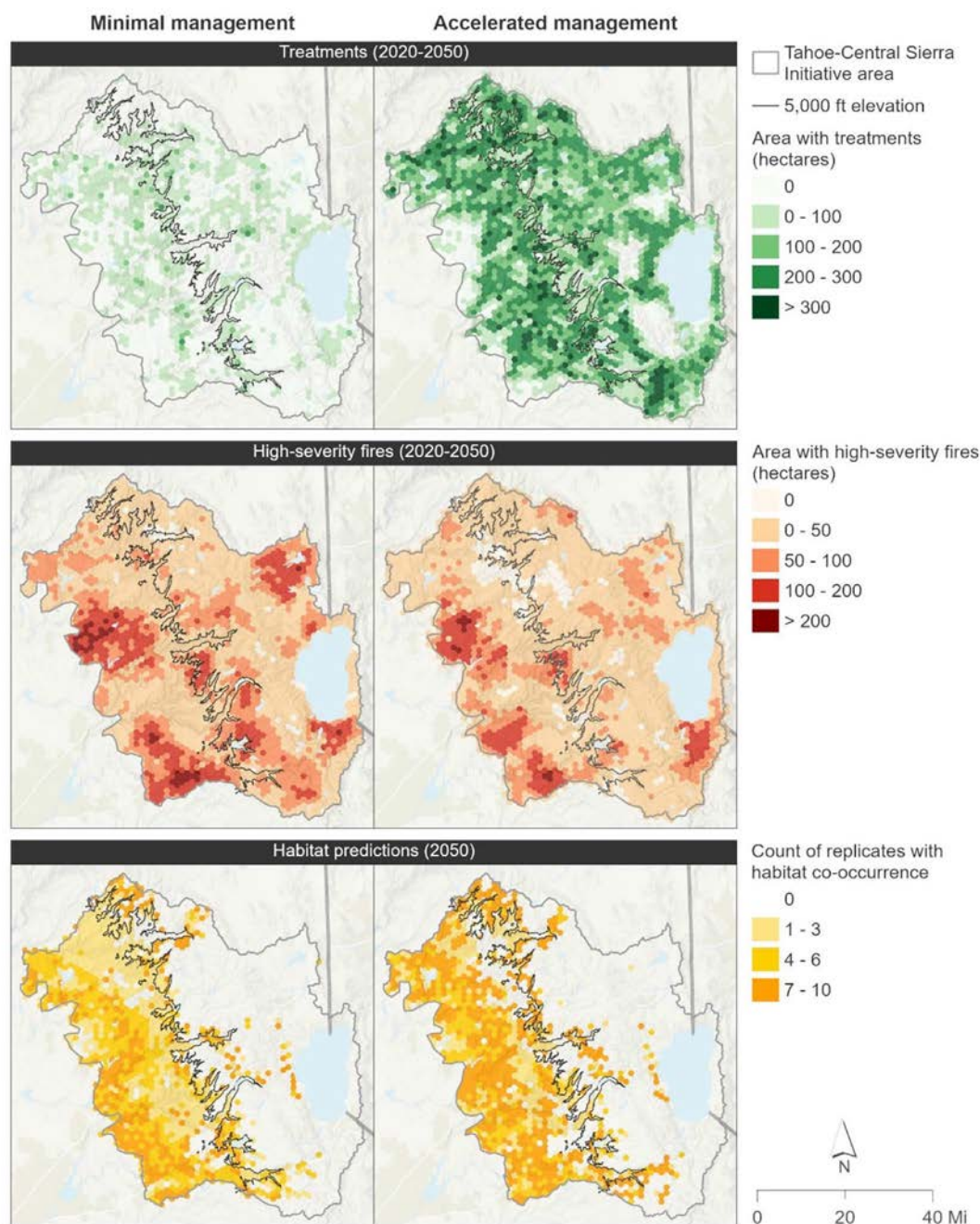


Figure 3 Spatial predictions of treatments (top row), high-severity fire extent (middle row) and landscape complementarity (bottom row) over our simulation period 2020–2050 under the minimal management scenario (left column) and the accelerated management scenario (right column). In the first and second 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

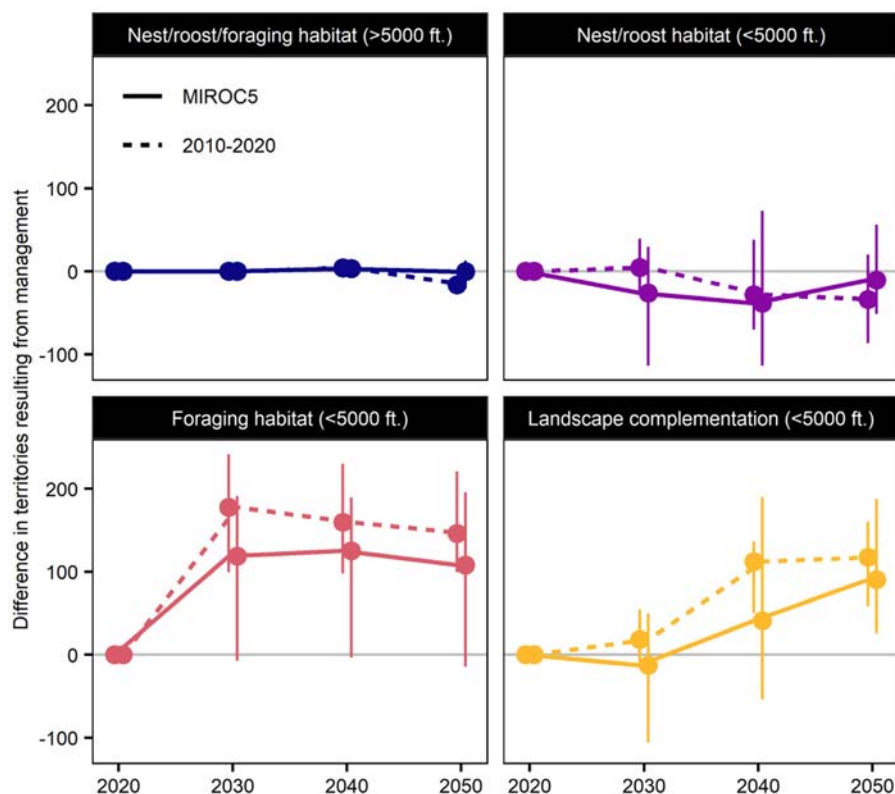


Figure 4 Predictions of spotted owl nest/roost habitat at high (upper left) and low (upper right) elevations; predictions of woodrat habitat at lower elevations (lower left); and predictions of the co-occurrence of nest/roost habitat and woodrat habitat at lower elevations (lower right) on the TCSI landscape. 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

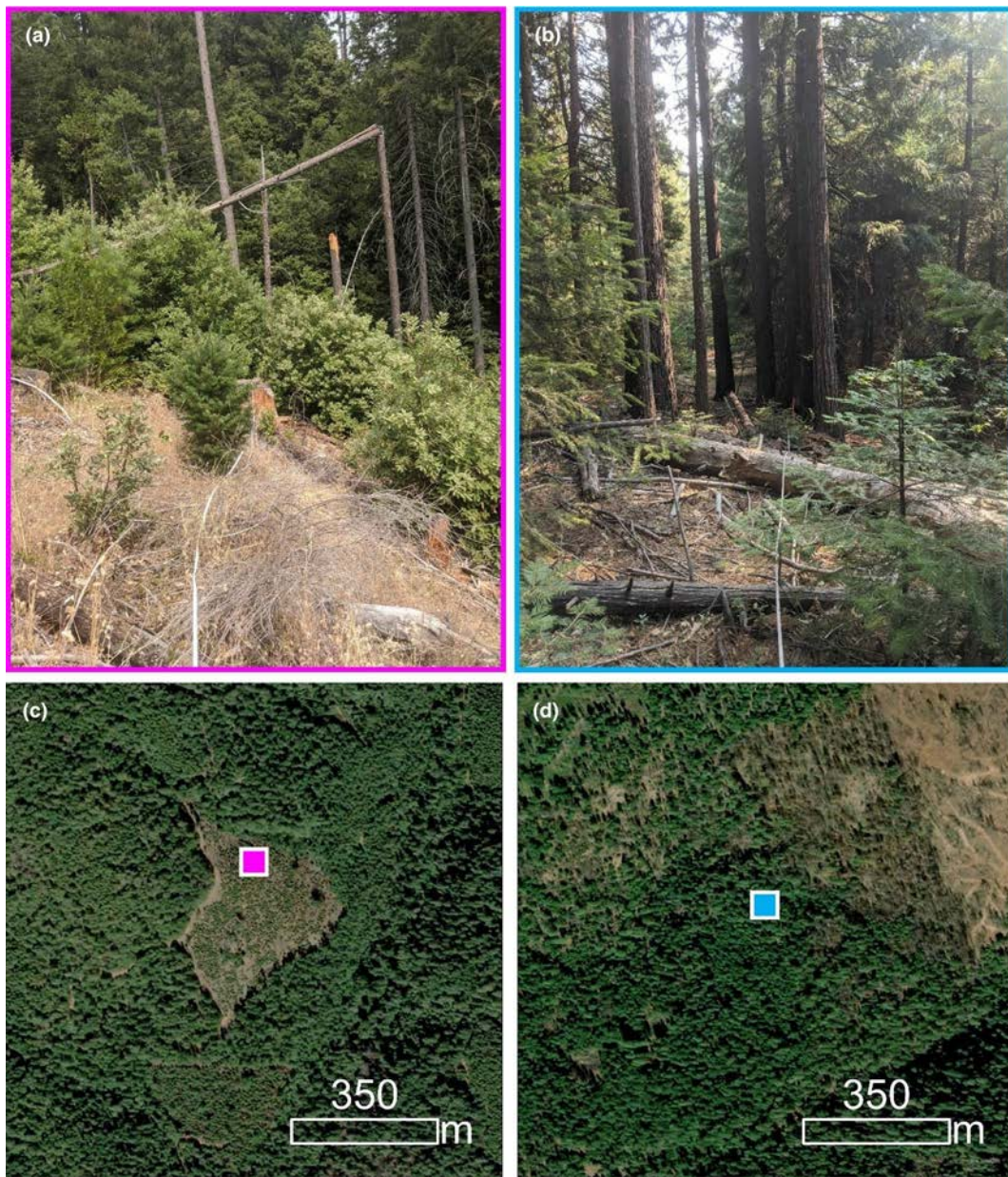


Figure 5 Examples of landscape complementation at an (a) intermediate patch scale and (b) micro-site scale on the Eldorado National Forest, California. Both photos show the juxtaposition of open, early-seral or brushy conditions that tend to be associated with woodrat habitat in the foreground, and later-seral, 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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California spotted owl habitat selection in a fire-managed landscape suggests conservation benefit of restoring historical fire regimes

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ABSTRACT

Wildland fire is a disturbance that shapes frequent-fire forest ecosystems and the life-histories of wildlife species that inhabit them. The California spotted owl (*Strix occidentalis occidentalis*) is an iconic old-forest species that evolved under a frequent-fire regime in western North America. While recent studies have focused on owl response to large, severe fire events, relatively little is known about how owls might respond to prescribed fires and wildfires managed for resource benefit. Therefore, understanding how owls use landscapes that are managed using fire may offer insight into how owls respond to fire management. We studied the breeding season nocturnal foraging habitat selection of 22 GPS-tagged California spotted owls in three national parks (Yosemite, Sequoia, and Kings Canyon) in the Sierra Nevada, California, USA where natural fires have largely been allowed to burn during the past 50 years and controlled burning has been used to target additional areas. Consistent with other studies of this species, owls selected forests dominated by medium and large trees and avoided areas with smaller trees within their home ranges based on step selection analysis. Owls neither selected nor avoided forests burned by low- and moderate-severity, or high-severity fires, yet avoided larger patches of severely-burned forest (odds of selection decreased by 20% for every 10 ha increase in severely-burned patch area). These results indicated the importance of patch characteristics, suggesting that larger patches reflected either lower quality foraging habitat or increased predation risk, even in these frequent-fire landscapes where “large” severely-burned patches were small compared to those common after megafires. Additionally, selection strength increased for areas burned recently by lower-severity fire and, to a lesser extent, by older fires (largely of lower severity) as the extent of these burned areas increased within individual home ranges. These results suggested that lower-severity fire benefitted spotted owls and that these benefits declined over time. Thus, our findings are consistent with the hypothesis that California spotted owls are adapted to historical frequent-fire regimes of overall lower-severity with small high-severity patches. We hypothesize that fire management, coupled with medium- and large-tree retention, likely maintains high quality spotted owl habitat and may contribute to the observed owl population stability in Sequoia and Kings Canyon National Parks, compared to declining populations on three national forests. Finally, our results indicated that fire management, as practiced in these national parks, could benefit owl conservation elsewhere if challenges to the reintroduction of frequent-fire regimes can be overcome.

Abbreviations: HRV, historical range of variability; DOP, dilution of precision; FRAP, CAL FIRE's Fire and Resource Assessment Program; GNN, gradient nearest neighbor; GPS, global positioning system; SSF, step selection function; KDE, kernel density estimate; LEMMA Lab, Landscape Ecology, Modeling, Mapping, and Analysis Lab, Oregon State University; MTBS, Monitoring Trends in Burn Severity; VHF, very high frequency; VEGCLASS, vegetation class

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1. Introduction

Wildland fire, ignited both naturally and intentionally by humans, has shaped ecosystems and the ecology of species living in them for millions of years (Clark, 1989; Bond and Keeley, 2005; Shakesby and Doerr, 2006; Johnstone et al., 2016). Despite the importance of wildland fires as a natural process, they can impact natural resources (e.g., trees, water) and environments (e.g., rural and urban areas) to such an extent that people have attempted to suppress them for many years and across many systems (Moritz et al., 2014; Kramer et al., 2019; Wood and Jones, 2019). Consequently, fire suppression has led to unnaturally high densities of vegetation in some areas (Parsons and DeBenedetti, 1979; Sugihara et al., 2006; Collins et al., 2011, 2017a). This situation is particularly true of dry forests in the western United States, such as those in California's Sierra Nevada forest ecosystems, where unnatural increases in vegetation density, warming and drying associated with climate change, and increasing human populations in the wildland-urban interface have increased both the size and severity of wildland fires (Gill et al., 2013; Abatzoglou and Williams, 2016; Westerling, 2016; Schoennagel et al., 2017; Stevens et al., 2017). Although many "fuels management" techniques are available to land managers to reduce the risk of large, severe fires in natural landscapes, some techniques (e.g., tree thinning and fire use) have been controversial partly because of their potential negative effects on sensitive wildlife species (Hanson et al., 2009; Collins et al., 2010; Stephens et al., 2019; Kuchinke et al., 2020). Thus, understanding wildlife responses to thinning and fire use intended to reduce high-severity wildfires, as well as wildlife responses to those severe fires themselves, will inform management decisions.

Managing dry forests with fire is considered an effective and economical method of mimicking historical fire regimes to restore forest resilience and reduce the risk of future severe fire (Hardy and Arno, 1996; Sugihara et al., 2006; van Wagtenonk, 2007; North et al., 2015; Stephens et al., 2019; Hiers et al., 2020). Both prescribed fire and managed wildfire are methods of fire use: prescribed fire refers to fires that are planned, ignited, and managed from start to finish (Stephens and Moghaddas, 2005; Stephens and Ruth, 2005; North et al., 2007; Hiers et al., 2020) and managed wildfires are naturally ignited fires that are allowed to burn if they are deemed to pose little or no threat to humans or ecosystems (Christensen et al., 1987; Parsons and van Wagtenonk, 1996; Parsons and Landres, 1998; van Wagtenonk and Lutz, 2007). Despite the benefits of fire use, this technique is not always compatible with management objectives, which differ among private landowners, non-profit organizations, and public land management agencies (Young et al., 2020). As a result, different groups often use different approaches to reduce the risk of severe fire. For example, mechanical "treatments" (thinning or harvesting trees and/or manually thinning the understory) may be used instead of or in combination with fire in order to offset the cost of fuel reduction treatments, to increase precision of treatment outcomes (by choosing the spatial pattern or altering species composition), or to avoid the liability and smoke associated with burning (Stephens and Moghaddas, 2005). Wildland fire size, severity, and frequency, as well as its socio-ecological impact, also vary across the western United States because of variation in management approaches, local climate, and ecosystems (Parsons and Landres, 1998).

The U.S. National Park Service has pursued a policy of encouraging the use of fire since the 1960s to restore or maintain natural ecosystem processes across the large, often remote landscapes of national parks. In these settings, fire is a relatively cost-effective management tool. In Yosemite, as well as Sequoia and Kings Canyon (the latter two parks are under joint management and hereafter referred to as Sequoia-Kings Canyon), National Parks located in the Sierra Nevada, fire policy allows not only prescribed fire, but also managed wildfire (Christensen et al., 1987; Parsons and van Wagtenonk, 1996; Parsons and Landres, 1998; van Wagtenonk and Lutz, 2007). Thus, compared to other forest lands

in this region managed under different guiding objectives, this policy has resulted in some national park landscapes that more closely resemble historical conditions and processes: more frequent fires burning at low- to moderate-severity with fewer and smaller patches of high-severity fire (Collins and Stephens, 2007; Collins et al., 2008; Stevens et al., 2017; Kane et al., 2019).

Within the seasonal dry forests of the western United States, some management-sensitive species like the spotted owl (*Strix occidentalis*) use forest conditions typical of both historical and fire-suppressed forests for nesting, roosting, and foraging if they contain large trees and dense canopies with available prey (Bias and Gutiérrez, 1992; Call et al., 1992; Jones et al., 2018; Atuo et al., 2019; Blakey et al., 2019). However, spotted owls can be negatively impacted by both large high-severity fires (Jones et al., 2016, 2020; Rockweit et al., 2017) and fuel reduction treatments, at least in the short term, that are designed to reduce fire risk (Stephens et al., 2014a; Tempel et al., 2014; Gallagher et al., 2019). Therefore, it is essential to understand the impacts and tradeoffs of wildfire, prescribed fire, and mechanical fuels treatments on spotted owls and other sensitive species to facilitate their conservation in the short and long term. How best to manage habitat for spotted owls, given the potential threat of "megafires" (fires with an area of at least ~ 40,500 ha; Stephens et al., 2014b), is complicated by research suggesting opposite effects of severe fire on spotted owls. Whereas some studies have reported negative effects of high-severity fire on spotted owls (e.g. Jones et al., 2016, 2019, 2020; Eyes et al., 2017; Rockweit et al., 2017; Lommler, 2019), others have reported no negative effects of high-severity fire on this species (e.g. Lee and Bond, 2015; Bond et al., 2016). Thus, the resolution of these different findings will require studies of owl response to prescribed, managed, and wildland fire to answer the following questions: what types and configurations of high-severity fire negatively impact owls and their habitats, and what types and configurations might not convey these negative consequences? Given such information, how can prescribed fire, managed wildfire, or even other vegetation management techniques be used to mitigate potential threats without also harming owls (Jones, 2019; Peery et al., 2019; Jones et al., 2020)?

California spotted owls (*S. o. occidentalis*) have been studied intensively for many years throughout the dry forests of the Sierra Nevada in California and only one of four populations studied on public lands (located in Sequoia-Kings Canyon National Parks) has shown a stable population trend (Franklin et al., 2004; Blakesley et al., 2010; Tempel et al., 2016). Although it is not known why this owl population has been stable while the three others on national forests have declined, it has been hypothesized that the presence of higher densities of large trees, differing prey resources, and the restoration of fire to this system through prescribed and managed wildfire may be contributing factors (Franklin et al., 2004; Blakesley et al., 2010; Jones et al., 2018). Additionally, and perhaps because of these differences in burning between these landscapes, prey type consumed by owls also differs between national parks and national forests, with the diet of spotted owls in national parks consisting of a higher proportion of (high-calorie) woodrats and pocket gophers compared to national forests (Hobart et al., 2019a). Therefore, the forest conditions that are maintained through restorative fire management in Yosemite and Sequoia-Kings Canyon National Parks provide a unique opportunity to understand owl habitat selection when prescribed and managed fire are used extensively within their home ranges. Indeed, a recent study in Yosemite National Park revealed neutral owl selection of recently burned territories when < 30% of the core area had burned at high-severity, indicating compatibility between owl occupancy and lower-severity fire (Schofield et al., In press). One explicit goal of restorative fire management is to reduce high-severity fire that has the potential to kill larger trees that are key features of both old-growth forests and owl habitat (Jones et al., 2018). The benefits of restorative fire also include a reduction in the size of patches of forest that burn at high-severity (Collins et al., 2008; Kane et al., 2014). Hence, conserving larger trees

and reducing the size of high-severity fire patches are two outcomes of restorative fire management that we predict will benefit spotted owls.

It is against this background and existing knowledge gaps that we studied California spotted owls in forests where fire is regularly used as a management tool. We formulated our study based on the hypothesis that owls evolved in forests characterized by frequent-fire regimes, including a patchy burn pattern with small areas of high-severity fire (Safford and Stevens, 2017), and that they would respond in predictable ways to the occurrence of fire in their home ranges. We predicted that in fire-restored landscapes, where high-severity patch size and characteristics are likely to be more closely aligned with the historical range of variability (HRV), (1) owls would show neutral or positive overall response to high-severity fire and higher levels of pyrodiversity (a mix of different burn severities and unburned area in close proximity), (2) owls would show no selection for or against high-severity patch characteristics, such as patch size, and they would equally forage along edges and far into larger patches of high-severity fire, and (3) owls would show neutral or positive response to low- and moderate-severity fire. These predictions were based on the assumption that in this landscape, high-severity patches created by a frequent-fire regime would fall within the HRV and therefore not adversely affect owl populations. Nevertheless, we acknowledge that severe fire even within the HRV could render some areas unsuitable for foraging by individual owls without adversely impacting populations. In addition, we tested whether habitat selection changed as a function of habitat availability within the home range (i.e., functional response) (Holbrook et al., 2019; Matthiopoulos et al., 2011; Mysterud and Ims, 1998). Our intent in testing these predictions was to help answer critical questions about the potential effects of fire to inform spotted owl conservation efforts.

2. Methods

2.1. Study site

We studied California spotted owl nocturnal habitat selection during the breeding season within three national parks: Yosemite and Sequoia-Kings Canyon. All three parks are located in the southern Sierra Nevada, California, and have experienced 50 years of active fire management (Fig. 1). Although fire restoration is still relatively recent in national parks, and “restored” areas encompass only 0.3% of the Sierra Nevada, Jeronimo et al., (2019) found that nearly 80% of these areas “restored” to the HRV fell within Yosemite and Sequoia-Kings Canyon National Parks, covering 3.7% of the area within these parks. Our study area encompassed these three parks, which spanned approximately 652,000 ha from the foothills (~500 m elevation) to the crest of the Sierra Nevada (> 4000 m elevation). The climate was Mediterranean, with cool, wet winters and warm, dry summers. Vegetation varied by elevation with oak woodlands and chaparral predominant at lower elevations, grading to mixed-conifer forests at middle elevations, and subalpine forests at higher elevations (Mayer and Laudenslayer, 1988; Sugihara et al., 2006). Logging is prohibited in national parks, which has resulted in the preservation of large, old trees (Beesley, 1996). Fire suppression began in the region during the late 19th century and continued until the late 1960s when new fire policies for national parks allowed the use of fire as a restoration tool (van Wagtenonk, 1991, 2007; Sugihara et al., 2006). Beginning in 1968 in Sequoia-Kings Canyon National Parks, and 1972 in Yosemite National Park, both prescribed and managed fire were used to facilitate restoration of historical fire regimes and to increase forest resilience within the parks (van Wagtenonk, 1991; Parsons and Botti, 1996).

2.2. Owl space use data

We captured 27 owls (males and non-nesting females) in the breeding season of 2018 (April and May) either by hand, pan trap, or using snare poles (Bull, 1987; Franklin et al., 1996). We then fitted owls

with small (7–10 g) tail-mounted dual GPS/VHF (very high frequency) tags (Lotek Pinpoint VHF 120, Newmarket, Ontario, Canada; GPS/VHF tags hereafter as “GPS tags”) that allowed remote downloading of on-board data. We recaptured owls to remove GPS tags when possible and expected tail-mounted tags of owls that we did not recapture to be shed during the next tail molt. We used the VHF capabilities to relocate tagged owls for recapture and GPS data retrieval, but in our habitat selection analyses, we used only the GPS locations. Accordingly, we programmed GPS tags to collect five hourly GPS locations per night (2200 to 0200), which we assumed primarily represented foraging activities because owls are nocturnal predators. However, owls engage in territory defense, resting, and returns to the nest at night that may also be reflected in these GPS locations (Forsman et al., 1984; Delaney et al., 1999).

2.3. Fire history and severity

We compiled fire history from CAL FIRE’s Fire and Resource Assessment Program (FRAP) database, where we downloaded perimeters of all fires in our study area that were at least 10 acres in size (<http://frap.fire.ca.gov/>, accessed May 2, 2018). This dataset also included information on whether a fire was a wildfire or a prescribed fire. We compiled fire severity data using the Monitoring Trends in Burn Severity (MTBS) database and additional data maintained by each national park. MTBS severity data (<http://www.mtbs.gov/>, accessed February 14, 2018) accounted for all fires in our study area over 1,000 acres (405 ha) in size that burned between 1984 and 2017 (Eidenshink et al., 2007). However, for smaller fires (100–1,000 acres) including wildfires and prescribed burns, we used spatially explicit severity data provided by Yosemite (personal communication, K. van Wagtenonk; Lutz et al., 2011) and Sequoia-Kings Canyon (personal communication, K. Folger) National Parks that used the same methodology as MTBS. Although these additional datasets included fires that burned before 2003, many older wildfires in the smaller size class (100–1,000 acres) lacked data on severity. Therefore, we used 2003 as the oldest date to include fire severity in our analyses.

We used the FRAP database of fire perimeters to check that our fire severity dataset included all wildland fires that burned over 100 acres between 2003 and 2017, with at least 30 acres of that burned area within an owl’s home range. We defined home range as the 95% kernel density estimate (KDE) from all filtered nocturnal GPS locations (see Habitat Selection Analysis section below for filtering methods) for each individual owl. However, a significant amount of fire severity data was missing for two owls, so we removed them from analysis. Four of 21 prescribed fires were missing information on fire severity, yet we found that only 1% of the area of the 17 prescribed fires in our dataset burned at high-severity. Thus, we assumed that these four prescribed fires only burned at low- and moderate-severity and that all fires smaller than 100 acres (for which we did not have information on fire severity) also burned at low- and moderate-severity. For fires that burned < 30 acres (12 ha) of an owl’s home range (home ranges were 750–3,000 ha), we included severity information, where available, and assumed that the area burned at low- and moderate-severity in cases when this information was not available.

We classified each burn location as follows: (a) burned 41 to 65 years prior (1953–1977), (b) burned 16 to 40 years prior (1978–2002), (c) burned at low- and moderate-severity (up to 75% overstory mortality) up to 15 years prior (2003–2017), and (d) burned at high-severity (over 75% overstory mortality) up to 15 years prior (2003–2017; Table 1). We grouped low- and moderate-severity fire (henceforth “lower-severity”) because others have shown that owl selection was similar between these areas (Bond et al., 2002; Eyes et al., 2017). We also used the definition of high-severity commonly used in other papers on spotted owls and wildfire (Jones et al., 2016; Eyes et al., 2017; Hobart et al., 2020), although we note that other thresholds for high-severity wildfire have been used (Bond et al., 2002;

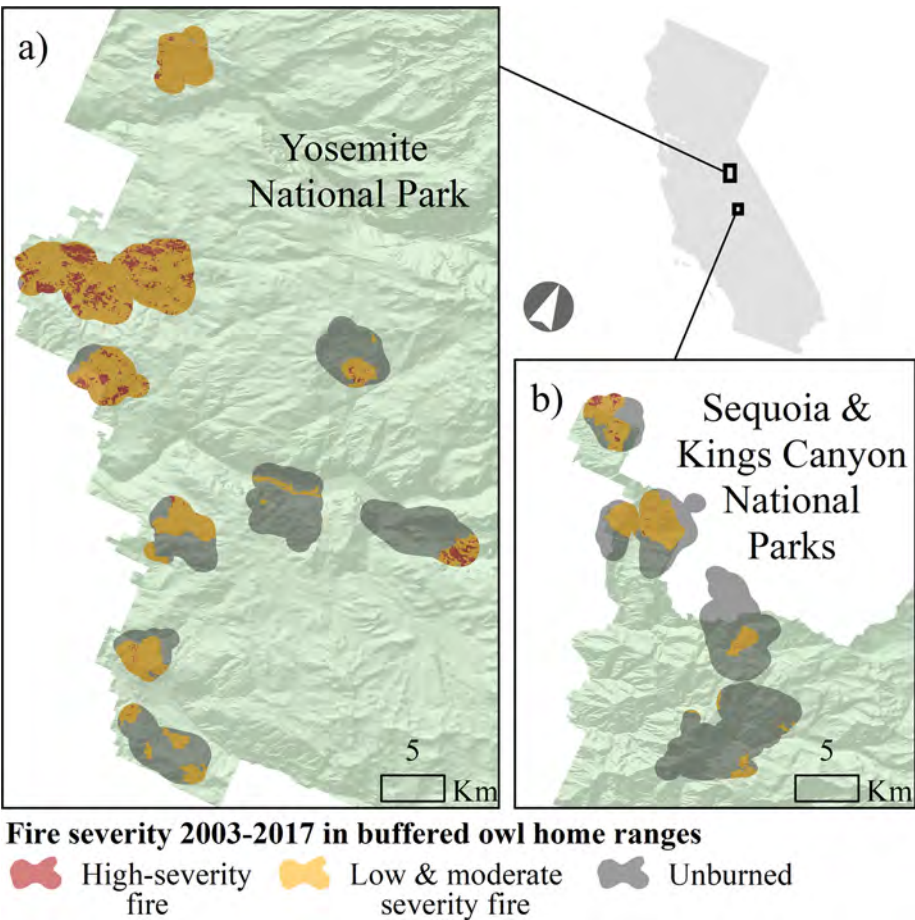


Fig. 1. Map of our California spotted owl study area in the Sierra Nevada, California, showing fire severity within buffered owl home ranges in (a) Yosemite National Park ($n = 13$ owls), and (b) Sequoia & Kings Canyon ($n = 9$ owls) National Parks. Home ranges represent the 95% kernel density estimate of all owl nocturnal GPS locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Lydersen et al., 2016; Collins et al., 2017b). If an area burned more than once between 2003 and 2017 (0.6% of assessment points in our analysis), we used the highest burn severity for that location for the classification because we expected high-severity fire to represent the predominant fire effects at that location. However, areas that burned in older fires were noted separately, such that an area could be coded as having burned during as many as three time periods, corresponding to the three time periods described above (e.g. an area that burned in 1967 and 1976, but not more recently would be coded as Burned₁₉₅₃₋

1977 = 1, Burned₁₉₇₈₋₂₀₀₂ = 0, Lower-severity = 0, and High-severity = 0; Table 1).

Spotted owl foraging patterns have been shown to be correlated with the spatial characteristics of high-severity patches (Jones et al., 2020). Thus, we calculated the size of each high-severity fire patch, the “permeation distance” of each point (the distance from the point to the patch edge, conditional on the point occurring within a high-severity patch), and the patch complexity (perimeter-area ratio of the patch; Table 1). We also computed a pyrodiversity index using data from fires

Table 1
Covariates used to model California spotted owl habitat selection in Sequoia, Kings Canyon, and Yosemite National Parks California, including the variable description, class, type, and values. Continuous variables were scaled so that values fell between 0 and 1. The class of each variable links it to the three stages of analyses, where stage I corresponds to landscape and disturbance covariates tested in a step selection function (SSF), stage II uses only high-severity patch covariates in an SSF, and stage III utilizes disturbance and patch covariates to test for functional response. Acronyms used in the table include digital elevation model (DEM), gradient nearest neighbor vegetation estimates (GNN), quadratic mean diameter (QMD), and monitoring trends in burn severity (MTBS).

Variable	Description	Class	Type	Range of values
Elevation	Elevation (m) based on a DEM	Landscape	Continuous	1000–2800
Medium-large trees	Proportion of area where dominant trees have medium and large diameters (as determined by 2016 GNN; QMD ≥ 25 cm) within 100 m radius (0–100%)	Landscape	Continuous	0–1
Small trees	Proportion of area where dominant trees have small diameters (as determined by 2016 GNN; QMD < 25 cm) within 100 m radius (0–100%)	Landscape	Continuous	0–1
Lower-severity	The point burned at low- and moderate-severity in 2003–2017	Disturbance	Categorical	0 or 1
High-severity	The point burned at high-severity in 2003–2017	Disturbance	Categorical	0 or 1
Burned _{1978–2002}	The point burned from 1978 to 2002	Disturbance	Categorical	0 or 1
Burned _{1953–1977}	The point burned from 1953 to 1977	Disturbance	Categorical	0 or 1
Pyrodiversity	Shannon diversity of 3-class (unburned; low/mod -severity; high-severity) MTBS classification within 100 m buffer for fires in 2003–2017	Disturbance	Continuous	0–1.09
Patch area	Area (ha) of severe fire patch ¹ that point falls in for fires in 2003–2017	Patch	Continuous	0–225
Patch complexity	Perimeter-to-area ratio of the severe fire patch ¹ that a point falls in for fires in 2003–2017	Patch	Continuous	0–0.133
Permeation distance	Distance (m) from point within severe fire patch to edge for fires in 2003–2017	Patch	Continuous	0–265

¹ High-severity patches were smoothed to remove patches under 4 pixels (0.36 ha)

that burned between 2003 and 2017, where we calculated the Shannon diversity of unburned, lower-severity, and high-severity fire within a 100-m radius of each point (Table 1). Thus, an area composed entirely of a single class (unburned, lower-severity, or high-severity) would yield a pyrodiversity index equal to 0, whereas an area composed of multiple classes would yield a pyrodiversity index > 0 .

2.4. Environmental variables

We determined the elevation at each point, which is related to spotted owl habitat preferences (Kramer et al., in revision). We also used Gradient Nearest Neighbor (GNN) maps of forest structure to classify the 2016 landscape into vegetation classes as follows: (i) forests where dominant trees were small in diameter (henceforth small trees), where canopy cover was at least 40% and the quadratic mean diameter of dominant trees was under 25 cm, (ii) forests where dominant trees were medium and large in diameter (henceforth medium-large trees), where canopy cover was at least 40% and the quadratic mean diameter of dominant trees was at least 25 cm, and (iii) open areas where canopy cover was under 40% (LEMMA Lab, Oregon State University, Corvallis, OR; using their VEGCLASS variable; Ohmann and Gregory, 2002). Note that we combined medium and large tree categories, given uncertainties in the accuracy of the GNN-based vegetation cover type classifications at fine scales. While there were two years between GNN habitat classification and bird tagging, there were minimal changes in forest structure to owl home ranges in our study area besides a few small fires (all under 10 acres between 2016 and when owl GPS data was collected in 2018), so we assumed these habitat classifications provided an acceptable representation of general forest structure.

2.5. Three stages of analysis

We used a three-part analysis to explore the effects of fire on spotted owl foraging habitat selection. In stage I of our analyses, we modeled selection relative to landscape and fire-related disturbance variables (Table 1) to examine how this broad range of environmental covariates shaped selection. In stage II of our analyses, we examined whether covariates related to the spatial characteristics of severely-burned areas could further explain patterns of selection related to the simple categorical severe fire effect from stage I. Therefore, we tested whether the spatial pattern and configuration of high-severity patches (area, complexity, and permeation distance; Table 1) influenced selection by owls. The third and final stage of analysis tested for a functional response in habitat selection to determine whether differing individual levels of exposure to the fire disturbance- and high-severity patch-related covariates (Table 1) also influenced habitat selection (see below) (Holbrook et al., 2019; Matthiopoulos et al., 2011; Mysterud and Ims, 1998). We examined these three stages of questions by developing models in each stage that allowed us to test and evaluate these questions.

2.5.1. Habitat selection analyses: Stages I and II

The analyses performed for stages I and II were similar, with the exception of the covariates used in the models. We examined patterns of habitat selection using a use-availability framework that compared habitat attributes at used locations to those at randomly generated available locations (Manly et al., 2002; Hooten et al., 2017). To improve spatial accuracy (to achieve median error of ~ 20 m) we only used GPS location points that had a dilution of precision (DOP) below five and whose coordinates were estimated by at least four satellites (Kramer et al., in revision). As a result, we excluded three individuals from analysis that had < 100 usable GPS points and two individuals that lacked sufficient fire severity data, which yielded an analysis sample of 22 individuals (13 from Yosemite and nine from Sequoia-Kings Canyon National Parks). Our sample owls had an average of 4.6 GPS points per night and 47 nights per individual. Because we

eliminated an average of only 0.4 points per night per owl, we were confident that our data filtering process did not result in substantive bias, even though it was possible that more points under dense canopy were eliminated due to fewer satellite hits (but see Frair et al., 2004).

We used a step selection function (SSF) to test for patterns in habitat selection (Duchesne et al., 2010; Fortin et al., 2005; Muff et al., 2020), where available habitat associated with a given owl location was conditional on where the individual occurred at the time of the previous GPS location during the same night (i.e. a “step”). While a “used” point refers to an owl GPS location, “available” points refer to 10 locations that were theoretically available for selection by that individual during that time period. For this reason, we calculated the position of these 10 available points by selecting random points that fit the spatial distribution of step lengths and step time intervals for any movement an owl made, while accounting for differences among individuals. Since some step intervals were 2–3 h long (because some GPS points were eliminated from analysis as described above), we created distributions of hourly, bi-hourly, and tri-hourly step lengths. All random points were located within a 400 m buffered 95% KDE. We used this buffer to avoid restricting the directionality of available steps near the edge of the owl's home range. Thus, turn angles were random and represented a uniform distribution, corresponding to non-directional random walks (Fortin et al., 2005).

We used mixed conditional Poisson regression models with stratum-specific intercepts, which are likelihood-equivalent to mixed conditional logistic regression models that yield equivalent parameter estimates and standard errors (Duchesne et al., 2010; Muff et al., 2020). We fitted the SSF using the Poisson formulation where the stratum-specific random intercept variance was fixed to a large value to avoid shrinkage, following Muff et al. (2020). By using conditional Poisson regression we were able to compare observed and available locations representing temporally correlated “matched pairs,” as was the case with our data.

Our response variable was binary (1 = used, 0 = available). In the stage I analysis that examined landscape characteristics and fire-related disturbance, we fitted a model that included elevation, pyrodiversity (2003–2017), small trees, and medium-large trees as continuous fixed effects and burned_{1953–1977}, burned_{1978–2002}, lower-severity burn (2003–2017), and high-severity burn (2003–2017) as categorical fixed effects. In the stage II analysis that focused on high-severity patch characteristics, we added to the stage I model continuous variables related to features of high-severity fire patches: patch size (2003–2017), permeation distance (2003–2017), and patch complexity (2003–2017). Since these variables were moderately- to highly-collinear with one another, we did not include them in the same model, but ran three separate SSF models. Because a SSF matches available points in close proximity to each used point, we did not include a variable for the distance from the nest or activity center of these central place foragers (Rosenberg and McKelvey, 1999). We tested for correlation among all continuous predictor variables and none were highly correlated (correlation coefficient > 0.7). We rescaled all continuous variables so that they would range between 0 and 1. Although we did not formally test for variability among individuals, we adopted the advice of Duchesne et al. (2010) that individual (random) coefficients should be included to avoid bias in the population-level (fixed) effects, allowing for more robust population-level habitat selection estimates, given individual heterogeneity. We used the R package glmmTMB version 0.2.0 to conduct the step selection analysis (Magnusson et al., 2017).

2.5.2. Functional response analysis: Stage III

A functional response to an available resource by an animal is indicated by an estimate for selection of that resource that changes as that resource also becomes more abundant (available) to the animal in its home range (Hebblewhite and Merrill, 2008; Holbrook et al., 2019; Jones et al., 2020; Mysterud and Ims, 1998). We tested for functional responses in habitat selection in our stage III analysis by including an interaction term between the habitat covariate of interest and a term representing its availability within a given individual's home range,

Table 2

Coefficient estimates from a mixed-effect step selection analysis from stage I (estimating California spotted owl selection relative to disturbance and land cover in the Sierra Nevada) and stage II (estimating California spotted owl selection relative to high-severity fire patch-related covariates). Column abbreviations correspond to: β , population-level (fixed) coefficient; SE, standard error of the mean; LCL, lower 95% confidence limit; UCL, upper 95% confidence limit; p, p-value for the effect of the population-level coefficient; σ^2 , variance of individual-level (random) effects for each parameter.

variable	β	SE	LCL	UCL	p	σ^2
<i>stage I</i>						
elevation	-0.46	0.71	-1.84	0.93	0.52	10.69
small trees	-2.43	0.93	-4.25	-0.61	0.01	13.94
medium-large trees	1.16	0.26	0.65	1.66	< 0.01	1.19
burned 1953-1977	-0.25	0.37	-0.97	0.48	0.51	1.47
burned 1978-2002	-0.30	0.17	-0.64	0.03	0.08	0.49
lower-severity	0.47	0.33	-0.17	1.11	0.15	1.59
high-severity	-0.50	0.41	-1.30	0.29	0.22	< 0.01
pyrodiversity	-0.91	0.35	-1.58	-0.23	< 0.01	1.65
<i>stage II</i>						
patch size	-4.52	2.15	-8.73	-0.31	0.04	12.18
permeation distance	-3.45	2.26	-7.89	0.99	0.13	9.64
patch complexity	1.18	0.92	-0.63	2.99	0.20	1.40

where availability was constant for each individual owl and represented the proportion of that resource among all available locations generated for the SSF within each individual's home range (Matthiopoulos et al., 2011; Aarts et al., 2013). We ln-transformed availability because functional responses are assumed to be non-linear (Myrsterud and Ims, 1998; Beyer et al., 2010). In all three analyses, we gauged the importance of fixed effects based upon their direction, effect size, and uncertainty (using 95% confidence intervals). We used R version 3.6.0 for analyses.

3. Results

We obtained 4,815 usable nocturnal GPS locations for the 22 GPS-tagged owls we monitored in 2018 that was composed of four females (all paired, but not nesting), and 18 males (all paired, with nine nesting and nine not nesting). These GPS locations provided data for 3,765 used steps (i.e., the first GPS point on any given night was the reference for subsequent steps and was not treated as a step itself) ranging from 118 to 188 used steps per owl (Table 1). We generated 37,650 available step locations corresponding to the 10 available steps generated for each used step. Owl home ranges were composed of 59.8% medium-large tree forest, 5.6% small tree forest, and 34.6% bare area (Fig. S1). Among all owls, 47.6% of used locations (steps) were in areas that had burned in the previous 15 years (between 2003 and 2017), with 46.2% of all used points having burned at lower-severity and 1.4% at high-severity (Fig. S1). The distribution of available locations (steps) was similar, with 44.1% falling in burned areas but with fewer available points in lower-severity burned areas (40.3%) and more in severely burned areas (3.9%). Among high-severity patches used, patch size ranged between 0.36 and 225 ha with a median of 18 ha (Table 1; Fig. S2). The overall distribution of high-severity patches within owl home ranges was skewed toward smaller patch sizes, with a maximum patch size of 225 ha (Fig. S2).

3.1. Landscape and disturbance selection analysis: Stage I

Spotted owls in our study areas selected forests with medium and large-sized dominant trees ($\beta_{\text{medium-large trees}} = 1.16$, 95% confidence interval [0.65, 1.66]) and avoided forests where dominant trees were small ($\beta_{\text{small trees}} = -2.43$ [-4.25, -0.61]; Table 2; Fig. 2). There was no apparent selection relative to whether an area had burned in older fires ($\beta_{\text{burned 1953-1977}} = -0.25$ [-0.97, 0.48]; $\beta_{\text{burned 1978-2002}}$

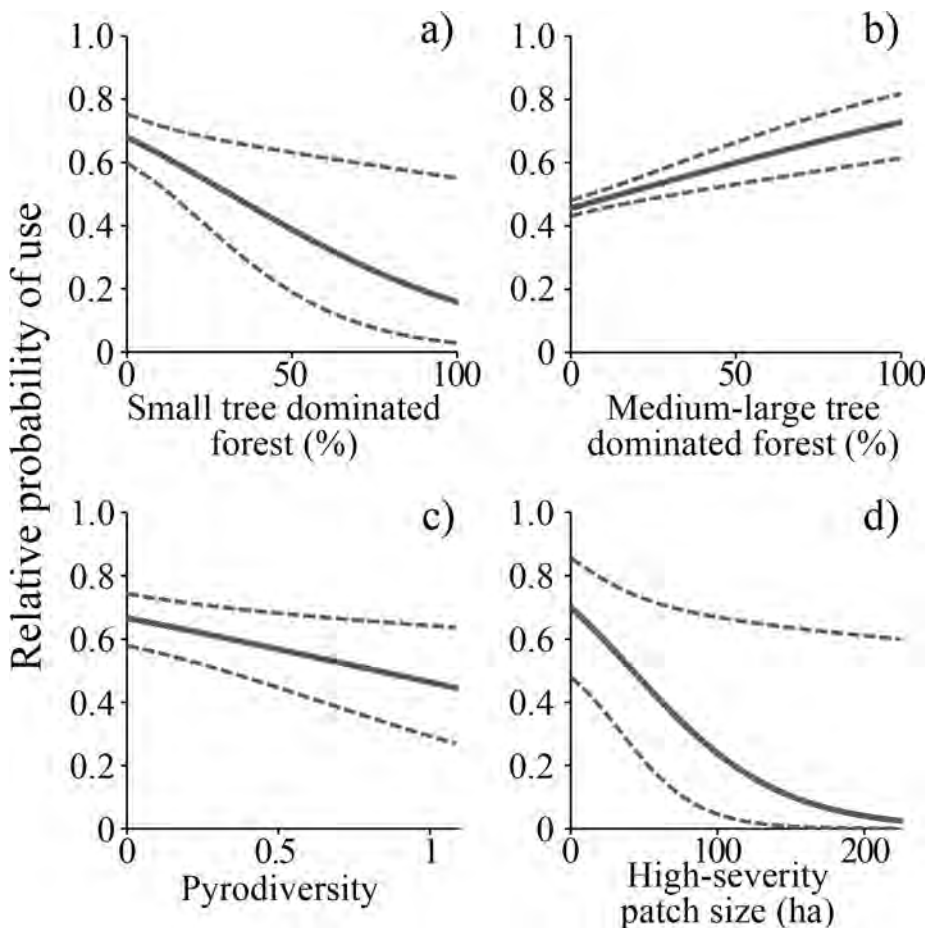


Fig. 2. Relative probability of use by California spotted owls in Sequoia, Kings Canyon, and Yosemite National Parks plotted against (a) the proportion of small tree dominated forest within 100 m, (b) the proportion of medium-large tree dominated forest within 100 m, (c) the pyrodiversity of fires that burned between 2003 and 2017 within 100 m, and (d) the size of a given high-severity fire patch (that burned between 2003 and 2017). The probability of use is shown as a solid line and the 95% confidence interval is bounded by dashed lines.

2002 = $-0.30 [-0.64, 0.03]$). There was also no apparent selection relative to the categorical effect of high fire severity ($\beta_{\text{high-severity}} = -0.50 [-1.30, 0.29]$) or lower-severity fire ($\beta_{\text{lower-severity}} = 0.47 [-0.17, 1.11]$) in more recent fires (Table 2). Owls selected areas that had lower pyrodiversity suggesting that, opposite to our prediction, they avoided areas that experienced a higher diversity of burn severities ($\beta_{\text{pyrodiversity}} = -0.91 [-1.58, -0.23]$; Table 2; Fig. 2).

3.2. High-severity patch selection: Stage II

When we compared selection or avoidance of patch characteristics by owls within severely-burned areas, owls showed avoidance of larger patches ($\beta_{\text{patch size}} = -4.52 [-8.73, -0.31]$) indicating that the odds of selection decreased by 20% for every 10 ha increase in severe fire patch size based on odds ratio and covariate scaling (Table 2; Fig. 2). Owls appeared to avoid traveling farther into severe fire patches ($\beta_{\text{permeation distance}} = -3.45 [-7.89, 0.99]$) and appeared to select more convoluted patches ($\beta_{\text{patch complexity}} = 1.18 [-0.63, 2.99]$), although the 95% CIs for both of these effects overlapped zero (Table 2).

3.3. Functional response analysis: Stage III

Owls selected areas that had burned in the past 16–40 years when this type of area was more abundant within their home range ($\beta_{\text{burned 1978-2002-FR}} = 0.48 [0.09, 0.87]$; Table S1; Fig. 3A). Similarly, owl selection for areas that burned at lower-severity in recent fires (up to 15 years old) increased as this type of burned area became more abundant within their home range ($\beta_{\text{lower-severityFR}} = 0.55 [0.04, 1.05]$; Table S1; Fig. 3B). There was no evidence for a functional response in the other six variables considered (see Table S1 and Fig. S3). Although Table S1 indicates weak evidence for a functional response to severe fire patch size ($p = 0.06$), inspection of the response curve indicates this effect was driven by a single owl that showed no change in selection based on patch size, while all other individuals showed relatively strong avoidance as patch size grew larger (Table S1; Fig. S3).

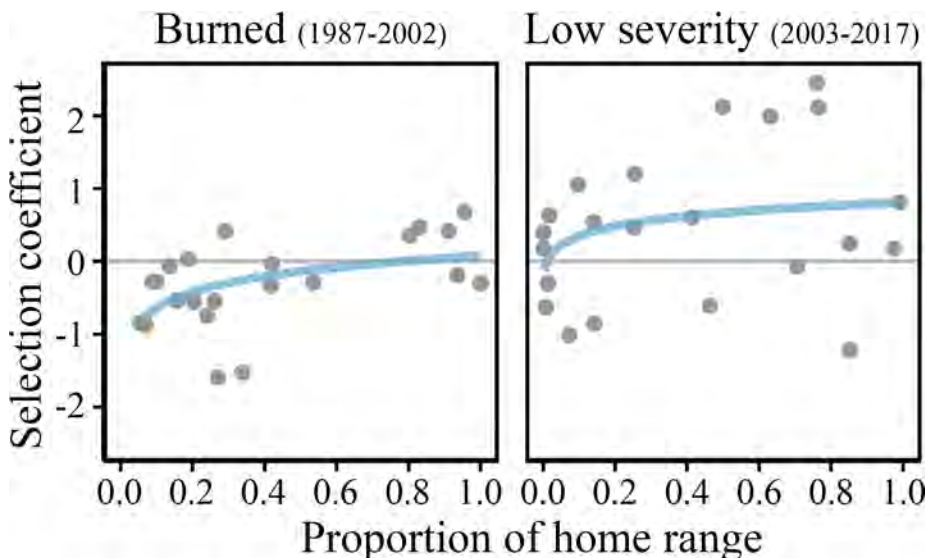


Fig. 3. Functional responses by California spotted owls in Sequoia, Kings Canyon, and Yosemite National Parks when selecting areas burned within their home ranges that were significantly different from zero, including the proportion of owl territory (a) burned at any severity between 1978 and 2002 and (b) burned at lower-severity between 2003 and 2017, with each dot representing an individual owl, and blue lines indicating significant trends. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.4. Discussion

We made two key discoveries about the way California spotted owls used burned forests in national parks that have significant implications for the conservation of this species in the Sierra Nevada and other frequent-fire forest ecosystems where they occur. First, spotted owls avoided larger patches of high-severity fire, a trend that was not

apparent in our stage I analysis in which only a categorical effect of severe fire was explored. This demonstrated the importance of including high-severity patch size in analyses of spotted owl habitat selection, even in these landscapes with partially restored fire regimes and relatively small severely-burned patches (Jones et al., 2020). Second, although owls neither preferentially selected nor avoided areas burned recently at lower-severity and areas burned by older fires, their strength of selection for these areas became stronger as their prevalence within home ranges increased – this functional response in habitat selection was a finding novel to studies of spotted owls in burned landscapes. Collectively, these two results suggested that owls were resilient, and likely adapted, to the patchwork of fire effects that characterize these landscapes with frequent-fire regimes (primarily low- and moderate-severity intermixed with small high-severity patches). Our findings support the hypothesis that spotted owls are adapted to frequent-fire regimes and when coupled with the retention of medium-large trees, may explain in part why spotted owl populations were stable in Sequoia-Kings Canyon National Parks (Franklin et al., 2004; Blakesley et al., 2010). Our results also suggest that spotted owl habitat can benefit from the restoration of frequent fires.

3.5. Selection for forest type

Spotted owls avoided forests dominated by small trees and selected for forests dominated by medium- to large-sized trees, a finding that was consistent with previous studies of both California (Call et al., 1992; Gutiérrez et al., 1992; Roberts, 2017) and northern spotted owls (Solis and Gutiérrez, 1990; Gutiérrez et al., 1995). Thus, despite our broad characterization of medium-large forest (QMD ≥ 25 cm) that covered 59.8% of owl home ranges (Fig. S1), our results emphasize that this forest type constitutes important foraging habitat for spotted owls in fire-managed landscapes, as is the case in other forested landscapes. Although we did not evaluate specific structures likely important to owls such as large trees and dense large-tree canopies (Bias and Gutiérrez, 1992; North et al., 2017), higher resolution representations of forest type and structure (e.g., with LiDAR) and prey studies would

further improve our understanding of the specific features used by owls for foraging in forests with frequent fire regimes.

3.6. Selection for burn severity class and patch characteristics

Owls avoided larger patches of severely-burned forest, suggesting that spotted owl selection/avoidance of forests burned at high-severity

could only be adequately interpreted in light of severe fire patch size. We expected that the largest high-severity patches on these fire-managed landscapes would be relatively small in comparison to previous studies and would thus not be avoided by owls. Indeed, high-severity patches within owl home ranges in this study were heavily skewed toward smaller patches, with a median of 18 ha and the largest patch measuring 225 ha and highly convoluted in shape (Fig. S2; Fig. S3). This pattern was consistent with the HRV for Sierra Nevada yellow pine mixed-conifer forests, where high-severity patches rarely exceeded 100 ha (Safford and Stevens, 2017). In comparison, in the 2014 King fire (a megafire), where Jones et al. (2020) found that owls avoided larger patches and patch interiors, the largest high-severity burned patch was 8,818 ha. Severe fire patches in this study were smaller and more complex than the patches within the King Fire (Collins et al., 2017b; Stevens et al., 2017) (Fig. S4). Therefore, although owls may use smaller severely burned patches, owls tended to avoid larger patches within their home range (but see Fig. S3), even in landscapes where patches of this type remain relatively small and often highly convoluted (Jones et al., 2016, 2019, 2020; Eyes et al., 2017). Although these patches were recently burned, their age ranged between one and 15 years old, with varying amounts of vegetative ingrowth. Despite this variation, owls may have avoided large patches of high-severity fire for several potential reasons such as predator avoidance, low prey availability (little vegetation on recently burned areas may decrease prey abundance, and dense shrub ingrowth longer after a fire may hinder prey capture by owls, even if prey abundance is high), and insufficient perches to support their hunting strategy (Forsman et al., 1984; Gutiérrez, 1985). Consistent with our finding that spotted owls avoided large patches of severe fire, Schofield et al. (in press) found that owls were less likely to occupy territories in Yosemite National Park that experienced high severity fire across > 30% of their core area. Thus, while owl populations may be relatively stable in landscapes with partially restored fire regimes, larger areas of high severity fire that make habitat less suitable for foraging also appear to have emergent effects that render territories less suitable for occupancy by owls in these landscapes.

Although confidence intervals for effects of permeation distance and patch complexity overlapped zero, our results suggested that owls may have selected more complex severe fire patches and may have avoided traveling further into severe fire patches (Table 2). The direction of the selection coefficient estimates were consistent with Eyes et al. (2017), who found that owls frequently foraged along the edges of severely burned patches, as well as Jones et al. (2020), who showed that spotted owls rarely traveled over 100 m into a severely-burned patch. Similarly, the maximum distance traveled into severely burned patches in our study was 169 m, and only 6% of locations that occurred within severely burned patches (0.08% of all locations) were farther than 100 m from the patch edge. Thus, our ability to detect significant effects may have been constrained by the small patches in this study. Even though we did not detect a significant effect of permeation distance, owls appeared to avoid making deep forays into larger patches of severe fire, regardless of tree size, in areas burned by both megafires (in the case of the King fire referenced above) and fires resembling historical regimes (reflected by our results for this study).

There has been disagreement in the literature about the effect of high-severity fire on spotted owls (Peery et al., 2019) because some studies have detected positive effects while others have detected negative effects (Ganey et al., 2017; Lee, 2018; Jones et al. In press). However, mounting evidence suggests these contrasting results could be explained in part by the spatial pattern and configuration of severely burned areas (Jones et al., 2020; this study). Our results indicated that owls avoided larger high-severity patches, even in a landscape where larger high-severity patches were relatively small, suggesting the importance of these characteristics to owl selection. Additionally, recent work on the King fire showed that while owls used some areas that burned at high-severity, they avoided both larger patches of severe fire

and avoided traveling deep into those patch interiors, even after accounting for the potential effects of salvage logging (Jones et al., 2019, 2020). Thus, the size and configuration of high-severity patches may determine the direction and strength of owl habitat selection. The absence of these high-severity patch characteristics in earlier studies (e.g., Bond et al., 2009, 2002) may potentially explain why adverse effects of high-severity fire were not detected, which would be similar to our results of neutral selection in our stage I analysis where we did not consider the characteristics of high-severity patches.

Questions have also lingered about the potentially confounding effects that salvage logging of severely burned areas could have on spotted owl response to high-severity fire. Although salvage logging was explicitly accounted for by Jones et al. (2020), who found avoidance by spotted owls of both salvage logging and large patches of severe fire after the King fire, there is strong interest in studies of owl response to severe fire in areas where salvage logging operations have not occurred at all (Bond et al., 2009; Lee and Bond, 2015). Our study in national park landscapes (also see Roberts et al., 2011; Eyes et al., 2017, and Schofield et al., in press) provided such an opportunity to formally examine the response of owls to severe fire in the absence of salvage logging while also accounting for patch characteristics that were not considered in many previous studies (e.g. Bond et al., 2009, 2016; Lee and Bond, 2015). Thus, our results suggested that in the absence of salvage logging (though we note the possibility of the occurrence of small areas of hazard tree removal along roads and other areas where hazard trees could endanger park visitors) spotted owls avoided larger patches of severely-burned forest, yet this relationship was only apparent when high-severity patch size was included in the analysis.

3.7. Selection for lower-severity burned areas

Our results supported our prediction that spotted owls are resilient to lower-severity fire, as well as older burned areas, the majority of which were likely of lower-severity (similar to trends in more recent fires). Owls in this study neither selected for nor against areas burned by recent lower-severity fire (within 15 years) or older fire (that burned 16–40 years before), each of which covered about 40% (with overlap) of owl home ranges in our study. Our results were supported by other studies that have shown spotted owls to be resilient to low- and moderate-severity fires (Bond et al., 2002; Ganey et al., 2017), perhaps partially due to their broader range of habitat use when foraging (Verner et al., 1992; Williams et al., 2011; Eyes et al., 2017; Hobart et al., 2019b).

Although owls exhibited neutral overall selection for recent lower-severity fire, the strength of selection for these conditions increased as the area of lower-severity fire increased within owl home ranges (Fig. 3). Indeed, a heterogeneous landscape of lower-severity burned and unburned areas likely promotes small mammal community diversity (Roberts et al., 2015) and could increase the abundance and availability of key prey species such as woodrats, pocket gophers, and flying squirrels – with emergent benefits to spotted owl populations (Hobart et al., 2019a, 2020). However, it could be that prey using lower-severity burned areas require larger areas of habitat to persist and maintain stable populations, especially as owls deplete those populations, making these areas beneficial to owls only if they cover a sufficiently large portion of an owl's home range. Alternately, small pockets of prey created by less overall burned area within an owl's home range may be less energetically efficient for an owl to find and utilize. Our functional response analysis also revealed a significant effect of the amount of older burned areas (which likely burned primarily at lower-severity) within an owl's home range on selection of those areas. Owls with little older burned area available to them avoided these older burned areas, whereas owls with greater amounts of older burned area showed neutral selection for those areas (Fig. 3). Together, these results suggest that the benefits of lower-severity fire may

attenuate over time, and that frequent, low-severity fire events might benefit owl populations and perhaps their prey.

The owl's use of lower-severity burned areas could also explain why owls avoided more pyrodiverse areas. Avoidance of pyrodiverse areas was in contrast to our prediction that owls foraging in heterogeneous landscapes shaped by fire would exhibit neutral or positive selection for areas with high pyrodiversity (Franklin et al., 2000; Franklin and Gutiérrez, 2002). Indeed, the most pyrodiverse locations were those containing a mix of burn severity classes (unburned, lower-severity, and high-severity fire), whereas areas of low pyrodiversity were those composed entirely of a single class of these three categories. Therefore, the composition of areas with low pyrodiversity becomes important for determining the direction and magnitude of owl selection. For instance, owls appeared to show weak selection for areas with high pyrodiversity in the King fire (Jones et al., 2016, 2020). However, areas of low pyrodiversity in the King fire predominately occurred in the large high-severity patch that owls avoided (and would have driven selection for greater pyrodiversity). In comparison, areas with low pyrodiversity in this study were most often composed of lower-severity or unburned area. Thus, neutral selection for lower-severity and unburned areas in our study may have resulted in an apparent avoidance of pyrodiversity unlike the owls in the King fire study (Jones et al., 2020; Fig. S5). Furthermore, the diversity of forest structure in unburned areas also may play a role in selection for pyrodiversity. Selection for more pyrodiverse areas may be more pronounced if pre-fire forest conditions are homogeneous, such that increased pyrodiversity might create structural heterogeneity preferred by owls, as may be the case on national forests and areas burned by the King fire (Jones et al., 2020). Regardless of the specific mechanism, our results suggest the importance of characterizing both pyrodiversity and structural diversity of unburned areas, especially when comparing selection for or against pyrodiversity among fires with different patterns of severity.

4. Conclusions and implications for using fire for owl conservation

Our study supports the long-held hypothesis that spotted owls are adapted to frequent-fire regimes, characterized by low- to moderate-severity fire with small patches of severe fire, such as those that have been reintroduced to the national parks that comprised our study area (Verner et al., 1992; Gutiérrez et al., 2017). Conversely, natural fire regimes on Sierra Nevada national forests have been altered by fire suppression, which has resulted in very different forest structures between the national parks we studied and other public lands in the Sierra Nevada. Hence, our study supports earlier speculation that the difference in management between these two general landscapes (fire managed and fire suppressed) may account for the difference in owl population trajectories – stable in Sequoia-Kings Canyon National Parks and declining on national forests (Franklin et al., 2004; Blakesley et al., 2010; Tempel et al., 2016). We do not know the mechanism(s) that confer higher fitness in fire-managed landscapes, but we propose that the benefit is conferred by (1) a positive influence of frequent low- and moderate-severity fire on prey habitat, (2) the change in forest structure that reduces the impact or spread of high-severity fires, and (3) the interaction of large trees and fire because large trees are relatively fire resistant and have helped facilitate the reintroduction of frequent lower-severity fire regimes. Therefore, we conclude that the effect of a natural fire regime is complex with positive benefits conferred on owls, the maintenance of forest systems, and reduction in high severity fire.

The habitat selection patterns revealed by owls in our study suggest that prudent use of fire, as practiced in the Sierra Nevada national parks we studied, could benefit spotted owl conservation in fire-suppressed landscapes such as national forests as previously proposed (Bond et al., 2002; Roberts et al., 2011; Eyes et al., 2017). However, the positive functional response owls exhibited to low-severity fire and the apparent attenuating benefits of lower-severity fire over time that we found

suggest that restoration of frequent fire regimes, rather than discrete (nonrepeating) fire treatments, will be needed to continue achieving benefits for owl foraging habitat. Hence, increasing the amount and frequency of lower-severity fire would serve a dual purpose of (1) reducing surface and ladder fuels that contribute to the large, high-severity fires that negatively affect owls and (2) promoting prey habitat for owls (Jones et al., 2016; Hobart et al., 2019a).

The extensive reintroduction of frequent lower-severity fire on national forests and other fire-suppressed areas within the range of spotted owls is constrained by social (e.g., air pollution, fear of escaped fire), economic (e.g., high cost), and ecological (e.g., escaped fire, unintended negative impacts on wildlife habitat) considerations (Collins et al., 2010; Young et al., 2020). In areas lacking frequent, lower-severity fire, mechanical treatments intended to remove surface and ladder fuels may serve as an intermediate step to the restoration of fire regimes, although they are also constrained by concerns of stakeholders – that logging to remove smaller trees may also have negative effects on spotted owls and other wildlife (Wood and Jones, 2019). Note that our study was limited to national parks, where such treatments do not occur, and so our results cannot provide direct insight on mechanical treatments. Nevertheless, if mechanical treatments are applied with rigorous guidelines designed to maintain key habitat features (e.g., retention of large trees and dense canopy of tall trees) of old forest ecosystems and sensitive species like spotted owls, fishers (*Pekania pennanti*), and others, the benefits of reducing severe fire through mechanical thinning may outweigh the adverse effect on spotted owl habitat, yet these areas need to be closely monitored because of high scientific uncertainty (Verner et al., 1992; Schwikl et al., 2009; Tempel et al., 2015; Jones, 2019). Increasing the use of fire as a management tool in fire-suppressed forests may increase the feasibility and spatial extent of restoration efforts compared to mechanical treatments alone (North et al., 2012). However, fire used in combination with mechanical treatments (e.g., removal of small and medium-sized trees) may be more effective in restoring vegetation structure with lower fuel loads than currently present, particularly in forests where the risks from prescribed or managed fire are now high (Schwikl et al., 2009). Thus, while much uncertainty and many obstacles remain, our study reinforces previous findings that owl conservation may benefit from restoration of frequent fire regimes in dry forests (Roberts et al., 2011; Jones et al., 2016, 2020; Eyes et al., 2017; Stephens et al., 2019).

5. Ethics approval and consent to participate

University of Wisconsin Institutional Animal Care and Use Protocol # A005367

6. Consent for publication

Not applicable.

7. Availability of data and materials

General data is available on request, but because of the sensitive status of these owls, specific owl locations will not be released.

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CRediT authorship contribution statement

Anu Kramer: Conceptualization, Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Gavin M. Jones:** Conceptualization, Methodology, Formal analysis, Visualization, Writing - original draft, Writing - review & editing.

Sheila A. Whitmore: Data curation, Writing - review & editing. **John J. Keane:** Writing - review & editing, Project administration. **Fidelis A. Atuo:** Conceptualization, Methodology, Writing - review & editing. **Brian P. Dotters:** Data curation, Writing - review & editing. **Sarah C. Sawyer:** Project administration. **Sarah L. Stock:** Writing - review & editing, Project administration. **R.J. Gutiérrez:** Writing - original draft, Writing - review & editing. **M. Zachariah Peery:** Conceptualization, Methodology, Writing - original draft, Writing - review & editing, 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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Appendix A. Supplementary material

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Elevational gradients strongly mediate habitat selection patterns in a nocturnal predator

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Abstract. Mountain ecosystems contain strong elevational gradients in climate and vegetation that shape species distributions and the structure of animal communities. Nevertheless, studies of habitat selection for individual species rarely account for such gradients that often result in species being managed uniformly across their range, which may not improve conservation as intended. Therefore, we characterized variation in nocturnal habitat selection by 18 GPS-tagged California spotted owls (*Strix occidentalis occidentalis*) along a 1400-m elevational gradient in the Sierra Nevada, California. We characterized three-dimensional forest structure with light detection and ranging data that we used in mixed-effects resource- and step-selection analyses of owl habitat selection. At lower elevations, owls selected stands with shorter trees, sites closer to hard edges between tall forests and open areas, sites with less diversity in forest seral types and sites with more ridge and southwest aspects. In contrast, owls at higher elevations selected the opposite. Within public forests that had taller trees and within their home range core (45% kernel density estimate of GPS points) areas, owls selected forests with less and more canopy cover at low and high elevations, respectively. Outside of their core areas, owls selected areas with fewer and more tall trees at low and high elevations, respectively. These findings may be explained by elevational gradients in prey distribution and variation in owl diet because owls consume more woodrats (*Neotoma* spp; earlier seral species) at lower elevations and more flying squirrels (*Glaucomys sabrinus*; older forest species) at higher elevations. Thus, at low elevations and in areas unlikely to support nesting, spotted owls could benefit from management that promotes woodrat habitat by encouraging oak regeneration and creating small brushy openings within forests with shorter (younger) trees. Conversely, at higher elevations, (1) enhancing flying squirrel habitat by promoting large trees and denser canopy on mesic sites and (2) managing for greater cover type diversity on southwest-facing slopes and ridgetops is more likely to improve foraging habitat quality for spotted owls. The patterns of owl selection over elevational gradients has not been explicitly considered in most habitat management plans but clearly would improve management throughout mountain ecosystems.

Key words: California; elevational gradient; forest management; habitat selection; light detection and ranging; predator; spotted owl; *Strix occidentalis*.

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INTRODUCTION

Elevation has a major influence on local and regional climatic and vegetation variation (Woodward 1987, Körner 2003), which, in turn, shapes the diversity and distribution of predator, competitor, and prey communities (Rahbek 1997, Callaway 1998). Although some species inhabiting mountain ecosystems may be restricted to narrow elevational ranges (Santhakumar et al. 2018, Khatiwada et al. 2019), other species, particularly larger and more mobile ones, occur over wider elevational gradients that span a range of environmental conditions, climate regimes, and ecological communities (Loiselle and Blake 1991, Rice 2008). For wide-ranging species, the life history strategies, behaviors, and choices made by individuals that confer fitness benefits at lower elevations may not confer fitness benefits at higher elevations and vice versa (Loiselle and Blake 1991). For example, the presence of a competitor, predator, or prey species at low elevations and its absence at high elevations could promote elevational niche partitioning and habitat selection patterns that vary as a function of elevation. Moreover, elevational gradients in local climate may interact with habitat or topographical features to create refugia for species from regional climate warming, providing opportunities for elevational-based conservation under climate change (Sears et al. 2011, Jones et al. 2016). Exploring how ecological relationships vary across elevations has important implications for understanding species' ecology and improving conservation outcomes in mountain ecosystems.

The conservation of wildlife species in mountain ecosystems has an important influence on forest management (US Forest Service 2004, Spies et al. 2018, Phalan et al. 2019). Habitat selection studies of focal species of conservation concern often provide information that forms the basis for decisions about how forest structure and composition will be managed, with substantial implications for other species and forest health (Bias and Gutiérrez 1992, Greenwald et al. 2005, Purcell

et al. 2009, Ackers et al. 2015). For example, evidence for the selection of a particular habitat element (i.e., greater use of large trees than expected based on their availability) by a species of conservation concern is often used to guide forest management activities that promote those conditions across the species' geographical range (Gutiérrez et al. 2017). However, when habitat selection by species is variable across elevations or latitudes, it complicates management strategies. Therefore, creating flexible forest management strategies to accommodate species' habitat selection patterns that vary along these gradients is likely to be a more effective conservation approach, which requires a better understanding of species' habitat selection over elevation and latitudinal gradients.

The spotted owl (*Strix occidentalis*) is distributed across broad elevational gradients in many montane forest ecosystems of western North America (Bias and Gutiérrez 1992, Gutiérrez et al. 2017). This species also has long resided at the epicenter of regional-scale forest management planning owing to its use of older forests (Simberloff 1987). Despite many studies of spotted owl habitat selection in forest ecosystems, individual habitat selection across elevational gradients has not been studied—information that is critical to managing this wide-ranging species. Thus, we hypothesize that elevation in the Sierra Nevada will have a strong influence on the selection of features such as forest height, tree species assemblages, canopy cover, and understory conditions by California spotted owls (*Strix occidentalis occidentalis*, hereafter referred to as spotted owls) because of its influence on climate, moisture, edaphic conditions, and fire regimes, which in turn influences the distribution and habitat associations of key spotted owl prey species such as woodrats (*Neotoma* spp.) and flying squirrels (*Glaucomys oregonensis*; Arbogast et al. 2017). Recent stable isotope-based work revealed that variation in the relative composition of these prey species in the spotted owl diet may partly explain differences in regional population dynamics (Hobart et al.

2019a). Woodrats, which prefer shrubby areas with masting oaks, may be particularly vulnerable to predation by owls near edges between relatively open area and closed-canopy forest (Sakai and Noon 1997, Innes et al. 2007), and were found to be a greater component of the spotted owl diet on private land and at lower elevations (Munton et al. 2002, Hobart et al. 2019a). Flying squirrels, which prefer areas of dense canopy and older, taller trees with abundant hypogeous fungi (Waters and Zabel 1995, Meyer et al. 2007, Holloway et al. 2012), were a greater component of owl diets at higher elevations, and also on US Forest Service land (Hobart et al. 2019a). Note that while Hobart et al. (2019a) was not able to discriminate woodrats from pocket gophers (*Thomomys* spp.) isotopically, woodrats constitute a considerably greater portion of spotted owl diets by biomass, and gradients in isotopically derived diets were thus assumed to be predominantly the result of a shift from woodrats at low elevation to flying squirrels at high elevations (Hobart et al. 2019a). Nevertheless, it is uncertain whether elevational gradients in spotted owl prey consumption lead to different forest habitat selection patterns.

In our study, we characterized habitat selection by GPS-tagged spotted owls along an elevational gradient in the Sierra Nevada, California, using high-resolution measurements of forest structure derived from aerial-based light detection and ranging (LiDAR) technology. We assessed how spotted owl nocturnal selection for different forest stand types, configurations, and forest structures varied as a function of elevation. Given our hypothesis that habitat selection varied by elevation, we predicted that owl foraging would reflect habitat features of their primary prey at lower (woodrats) and higher (flying squirrels) elevations. We further predicted that these patterns of stand selection would be consistent across ownerships, as well as when limited to public forests with taller trees (henceforth taller public forests).

METHODS

Study area

Our study area covered 270 km² that encompassed the home ranges of 18 spotted owls located primarily on the Tahoe National Forest in

the central Sierra Nevada of California, USA, but also had private land interspersed within and bordering the National Forest (Fig. 1). Lands within the study area were managed by the US Forest Service (61%) and private owners (39%), and thus, forests were a mix of plantations and recent clear cuts as well as unlogged and selectively logged forest that was more mature with a closed canopy. The climate was Mediterranean with warm, dry summers and cool, wet winters. Elevations ranged from 400 to 1800 m. The dominant tree species of these Sierran mixed conifer forests included ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), Douglas-fir (*Pseudotsuga menziesii*), California black oak (*Quercus kelloggii*), and white fir (*Abies concolor*) (Mayer and Laudenslayer 1988). These were intermixed with Jeffrey pine (*Pinus jeffreyi*) and red fir (*Abies magnifica*) at high elevations and live oak (*Quercus chrysolepis* and *Quercus wislizeni*), tanoak (*Notholithocarpus densiflorus*), and Pacific madrone (*Arbutus menziesii*) at lower elevations (Mayer and Laudenslayer 1988).

GPS-tagged owl data

We captured and GPS-tagged 18 adult (four females and 14 males) spotted owls between March and May, 2017 and 2018, which we then monitored during the breeding season (May–August) of the year they were captured. Two of the four paired females were nesting. One male was single, while the remaining 13 paired males were split between six nesting and seven non-nesting. We captured owls opportunistically, but all were well within the geographic area of LiDAR coverage taken 5 yr before the owls were tagged and included a range of elevations, forest conditions, and land ownerships that we believed was representative of the broader landscape (Fig. 1). We captured owls by hand or with snare poles using modifications of the methods used by Franklin et al. (1996) before or early in the breeding season and fitted birds with backpack- or tail-mounted dual GPS/VHF tags that allowed remote downloading of data (Pinpoint VHF 120; Lotek, Newmarket, Ontario, Canada; hereafter “GPS tags”). Tags and harnesses weighed 7–10 g (under 2% of average spotted owl body weight). We recaptured most owls to remove the GPS tags, but owls that we did not recapture all had tail-mounted transmitters,

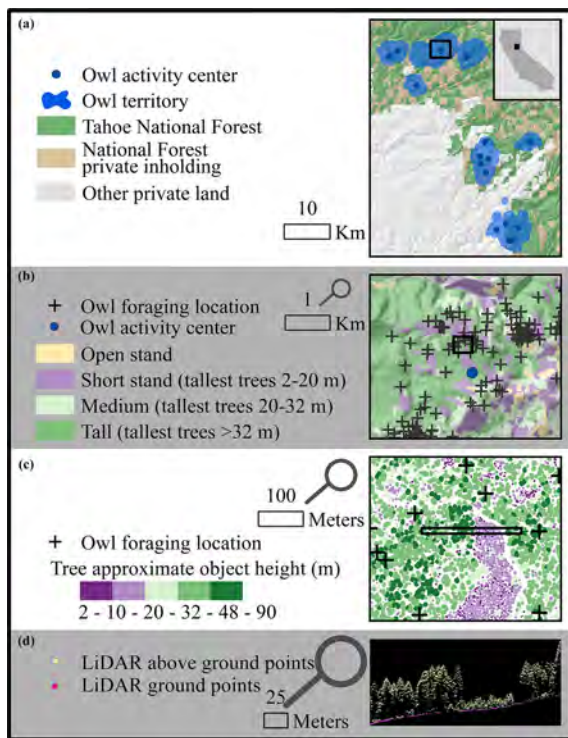


Fig. 1. The study area, showing (a) the location in the state of California, owl 400-m buffered 95% kernel density estimate polygons, the Tahoe National Forest, and private inholdings on the National Forest, (b) landscape classifications into open, short, medium, and tall stands generated by the LiDAR (light detection and ranging), as well as used owl GPS points, (c) tree-approximate objects generated by the LiDAR, and (d) a cross-sectional view of the LiDAR point cloud itself as it crosses from tall to short to tall stands. Note that the scale bars listed to the left of each map show the scale for that map, whereas the black box on each map shows the boundaries of the subsequent map, for instance, the wide rectangle shown in map (c) corresponds to the boundaries of the data presented in map (d).

which we expected to be shed during the subsequent molt. All habitat selection analyses were conducted using GPS locations derived from the transmitters, whereas VHF was used to relocate tagged owls for recapture and GPS data retrieval. GPS tags were programmed to collect five hourly GPS locations per night (22:00–02:00 or 23:00–03:00) and one diurnal location. We removed all diurnal GPS point locations from

analyses, and because owls are nocturnal predators, we assumed that nighttime GPS locations primarily represented locations of foraging activities, but we acknowledge that they could represent other activities such as territory defense and social interactions (Forsman et al. 1984, Delaney et al. 1999). For the two nesting females, we removed all GPS points within 50 m of the nest from our analyses to reduce the potential biases associated with nesting rather than foraging activities. This eliminated 20% and 23% of GPS points, respectively, for each nesting female, but left sufficient foraging locations (over 250 GPS points, mostly from later in the summer) to conduct our analyses.

Habitat selection analyses

To test our prediction that spotted owls would select putative nocturnal foraging sites characteristic of woodrat habitat at lower elevations and flying squirrel habitat at higher elevations, we conducted two parallel analyses that examined these relationships under different spatial filters and management strategies, taking advantage of different GPS accuracy thresholds to filter owl locations. The first analysis (hereafter “mixed ownership stand selection”) was an examination of habitat selection across multiple land ownerships (US Forest Service and private) at the stand scale that focused on the spatial distribution of relatively coarse vegetation height classes that approximated forest seral stage (described below and in Table 1) in relation to where owls moved from one hour to the next. In the mixed-ownership stand selection analysis, we used a greater proportion of owl movement data with a more inclusive GPS accuracy threshold (see section *Mixed-ownership stand selection* below) with the goal of assessing movement patterns and habitat selection across the broader landscape that included both public and private lands. The second analysis (hereafter “selection of structure within taller public forests”) was an examination of the nocturnal habitat selection of forest structure by owls on US Forest Service land only and relied on high spatial accuracy of both the owl GPS points and the LiDAR-derived environmental variables. We focused these analyses on National Forest lands and stands with medium and tall trees in light of current efforts to integrate spotted owl habitat management with

forest restoration activities intended to reduce large severe fires and drought-related tree mortality on this landownership (North 2012, USDA Forest Service 2019). The invasive barred owl (*Strix varia*) has been documented in our study area and may have affected habitat selection of spotted owls, but only one barred owl was detected in our study area in 2019. Therefore, we suggest that there was minimal influence by barred owls on spotted owl habitat selection.

LiDAR data

Discrete-return LiDAR was flown by the National Center for Airborne Laser Mapping (NCALM) for the study area during 2013 (October 24–November 24) and 2014 (June 10–30), with an average pulse density of 8.56 pulses/m². Although the 2013 LiDAR flight occurred late in the season, we confirmed that deciduous hardwood canopies (such as California black oak) had likely not yet dropped their leaves and were recognized as tree canopies in the LiDAR point cloud. However, because hardwood and conifer canopies were mixed together in the LiDAR point cloud, we were not able to differentiate hardwood from conifer foliage. We used different LiDAR-derived metrics to characterize stand size and forest structure for the mixed-ownership stand selection analysis and the analysis examining the selection of structure within taller public forests, respectively. For the mixed-ownership stand selection analysis, we processed the raw point clouds using FUSION software (McGaughey 2012) to produce 30-m rasters of average canopy height and the 95th percentile LiDAR height (representing the height of the dominant trees in each pixel). These rasters were used to classify the landscape into four height-based forest stand types: (1) open, canopy height under 2 m, (2) short, tallest trees ≥ 2 and < 20 m, (3) medium, tallest trees ≥ 20 and < 32 m, and (4) tall, tallest trees ≥ 32 m tall (Table 1; Fig. 2).

We estimated forest structure using a combination of LiDAR-derived metrics from the area within 30 m of each point and a suite of metrics utilizing tree-approximate objects (TAOs). The watershed transform algorithm, like almost all LiDAR tree identification algorithms, identifies overstory trees directly visible to the LiDAR instrument. Subordinate trees, which often are the most numerous on a site, are not detected.

We adopted the TAO paradigm where each TAO represents an identified tree that may have none to several subordinate trees beneath its outer crown surface (North et al. 2017, Jeronimo et al. 2018, 2019). Treating tree detection results as TAOs is a way to make use of tree-scale measurements while explicitly recognizing that subordinate trees are not identified. We estimated (1) vertical complexity, the coefficient of variation in all LiDAR points over 2 m, (2) average, (3) maximum tree height, estimated using TAOs, (4) tall tree density, the density of TAOs over 32 m, (5) shrub/understory density, the relative density of LiDAR points 0.5–2.0 m (Wing et al. 2012, Kramer et al. 2016), and (6) percent canopy cover: the percent area of TAO coverage (North et al. 2017, Jeronimo et al. 2018, Kane et al. 2019, Table 1). TAOs were used to calculate canopy cover defined as the total horizontal area covered by tree canopy (Table 1).

We assumed that vegetative growth between the 2013–2014 LiDAR acquisition and the 2017–2018 collection of owl GPS data would not affect our results, but we accounted for disturbance that significantly altered vegetative structure. To identify areas that had changed as a result of timber harvest, fire, or drought mortality between 2013 and 2014 and 2017 and 2018, we used a combination of (1) 5-m RapidEye imagery from 2017 and 2018 (to match the year that the owl had been tagged; downloaded from PlanetLabs (<https://www.planet.com/>)) and (2) the eDaRT forest change product (USFS Pacific Southwest Region Remote Sensing Lab and UC Davis CSTARS; Slaton et al. 2016, Koltunov et al. 2018, 2020), which highlighted areas that had changed between the baseline year of 2007 and 2018. Using these two products, we hand-digitized all areas that had visibly changed, which comprised 2% of the 1 km buffered 95% kernel density estimates (KDE) for each owl.

KDEs were generated using the reference bandwidth and the adehabitatHR package in R (Calenge 2011, Silverman 1986). We excluded areas that had been altered, but where trees were still present (due to partial harvesting or drought mortality), from further analyses, since these changes could not be accurately updated in the LiDAR. In areas where all trees were removed, we reclassified the cover to open for the mixed-ownership stand selection analysis (open areas

Table 1. Habitat variables and a description of how each variable was calculated in the analyses of (a) mixed-ownership stand selection and (b) selection of structure within taller public forests.

Habitat variable	Description
(a) Mixed-ownership stand selection	
% Short stand area	Proportional area within 100 m of owl location where 95% LiDAR height <20 m and mean canopy height >2 m
% Medium stand area	Proportional area within 100 m of owl location where 95% LiDAR height between 20 and 32 m and mean canopy height >2 m
% Tall stand area	Proportional area within 100 m of owl location where 95% LiDAR height ≥32 m and mean canopy height >2 m
Distance to soft edge (m)	Euclidian distance from point to nearest soft edge between smoothed† cover classes (open, short, medium, and tall)
Distance to hard edge (m)	Euclidian distance from point to nearest hard edge between smoothed† open and tall stand types
Seral stage diversity	Shannon-Weiner diversity index of all four cover types within 100 m of the point on unsmoothed, classed data
Distance to stream (m)	Euclidian distance to perennial stream from the USGS National Hydrography Dataset (https://www.usgs.gov/core-science-systems/ngp/national-hydrography)
% Ridge	The proportion of ridge topographic position class within 100 m (North et al. 2012)
% SW aspect	The proportion of southwest topographic position class within 100 m (North et al. 2012)
Elevation (m)	Elevation above sea level in meters
(b) Selection of structure within taller public forests	
Elevation (m)	Elevation above sea level in meters
Vertical complexity	Coefficient of variation for all LiDAR points over 2 m and within 30 m of the owl point
Max tree height (m)	Maximum height of LiDAR-derived TAOs within 30 m
Tall tree density (per ha)	The density of tall (over 32 m) LiDAR-derived tree-approximate object centroids within 30 m
Shrub/understory density	Relative LiDAR point density for Stratum (0.5, 2), where R_x = the number of returns at or below height x and $\text{Stratum}_{a,b} = \frac{R_b - R_a}{R_b}$
% Canopy cover	Proportional area of LiDAR-derived TAOs within 30 m
Distance to activity center (m)	Euclidian distance to owl activity center (m)
Squared distance to activity center (m ²)	The squared distance to owl activity center (m ²)—included to account for an exponential relationship between distance and behavior

Notes: LiDAR, light detection and ranging; TAOs, tree-approximate objects.

† We smoothed polygons by simplifying edges when converting from raster to polygon and eliminating slivers with area <1 ha to address uncertainty with owl location and to better identify continuous areas of cover.

were not considered in the analysis that focused on the selection of structure within taller public forests).

Mixed ownership stand selection

The mixed-ownership stand selection analysis was intended to elucidate patterns of foraging habitat selection at a coarse scale of forest stands, testing whether elevation influenced selection for different spatial configurations of cover types across the range of forest conditions present within spotted owl home ranges. We considered all area present within owl home ranges, classifying 30-m pixels by maximum canopy height, as described above (i.e., open, short, medium, and

tall; Table 1), grouping same-height pixels into putative stands, and merging single-pixel stands with the most common neighboring stand type to create relatively homogeneous stands (in terms of the height of the tallest trees) that ranged in size between 0.18 and 18.06 ha (Fig. 2). We excluded areas that had undergone significant forest changes between the LiDAR acquisition and the owl monitoring (described above).

We characterized patterns of selection for habitat characteristics of stands based on all locations (~5 per night collected at hourly intervals) obtained by the GPS tags. Because this analysis focused on attributes of stands and was thus a coarse characterization of the landscape, we



Fig. 2. Representative photographs of areas with nearby owl use categorized into different forest and edge types: (a) hard edge between open and tall stands, (b) open, (c, d) short forest, (e) medium forest, and (f) tall forest. Due to our method of classifying the forest by the tallest tree per 30-m pixel, short forest included areas that were fairly dense (c), as well as much more open, with widely spaced trees (d). Note that (a) was taken on the edge between private and public land, (b) and (c) were taken on private land, and (d–f) were taken on public land.

expected it would be relatively insensitive (compared with our second analysis of forest structure) to positional error of GPS locations. As such, we used relatively relaxed criteria for including GPS locations (dilution of precision (DOP) between 0 and 5 and at least four satellites), which resulted in the retention of a mean of 4.02 near-hourly locations per night, and an estimated median accuracy of 20 m overall and 29 m in forested areas (Appendix S1). Removing GPS points that did not meet the threshold may have resulted in GPS bias, but we assumed this would be minimal because of the low reduction in locations per night (from 5 to 4.02) and the assumption that this bias would remain fairly constant across the elevational gradient (but see Frair et al. 2004). We removed two owls that had

less than 100 locations because of insufficient data, which left 16 owls for this analysis.

Step-selection analysis.—A step selection function (SSF; Fortin et al. 2005) takes advantage of non-independent GPS points collected as an animal moves from one location to the next over time, allowing us to make use of the multiple nightly GPS locations we had collected for each owl. We used SSF (Fortin et al. 2005, Duchesne et al. 2010, Muff et al. 2020) to test for patterns in habitat selection with a use-vs.-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. Hereafter, we refer to “used” points as the owl GPS locations retained for the analysis and “available” points as potential locations that the owl could have chosen according to an empirical distribution of step length and turn angles. The mean covariate values for used and available points are provided in Appendix S2: Table S1. Used and available points were compared in the modeling framework to determine foraging habitat selection patterns. We generated 10 available points for each observed hourly step made by owls by first generating thousands of randomly placed points within the 400 m buffered 95% KDE of each owl. We used a 400-m buffer to allow the random steps the opportunity to go in any direction. From these random points, we chose those where the step length to a given used point matched the frequency distribution of step lengths for that owl (to account for differences in individual behavior), based on the length of time since the last GPS reading. For example, if 10% of 1-h step lengths for a given owl were between 400 and 500 m, then 10% of available points for that owl were 400–500 m from the owl’s GPS point an hour earlier. Because there was variability in the times between steps by owls (owl GPS points that did not meet the DOP and satellite thresholds were excluded, so some steps were 2 or 3 h apart), we used distributions of hourly, bi-hourly, and tri-hourly step lengths. Turn angles were random and represented a uniform distribution (corresponding to non-directional random walks [Prokopenko et al. 2017]).

In order to include differences in habitat selection preferences among individuals in the SSF framework, we estimated the relative probability

of use using mixed conditional Poisson regression models with stratum-specific intercepts, which are likelihood-equivalent to mixed conditional logistic regression models (Duchesne et al. 2010, Muff et al. 2020) and yielded equivalent parameter estimates and standard errors (Muff et al. 2020). The model was formulated as:

$$E(y_{ijk}) = \mu_{ijk} = \exp(\alpha_{ik} + \beta^T x_{ijk} + u_i^T z_{ijk})$$

$$\text{with } y_{ijk} \sim \text{Po}(\mu_{ijk}),$$

where $i = 1, \dots, I$ individuals, $j = 1, \dots, J$ indexed used or available locations at a given time, and $k = 1, \dots, K$ strata, α_{ik} was the stratum-specific intercept with $\alpha_{ik} \sim N(0, \sigma_\alpha^2)$ and σ_α^2 fixed to a very large value (i.e., 10^4), β^T was the transposed of the vector of coefficients being estimated, x_{ijk} was the covariate vector, u_i^T was the vector of individual-specific random slopes, and z_{ijk} was the design vector. The Poisson formulation allows the SSF to be fitted in a single step using standard statistical software where variance for the stratum-specific random intercept effect can be fixed to a large value (Muff et al. 2020). Conditional Poisson (logistic) regression approaches allow for the testing of habitat selection when observed and available locations represent matched pairs (strata) because of the underlying temporally correlated data generating process, as was the case with our data.

We treated owl location (coded as 1) vs. available location (0) as the response using the package glmmTMB version 0.2.0 (Magnusson et al. 2017). We tested covariate correlation and found none with a correlation coefficient >0.7 (Appendix S2: Fig. S1). However, preliminary analysis suggested high multicollinearity (variance inflation factor) for the three tree height classes (short, medium, and tall stand area), which was remedied by excluding one of the three tree height classes from the model. We included the following continuous variables as fixed effects: (1) proportion of medium and tall stand area; (2) distance to soft edge; (3) distance to hard edge; (4) seral stage diversity; (5) distance to stream; (6) proportion of ridge and southwest aspect (representing topographic position (sensu North et al. 2012); and (7) elevation of each GPS location. We also obtained a coefficient for short stand area by fitting an additional model, substituting the short term for the medium and tall

model terms. The abundance and distribution of hardwoods are key habitat factors that may vary by elevation, but data were not available to include in this analysis. Soft edge was defined as the boundary between two stand types after smoothing, while hard edge was the boundary between open and tall stands only (after smoothing). We smoothed stands to ensure that we were measuring edges between large patches by removing all stands <1 ha in area and merging them with the most common nearby stand. We estimated seral stage diversity using the Shannon-Wiener diversity index among the proportional area of all four vegetation height types within 100 m of each used and available point, assuming that diversity of stand heights would also indicate a diversity in seral stage. We considered interactions between elevation and other predictors, which provided a means to test whether habitat selection was mediated by elevation. For example, spotted owls might be more likely to use open and shorter stands, hard edges, and a greater seral stage diversity at lower elevations, where woodrats are more prevalent, than high elevations where flying squirrels are more common (Jones et al. 2016, Gutiérrez et al. 2017).

In addition to fixed effects, we estimated random slope effects for each additive main effect (excluding interactions) that varied by individual owl. We included random slopes not to assess individual variation, but to account for it so as to avoid bias in the fixed effects. Therefore, this approach provided unbiased estimates of population-level selection in the presence of individual heterogeneity (Duchesne et al. 2010). Then, following Muff et al. (2020), we treated the strata-specific intercepts as a random effect with a very large ($\sim 10,000$) fixed variance to facilitate model fitting and prevent shrinkage toward an overall mean. We evaluated the support of each fixed effect by examining whether 95% confidence intervals for coefficients overlapped zero, but did not use this as a strict threshold for assessing potential variable importance to avoid possible Type II error (Amrhein et al. 2019); thus, we also considered effects with 90% confidence intervals that did not overlap zero to be potentially meaningful. We evaluated model goodness of fit by calculating the conditional coefficient of determination for generalized linear mixed-effects models (R_{GLMM}^2 ; Nakagawa and Schielzeth

2013, Johnson 2014, Nakagawa et al. 2017) using the MuMIn package in program R (Barton 2020). We used odds ratios, which can facilitate linear interpretation of covariate effects in logistic models containing interactions (Jones and Peery 2019), to understand the potential management effects of altering forest characteristics by small amounts (e.g., 10% increase in tall trees) at lower (1000 m; 16th percentile) and higher (1500 m; 87th percentile) elevations for covariates that interacted significantly with elevation. We expressed odds ratios as proportional changes in effects, so odds ratios between 0 and 1 represent a decrease in the odds of selection, and odds ratios >1 represent an increase in the odds of selection. For example, an odds ratio of 1.33 indicates that the odds of selection increase by a factor of 1.33, or in other words, owls are 1.33 times as likely to select that given habitat, whereas an odds ratio of 0.75 indicates that the odds of selection decrease by a factor of 1.33 (the inverse of 0.75 or 1 divided by 0.75).

Selection of structure within taller public forests

In our analysis of selection of structure within taller public forests, we tested whether elevation affected spotted owl nocturnal habitat selection of forest structural characteristics, limiting our area of interest to public forests with taller trees (the medium and tall forest stand classes used in the mixed-ownership stand selection analysis where the tallest trees measured at least 20 m in height; Table 1). A better understanding of very fine-scale selection for forest structure is needed to guide forest restoration efforts on national forests, given that retaining owl habitat and managing for wildfire resilience are often at odds. Following historical logging of large trees and over a century of fire suppression, forests are now primarily composed (80%) of homogenized medium and tall stands in our study area. Because this analysis required substantial locational precision to match the finer-scale LiDAR metrics used to estimate forest structure, we used a stricter criterion for including GPS locations ($0 < \text{DOP} < 3$ and at least five satellites), which resulted in a median error of 17.5 m under forest canopy (Appendix S1).

Resource selection analysis.—This stricter criteria yielded fewer GPS locations and fewer points in a given night for each owl (2.8 points per owl,

per night, on average), making SSF a less appropriate analytical framework (Appendix S1). As a result, we instead used a resource selection function (RSF) approach in which the locations of used and available points were not treated as conditional on the location of the previous used location. While the stricter DOP and satellite threshold may have resulted in some GPS bias in our data (eliminating more points under denser canopy because they reached relatively fewer satellites), we assumed that this bias was constant across the elevational gradient and thus would not have a large effect on our findings (but see Frair et al. 2004). For our analysis of selection of structure within taller public forests, we generated five available points for every used point within the area of interest. The mean covariate values for used and available points for this analysis are provided in Appendix S2: Table S2.

We ran two models to test for selection of structure within taller public forests that differed in the portion of the home range considered in the model. We split the 400 m buffered 95% KDE for each owl into inner and outer portions because (1) as central place foragers (Carey and Peeler 1995), owls tend to concentrate activities in areas closer to nests and roost sites; and (2) these often have different habitat characteristics than areas further from nest and roost sites that can lead to different patterns of nocturnal habitat selection (Atuo et al. 2019). The inner portion was defined as the 0–45% (KDE), hereafter referred to as “home range core,” and the outer portion was defined as the 45–95% KDE and hereafter referred to as “outer home range.” We assumed that when multiple GPS points were recorded in either the outer home range or home range core in a single night that they were spatially independent because fixes were typically separated by several hours. We excluded owls with fewer than 10 used points for each RSF analysis (reducing our sample size from 18 to 14 owls for the analysis of the home range core and 11 owls for the analysis of the outer home range). The high proportion of private land within either the owl home range core, outer home range, or both was the key reason that owls were removed by these analyses with the exception of one owl (this one owl had few GPS points overall, likely because of a failing GPS transmitter). While this

was not a large sample of owls, it was within the range of other such spotted owl GPS studies and we expected that the many used locations for each owl, combined with our multi-faceted analyses, would reveal any strong underlying selection patterns relative to what had previously been reported for spotted owls.

We used mixed-effects logistic regression models (1 = used, 0 = available) to test for patterns of selection of structure within taller public forests. As in the SSF above, we allowed intercepts as well as slopes (regression coefficients) to vary by individual owl. The probability π_{ij} that used/available point $y_{ij} \sim \text{Bern}(\pi_{ij})$ was used by individual $i = 1, \dots, I$ at location $j = 1, \dots, J_i$ was modeled as:

$$\text{logit}(\pi_{ij}) = \mu + \alpha_i + \beta^T x_{ij} + b_i^T z_{ij},$$

where μ was the overall mean (intercept), α_i was the individual-specific random deviation from the intercept, β^T and x_{ij} were the vectors of fixed-effects coefficients and covariate values, respectively, b_i^T was the vector of individual-specific random slope coefficients, and z_{ij} was a design vector (Muff et al. 2020). For each used and available point, we analyzed the LiDAR point cloud within 30 m of the point to calculate the (1) elevation, (2) vertical complexity, (3) max tree height, (4) tall tree density, (5) shrub/understory density, (6) % canopy cover, (7) distance to activity center, and (8) squared distance to the activity center, as well as the interaction between each of the above terms and elevation (Table 1). We chose not to examine horizontal diversity in this analysis because the plot area was small and vertical diversity has been shown to be strong predictor of California spotted owl site selection (e.g., Bias and Gutiérrez 1992, Gutiérrez et al. 1992). As with the SSF, we tested covariates for high correlation (correlation coefficient >0.7; Appendix S2: Fig. S2). We also considered interactions between elevation and habitat variables to test whether selection varied as a function of elevation and reported odds ratios for covariates that interacted significantly with elevation. As in the SSF analysis, we evaluated the support for each fixed effect by examining whether the 90% or 95% confidence intervals for coefficients overlapped zero, and evaluated goodness of fit for both the home range core and outer home range using the R^2_{GLMM} (Nakagawa and Schielzeth

2013, Johnson 2014, Nakagawa et al. 2017) using the MuMIn package in program R (Barton 2020).

RESULTS

Mixed ownership stand selection

We tracked owls included in the mixed-ownership stand selection analysis for a mean of 50 nights (range 15–88 nights, $n = 16$ owls) and recorded a mean of 3.5 steps per owl-night, which resulted in a mean of 173 steps (range 130–237 steps) per owl and a total of 2765 used locations (Appendix S2: Table S3). The mean 95% KDE with a buffer of 400 m for owls included in this analysis was 2134 ha (range 832–5985 ha, $n = 16$; Appendix S2: Table S3). See Appendix S2 for additional tables and figures describing mean values for each input variable used in each analysis (Appendix S2: Tables S1, S2), correlations between these variables (Appendix S2: Fig. S1; Appendix S2: Fig. S2), distribution of each variable across elevations (Appendix S2: Figs. S3, S4), description of the owl sample sizes and areas (Appendix S2: Table S3), and the parameter estimates, confidence intervals, and standard errors for each model (Appendix S2: Tables S4–S6).

The mixed conditional SSF revealed that mixed-ownership stand selection was generally dependent on elevation, with multiple significant interactions between elevation and other variables (Fig. 3, Appendix S2: Table S4). The interaction between elevation and short stand area ($\beta_{e*sh} = -0.68$, 95% CI = -1.24 to -0.12) indicated that owls tended to select areas with proportionally less short stand area at higher elevations but with proportionally more short stand area at lower elevations (Fig. 3a). Odds ratios (hereafter “OR”) indicated that owls were more likely (selection increased by a factor of 1.41; OR = 1.41) to select areas with 10% more short stand area (e.g., increasing from 5% to 15%) at lower elevations, but less likely (selection decreased by a factor of 0.70; OR = 0.70) to select areas with 10% more short stand area at higher elevations (Table 2). Conversely, the interaction between elevation and medium stand area ($\beta_{e*med} = 0.79$, 95% CI = 0.02 – 1.56), as well as tall stand area ($\beta_{e*tall} = 0.88$, 95% CI = 0.14 – 1.63) indicated that at higher elevations owls tended to select areas with proportionally more medium

and tall stand area (OR = 1.33 and 1.35, respectively, for every 10% increase in medium and tall stand area) with an opposite trend at lower elevations (Fig. 3b,c; Table 2).

There were also interactions between elevation and each of the following variables: distance to hard edge ($\beta_{e*hed} = 1.49$, 95% CI = 0.62–2.36), seral stage diversity ($\beta_{e*ssd} = 0.67$, 95% CI = 0.09–1.24), ridge area ($\beta_{e*ridg} = -0.83$, 95% CI = -1.49 to -0.17), and SW slope area ($\beta_{e*sw} = -1.37$, 95% CI = -1.98 to -0.75; Fig. 3). Odds ratios indicated that owls at higher elevations selected areas further from hard edges (OR = 1.11 for each 100 m increase in distance from a hard edge), with proportionally more seral stage diversity (OR = 1.14 for every 10% increase in seral stage diversity), and proportionally less ridge and SW aspect area (OR = 0.84 and 0.83, respectively, for every 10% increase in ridge and SW aspect area; Table 2). At low elevations, owls selected the opposite. The goodness-of-fit test statistic suggested the SSF model explained a moderate amount of the total variation ($R^2_{GLMM} = 0.47$).

Selection of structure within taller public forests

Within taller public forests, we analyzed 580 used points in the home range core of 14 birds over a mean area of 166 ha (Appendix S2: Table S3). Mean values for used and available points for independent variables are in Appendix S2: Table S2. The models for selection of structure within taller public forests for the home range core showed a positive interaction between elevation and canopy cover ($\beta_{e*cc} = 1.18$, 95% CI = 0.14–2.22; Fig. 4a; Appendix S2: Table S5). This interaction suggested that within taller public forests in the home range core, owls tended to select areas with proportionally more canopy cover at higher elevations (OR = 1.59 for every 10% increase in canopy cover), but with less canopy cover at lower elevations (OR = 0.14 for every 10% increase in canopy cover; Table 2). Note that areas available to owls all had relatively high levels of canopy cover (mean = 93% in the home range core; Appendix S2: Table S2). The goodness-of-fit test statistic suggested the model describing the home range core explained approximately 68% of the total variation ($R^2_{GLMM} = 0.68$).

We also analyzed 276 used points in taller public forests in the outer home range of 11 birds over a mean area of 487 ha (Appendix S2: Table S3). There was a positive interaction between elevation and the tall tree density ($\beta_{e*tall} = 0.89$, 95% CI = -0.07 to 1.86; Fig. 4b; Appendix S2: Table S6), although the 95% CI slightly overlapped zero. These results, combined with odds ratios, suggested that within taller public forests in the outer home range, owls tended to select areas with more tall trees at higher elevations (OR = 1.49 for each additional 20 tall trees/ha) but with fewer tall trees at lower elevations (OR = 0.04 for each additional 20 tall trees/ha; Fig. 4b; Table 2). Also note that areas available to owls all had relatively high tall tree densities (mean = 51 tall trees/ha [over 32 m tall] in the outer home range; Appendix S2: Table S2). The goodness-of-fit test statistic suggested the outer home range model explained approximately 46% of the total variation ($R^2_{GLMM} = 0.46$).

DISCUSSION

Spotted owl nocturnal habitat selection patterns at higher elevations in this study were generally consistent with the results presented in previous studies (Gutiérrez et al. 1992, 2017, Irwin et al. 2007, Atuo et al. 2019, Blakey et al. 2019, Gallagher et al. 2019). However, habitat selection at lower elevations exhibited a different pattern and was consistent with our hypothesis of elevation-dependent habitat selection. Despite our modest sample of owls, these elevational trends were apparent across our analyses. We also observed trends consistent with our prediction that the differences in selection would correspond with habitat features associated with owl primary prey—flying squirrels at high elevations and woodrats at low elevations. Our analyses showed that spotted owls at higher elevations selected interior areas of forest stands with medium and tall trees and with higher seral stage diversity overall and less ridge and southwest aspects. When limited to taller forests on publicly owned land, spotted owls at higher elevations selected sites with higher canopy cover inside their home range core and more large trees outside their home range core. By contrast, spotted owls at low elevations selected more homogeneous stands with shorter trees that were closer

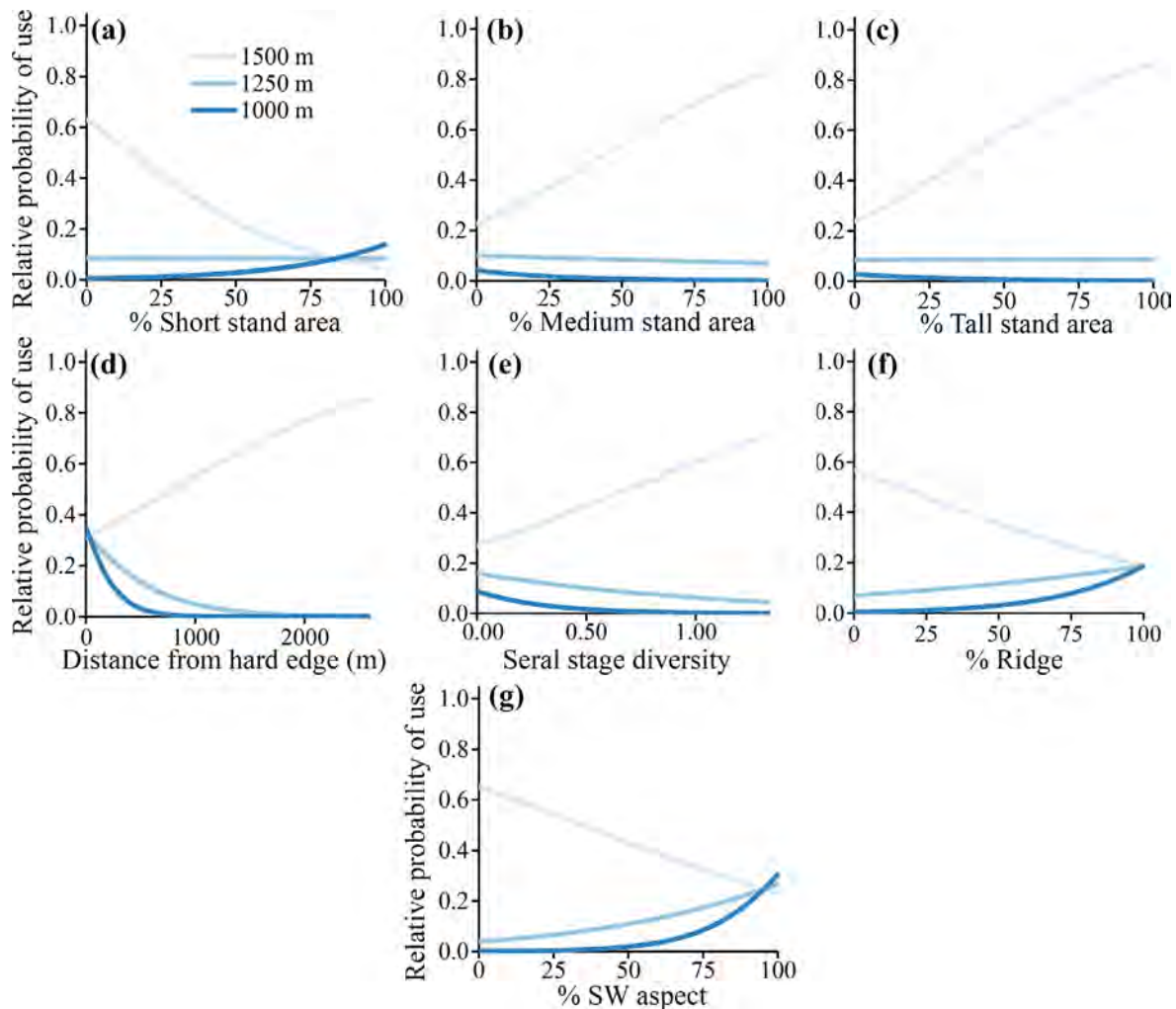


Fig. 3. Graphical depiction of results from the mixed-ownership stand selection analysis derived from a SSF. Covariates displayed are those that revealed significant interaction with elevation in the model. Panels (a–g) show the SSF fixed-effect interaction between the focal x -axis variable and elevation. Note that the model-based interaction term included elevation as a continuous term but here we have displayed elevation as discrete values for easier visualization and interpretation. The legend in panel (a) applies to all panels. For all panels, the intercept term used for graphical display of fixed effects was the median of all stratum-specific intercepts. Note that the apparent slopes of the lines are influenced by the intercept, and while the slope of the low-elevation line in panel (c) is close to 0, this does not equate to a weak effect. Odds ratios should be used to determine the difference in owl selection at low vs. high elevations for each variable. For example, panel (a) shows a higher relative probability of use of short-tree stands for birds at low elevations compared with high, but odds ratios provide the specific change in use probability at a given elevation as the proportional area of nearby short-tree forest changes by a given amount (Table 2).

to edges and that included more ridge and southwest aspect. Within taller public forests, owls at lower elevations selected areas with more open canopies inside their home range core and

fewer large trees outside their home range core. While our results do not preclude elevationally consistent and potentially stronger (Blakey et al. 2019) selection for older and more closed canopy

conditions at landscape scales (i.e., second-order selection; sensu Johnson 1980), they provided strong evidence that spotted owls selected for putative foraging habitat differently at low vs. high elevations within their home ranges, which was predicted by Gutiérrez et al. (1992).

Elevational gradients in habitat selection

We predicted that variation in spotted owl habitat selection by elevation would reflect the habitat preferences of their woodrat and flying squirrel prey that are relatively abundant at high and low elevations, respectively (Gutiérrez et al. 1992, Munton et al. 2002, Hobart et al. 2019b). Woodrats are often associated with younger, shorter forests containing hardwoods and brushy understories (Sakai and Noon 1993, Innes et al. 2007, Hamm and Diller 2009), such that selection for shorter forests by GPS-tagged owls at lower elevations may have reflected a woodrat-focused foraging strategy. Although there were generally few areas with short trees, their availability was reasonably consistent across elevations, suggesting that observed patterns in selection were simply not the result of the differences in availability of cover types (Appendix S2: Fig. S3). Moreover, selection for hard edges (between open and tall stand types) may be indicative of use as a movement corridor while avoiding open areas or using taller forests for perch sites adjacent to shorter forests containing relatively dense woodrat populations (see Fig. 2a for a photograph of a hard edge visited repeatedly by one individual owl), consistent with previous research (Sakai and Noon 1993, Zabel et al. 1995, Franklin et al. 2000). Similarly, spotted owls may have selected southwest-facing slopes and ridgetops, which tend to have more open, shrubby vegetation cover, as a strategy to prey on woodrats. However, we acknowledge that selection for some covariates in our analysis might also reflect non-foraging behaviors, as some short forest areas used by owls had widely spaced trees and occurred on ridgetops that could potentially be serving as territorial calling locations (see Fig. 2d). Finally, and somewhat surprisingly, we did not detect selection or avoidance for the shrub/understory covariate at any elevation. Dense shrub cover could make successful foraging by spotted owls difficult, which could moderate its impact on foraging habitat

selection, despite potentially higher densities of woodrats, as suggested by Sakai and Noon (1993). Our finding of neutral selection for shrub density could also be explained by differences in the composition of those shrubs, with potentially positive selection for hardwood shrubs that provide food for woodrats canceled out by potentially negative selection for areas with dense coniferous understory that might be avoided by woodrats (Sakai and Noon 1993). However, LiDAR and other current remote sensing products are not able to discriminate among the various tree or shrub species in the understory, so we were unable to investigate this question further (Su and Bork 2007, Martinuzzi et al. 2009).

The selection of putative foraging sites that had tall trees and closed canopies at higher elevations was consistent with a foraging strategy targeting flying squirrels (Waters and Zabel 1995, Munton et al. 2002, Meyer et al. 2007). Studies have shown that flying squirrels are typically associated with older coniferous forests, where they consume fungi and lichen found in these forests (McKeever 1960, Waters and Zabel 1995, Meyer et al. 2007, Sollmann et al. 2016). But selection for closed canopy forests in the home range cores and large trees in the outer home ranges at higher elevations may also have reflected a trade-off between forest conditions providing concealment from predators (canopy cover) near activity centers and key prey habitat elements (large trees) in foraging areas. Consequently, the selection of sites with greater seral stage diversity at higher elevations and lower seral stage diversity at lower elevations was opposite of what we expected, given our hypothesis that owls preyed on species that reach their highest abundance under conditions opposite of this (Sakai and Noon 1993, Hobart et al. 2019a). Still, it is possible that the higher seral stage diversity within owl home ranges at higher elevations may be linked to diet diversification beyond smaller-bodied flying squirrels (Munton et al. 2002) or may be a strategy to mitigate prey depletion in primary foraging patches (Carey et al. 1992, Ward Jr et al. 1998).

The gradients we observed in habitat selection by spotted owls, which we posit were proximately mediated by changes in prey communities, could ultimately have been driven by elevational gradients in both environmental

Table 2. Expected odds ratios associated with a 10% increase in a given habitat variable at lower (1000 m) vs. higher (1500 m) elevations in the analyses of (a) mixed-ownership stand selection and (b) selection of structure within taller public forests.

Variable	Variable change	Low elevation	High elevation
(a) Mixed-ownership stand selection			
% Short stand area	10% increase	1.41	0.70
% Medium stand area	10% increase	0.70	1.33
% Tall stand area	10% increase	0.74	1.35
Distance to hard edge (m)	100 m further	0.57	1.11
Seral stage diversity	10% increase	0.71	1.14
% Ridge	10% increase	1.49	0.84
% SW aspect	10% increase	1.86	0.83
(b) Selection of structure within taller public forests			
% Canopy cover†	10% increase	0.14	1.59
Tall tree density (per ha)‡	20 trees/ha increase	0.04	1.49

Notes: All covariates showed significant interaction with elevation in the underlying step or resource selection model (see Appendix S2 for parameter estimates and associated measures of uncertainty). For example, owls were more likely (selection increased by a factor of 1.41; odds ratio = 1.41) to select areas having 10% more short-tree stand area (e.g., increasing from 5 to 15% short stand area) at lower elevations, but less likely (selection decreased by a factor of 0.70; odds ratio = 0.70) to select areas with 10% more short stand area at higher elevations.

† Home range core.

‡ Outer home range where tall trees are over 32 m in height.

conditions and management practices. Certainly, natural gradients in woodrats and flying squirrels occur in Sierra Nevada mixed coniferous forests, and this pattern likely shaped the change in the importance of large trees when analyses were limited to taller public forests. However, low-elevation landscapes contain a higher fraction of privately owned forests (primarily industrial) managed in ways that could benefit woodrats at the expense of flying squirrels (Hobart et al. 2019b). Thus, we suspect that stronger selection for, for example, shorter forests and lower elevations was the result of some combination of private lands management (e.g., that creates brushy open or young areas) and ecological conditions (e.g., the presence of hardwoods) that promote woodrat populations in shorter forests at low but not high elevations. Distinguishing between the relative importance of management vs. environmental conditions in shaping elevational gradients in habitat selection is challenging and beyond the scope of this study, but would enhance the ability to manage prey populations for the benefit of spotted owls across the elevations at which they occur.

Barred owls have the potential to affect habitat selection by spotted owls (Gutierrez et al. 2007, Wiens et al. 2014). Although one barred owl was detected close to the home range boundaries of

two owls in this study, it was not detected until the following year (N. Kryshak and D. Hofstadter, *unpublished data*). Thus, the low density of barred owls (possibly not even present during our study) combined with our inclusion of random effects to account for variation among individual owls should have minimized any differences in behavior of these two owls.

Population implications of elevational gradients in selection and future research

In conjunction with previous studies (Zabel et al. 1995, Munton et al. 2002, Hobart et al. 2019b), our results suggest that the elevational gradients in habitat selection, which are likely a response to the distribution of primary prey, have consequences for spotted owl populations. At lower elevations, spotted owl territory occupancy and breeding probabilities tend to be higher, home ranges smaller, and woodrats more prevalent in the diet (Zabel et al. 1995, Hobart et al. 2019a, b). Moreover, spotted owl breeding probabilities can be positively associated with the prevalence of younger forests at low elevations where there is a significant hardwood component (a forest type that likely harbors relatively abundant woodrat populations) in owl territories (Thome et al. 1999, Hobart et al. 2019b). But territory occupancy can be

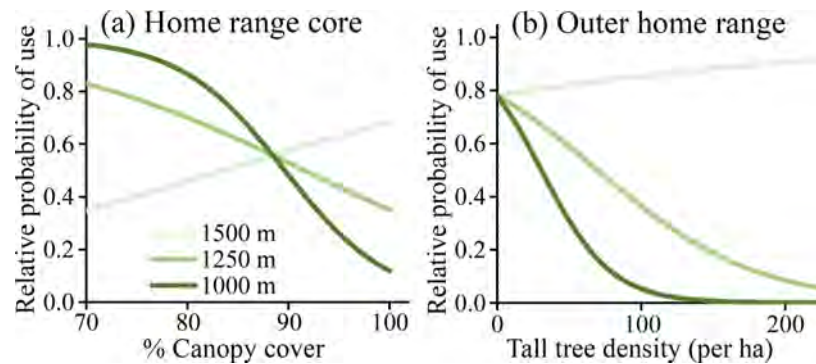


Fig. 4. Graphical depiction of results from the analysis of selection of structure within taller public forests derived from a resource selection function (RSF) analysis. Covariates displayed are those that significantly interacted with elevation in the model. Fixed-effect interactions between the focal x -axis variable and elevation input are shown at two spatial extents: (a) home range core, defined as the 0–45% kernel density estimate, and (b) outside the core area, defined as the 46–95% kernel density estimate. Note that the model-based interaction term included elevation as a continuous term but here we have displayed elevation as discrete values for easier visualization and interpretation. Also note that while the minimum canopy cover in used locations was 48%, we set a lower bound of 70%, which represents nearly a 99% confidence interval of canopy cover at available locations. As in Fig. 3, the apparent slopes of the lines are influenced by the intercept, and odds ratios should be used to determine the difference in owl selection at low vs. high elevations for both variables.

more sensitive to variation in the amount of closed canopy forest within territories at higher elevations, potentially because of spotted owls' greater reliance on flying squirrels at higher elevations (Jones et al. 2016). Certainly, several studies have shown that older and closed canopy forests benefit spotted owl territory occupancy and demographic rates (Seamans and Gutiérrez 2007, Blakesley et al. 2010, Tempel et al. 2014, 2016, Jones et al. 2018), but—unlike Jones et al. (2016)—these studies did not consider the potential mediating effects of elevation or latitude on relationships between habitat and populations.

Thus, our finding that habitat selection varies across elevation supports a growing body of research that links elevational-dependent distributions of small mammal communities with emergent effects on individual fitness and population metrics such as population density and trend (Jones et al. 2016, Hobart et al. 2019a, b). Collectively, these results suggest that lower elevations within the range of the spotted owl in the Sierra Nevada are particularly important for maintaining viable populations of this species—acknowledging that, in the future, the potential adverse effects of anthropogenic climate change

on spotted owls might be greatest at lower elevations (Peery et al. 2012).

Management implications

Our results provide further indication that managing forests for conditions that promote access to abundant woodrat—and perhaps pocket gopher—populations could benefit spotted owl populations within the lower elevations of the species' range if sufficient nest and roost habitat are available (Hobart et al. 2019b). In particular, managing for heterogeneous forests within spotted owl home ranges, such as a juxtaposition of owl nesting habitat (older forests) and woodrat habitat that includes smaller patches of younger forests with a significant shrub and hardwood component could benefit both spotted owl reproduction and territory occupancy (Sakai and Noon 1997). In northwestern California, Franklin et al. (2000) found that the juxtaposition of nesting with non-nesting habitat for spotted owls increased fitness presumably by facilitating access to woodrats as prey. Moreover, promoting woodrat food resources such as masting California black oak and nesting resources such as cavities in snags and large diameter logs (Innes et al. 2007) would not only boost woodrat abundance,

but would also increase habitat suitability for other species such as pacific fisher (*Pekania pennanti*) and owls (Long et al. 2016).

Nevertheless, promoting woodrat habitat at lower elevation without adverse effects to spotted owl populations is challenged by several considerations. First, spotted owls at lower elevations in our study area consume flying squirrels as well as woodrats based on pellet analyses (R. J. Gutiérrez, *unpublished data*), such that promoting sufficient habitat for both species—including older, closed canopy forests for flying squirrels—could buffer spotted owls from variability in the populations of either prey species. Second, spotted owls use forests characterized by tall, old trees, and more complex canopies for nesting and roosting in the Sierra Nevada regardless of elevation (Verner et al. 1992, Gutiérrez et al. 2017, North et al. 2017). Creating gaps in older, more complex-canopied forests that are being used by the owls for nesting and roosting could compromise the nesting habitat quality by increasing predation risk as well as the thermal exposure (Barrows 1981). Therefore, potentially suitable areas for such gap creation (thus increasing seral stage diversity) could include dense canopy forests without a large-tree component and drier sites unlikely to support tall trees and dense cover (sites less suitable for nesting by spotted owls; Fricker et al. 2019). Third, canopy cover was high at used sites within the owl home range cores across elevations, averaging 93% (as measured using TAO area derived from LiDAR; Appendix S2: Table S2). For instance, 99% of available points had 69–100% canopy cover, but reducing forest cover below this level over significant portions of a home range core could have unknown effects on foraging habitat, even at lower elevations. Fourth, the tendency for individuals to avoid high seral stage diversity at lower elevations (Fig. 3) suggests limits to the extent to which owls will benefit from heterogeneity—at least as we defined and measured it. Fifth, few researchers have studied spotted owl diet and foraging habitat selection during the winter, when starvation is likely a higher risk than during our study period and prey dynamics may shift to species that are more prevalent or easier to locate and capture when snow is present. Greater knowledge of winter behaviors would contribute to a

more complete understanding of spotted owl conservation. Finally, while spotted owls tended to select hard edges in this study, and non-juvenile survival rates appear to benefit from edge between similar edge types (Tempel et al. 2014), relatively high levels of edge have also been associated with reduced territory occupancy in the Sierra Nevada and tendency to avoid nesting close to edges (Phillips et al. 2010, Tempel et al. 2016). Certainly, some of this ambiguity could have resulted from previous studies not considering how the effects of edge may vary across elevations, or alternatively because studies examined properties that occur at different spatiotemporal scales (i.e., population responses vs. individual movement processes). Caution is merited when considering the creation of edge as a management tool owing to potential negative impacts of predation, increased thermal profile, and forest fragmentation on owls.

By contrast, selection of forest conditions typically associated with abundant flying squirrel populations, coupled with the dietary shift from woodrats to flying squirrels at higher elevations (Munton et al. 2002), suggests that maintaining older, closed canopy forests is more likely to provide high-quality foraging habitat at those high elevations (see Jones et al. 2016), as long as sufficient habitat diversity is promoted. Flying squirrels are typically more abundant in forests with a greater basal area of larger trees and higher canopy cover, and can decline following forest thinning activities (Meyer et al. 2007, Holloway et al. 2012, Sollmann et al. 2016), although declines are not universal (Rosenberg and Anthony 1992, Ransome et al. 2004, Gomez et al. 2005) and responses can be scale-dependent (Sollmann et al. 2016). Thus, at higher elevations, managing for forest conditions such as tall (older) trees that promote flying squirrel populations could benefit spotted owls, whereas opening forests or removing tall trees at higher elevations is more likely to have an adverse effect, especially given the population decline at higher elevations, on spotted owl foraging habitat than at lower elevations. Areas of high cover provided by tall trees may currently be a limiting factor for spotted owl and their prey at higher elevations (North et al. 2017) and due to the legacy of fire suppression and historic logging practices, restoration of this cover type likely requires tree density

reductions (of smaller trees) to reduce competition for limited resources (and promote growth in taller trees; see also Eyes et al. [2017] and Kramer et al. [2021] for owl response to fire use). Thus, managing higher elevation forests to increase seral diversity could benefit spotted owls through both the diversification of their prey base and the promotion of tall tree growth and resilience through reduced resource competition. Given that owls at higher elevation tend to select against southwest-facing slopes and ridges, these may be appropriate locations to reduce tree cover densities and increase seral stage diversity when forest cover is homogenous—objectives consistent with forest restoration objectives (North 2012)—while minimizing potential effects to spotted owls.

Our results, combined with other studies (Hobart et al. 2019a), suggest that increasing woodrat populations at higher elevations via forest management could have potential benefits to spotted owls, though more research is needed on prey populations and spotted owl dietary and movement patterns (e.g., are woodrat populations limited by high elevation climatic and biotic factors; e.g., diet and predation; even if suitable habitat is created; does owl diet shift seasonally in areas with heavy snowfall to rely on flying squirrels more heavily in the winter, or do owls migrate downslope, as indicated by Laymon 1989). But such management efforts are most likely to be successful in higher elevation areas that currently contain woodrats at low densities while less likely to be successful in the highest areas of owl distributions where woodrats are often absent potentially because of unsuitable climate rather than vegetation conditions. In addition, several species of woodrats occur in the Sierra Nevada, each with different elevational distributions and habitat associations, which complicates their management (Carey et al. 1999, Innes et al. 2007, Hobart et al. 2019a). Thus, more research is needed on range, abundance, and limiting factors of these prey species across elevation and latitudinal gradients to assess the potential effectiveness of such an approach for woodrats at higher elevations—especially in light of future climate change. We also caution against developing management prescriptions directly from the elevational values presented in this study (e.g., Figs. 3, 4) given that latitudinal gradients interact

with elevation to shape vegetation and thus prey communities. The transition between a mixed woodrat-flying squirrel diet to a primarily flying squirrel diet likely occurs at higher elevations in the southern Sierra Nevada and lower elevations in the northern portion of the range as a result of latitudinal change in climate and forest conditions (Gutiérrez et al. 2017).

Beyond spotted owls, we recommend future research focused on habitat selection patterns by species in montane ecosystems consider how selection varies along elevational gradients. Such assessments can be conducted in a straightforward manner—as we did here—by evaluating support for resource selection models containing interactions between elevation and covariates representing habitat features of interest such as canopy cover, tree size, and vertical structure. Linking such assessments with detailed studies of prey ecology would help untangle what are inevitably complex relationships between forest structure and composition, prey abundance and availability, and foraging strategies and population outcomes. Regardless, these previously underappreciated elevational gradients revealed here merit additional study in additional systems and could provide key insights leading to more effective habitat management for montane species of conservation concern.

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SUPPORTING INFORMATION

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ARTICLE

Landscape heterogeneity provides co-benefits to predator and prey

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Abstract

Predator populations are imperiled globally, due in part to changing habitat and trophic interactions. Theoretical and laboratory studies suggest that heterogeneous landscapes containing prey refuges acting as source habitats can benefit both predator and prey populations, although the importance of heterogeneity in natural systems is uncertain. Here, we tested the hypothesis that landscape heterogeneity mediates predator–prey interactions between the California spotted owl (*Strix occidentalis occidentalis*)—a mature forest species—and one of its principal prey, the dusky-footed woodrat (*Neotoma fuscipes*)—a younger forest species—to the benefit of both. We did so by combining estimates of woodrat density and survival from live trapping and very high frequency tracking with direct observations of prey deliveries to dependent young by owls in both heterogeneous and homogeneous home ranges. Woodrat abundance was ~2.5 times higher in owl home ranges (14.12 km²) featuring greater heterogeneity in vegetation types (1805.0 ± 50.2 SE) compared to those dominated by mature forest (727.3 ± 51.9 SE), in large part because of high densities in young forests appearing to act as sources promoting woodrat densities in nearby mature forests. Woodrat mortality rates were low across vegetation types and did not differ between heterogeneous and homogeneous home ranges, yet all observed predation by owls occurred within mature forests, suggesting young forests may act as woodrat refuges. Owls exhibited a type 1 functional response, consuming ~2.5 times more woodrats in heterogeneous (31.1/month ± 5.2 SE) versus homogeneous (12.7/month ± 3.7 SE) home ranges. While consumption of smaller-bodied alternative prey partially compensated for lower woodrat consumption in homogeneous home ranges, owls nevertheless consumed 30% more biomass in heterogeneous home ranges—approximately equivalent to the energetic needs of producing one additional offspring. Thus, a mosaic of vegetation types including young forest patches increased woodrat abundance and availability that, in turn, provided energetic and potentially reproductive benefits to mature forest-associated spotted owls. More broadly, our findings provide strong empirical evidence that heterogeneous landscapes

containing prey refuges can benefit both predator and prey populations. As anthropogenic activities continue to homogenize landscapes globally, promoting heterogeneous systems with prey refuges may benefit imperiled predators.

KEYWORDS

forest management, heterogeneity, predator conservation, predator–prey, spotted owl, woodrat

INTRODUCTION

Predator populations are declining globally, often precipitated by habitat loss and changes in trophic interactions (Estes et al., 2011; Ripple et al., 2014). Many predators occur, and presumably evolved, in complex landscapes with heterogeneously distributed resources that shape many of their ecological interactions (Hunter & Price, 1992; Wiens, 1995). Among these, the composition and configuration of habitat patches can mediate predator–prey interactions, with consequences for population dynamics for both predators and their prey (Fahrig et al., 2011; Schmitz, 1998; Wilson et al., 2019). As anthropogenic land-use change increasingly homogenizes landscapes, there is a growing need for empirical studies on the effects of heterogeneity (variability of an environmental property in time and space; Li & Reynolds, 1995) in predator–prey systems (Bullock et al., 2022; Layman et al., 2007). However, to date most studies on the effects of heterogeneity on predator–prey interactions have been theoretical or conducted within controlled experimental settings subject to many simplifying assumptions (Hastings, 1977; Sih, 2005). Further, empirical studies are typically conducted at patch rather than landscape scales, do not involve mobile predators capable of accessing many patches, or fail to account for alternative prey (Ryall & Fahrig, 2006).

Landscape heterogeneity is most likely to affect predator–prey dynamics through effects on prey abundance or vulnerability. In heterogeneous systems, landscape-scale abundance of prey is an emergent property of the composition of habitat patches of varying quality, with landscapes containing a greater area of high-quality habitat patches expected to have higher prey abundance (Holt, 1985; Iles et al., 2018). However, dispersal from high-density source patches can increase densities within lower-quality patches (Holt, 1985), decoupling local abundance from habitat quality (Ehrlén & Morris, 2015; Iles et al., 2018). In some cases, landscape-scale abundance may even exceed the combined carrying capacity of all representative patches (Holt, 1985; Zhang et al., 2017). When predation rate is determined by prey density (i.e., the functional response), these patch- and landscape-scale differences in prey abundance can have

profound effects on predator populations (Coulson et al., 2006; Holling, 1959), which may be most pronounced when predators exhibit differential hunting success among patches (Hopcraft et al., 2005).

Landscape heterogeneity can affect prey vulnerability by creating refuges that reduce predation risk—that is, the likelihood of a predator encountering or capturing prey (Sih, 1987). When predator and prey prefer different habitats, the relative amounts and arrangements of safe (difficult for the predator to successfully capture prey) versus risky (easier for the predator to successfully capture prey) patches can decouple prey availability from abundance (Hebblewhite et al., 2005; Laundré, 2010), with ostensible tradeoffs when either habitat type predominates. Homogeneous landscapes dominated by risky habitat may increase prey accessibility but limit abundance or advance prey depletion (Coulson et al., 2006; Huffaker et al., 1963), while landscapes dominated by safe habitat may increase prey abundance but limit capture opportunities (Hopcraft et al., 2005). By reducing top-down control on prey abundance, refuge use can also promote density-driven dispersal into adjacent risky patches (Holt, 1985) and provide foraging opportunities along the edges of the two habitat types (Laundré & Hernández, 2003; Zulla et al., 2022). Therefore, compared to homogeneous landscapes where predator habitat predominates, heterogeneity may decrease the availability of hunting patches for predators but increase the encounter probability within those that remain, potentially increasing hunting success (Hopcraft et al., 2005; Zulla et al., 2022). In summary, the relationship between habitat characteristics and predation rates often depends on the landscape context, although studies need to be conducted across a gradient of heterogeneity in natural systems—that is, complex landscapes containing a mosaic of prey refuges and patches of varying density and catchability versus homogeneous ones dominated by a single habitat type and uniform catchability of prey.

We assessed how landscape heterogeneity mediates predator–prey interactions between a mature forest predator, the California spotted owl (*Strix occidentalis occidentalis*), and one of its primary prey species, the dusky-footed woodrat (*Neotoma fuscipes*). While spotted

owls consume a variety of small mammals and other taxa, woodrats represent the largest-bodied (Ward Jr et al., 1998) and, thus, most energetically profitable prey when present (Weathers, 1996). As such, woodrat consumption can drive patterns in fitness, occupancy, and space use for spotted owls (Franklin et al., 2000; Hobart, Jones, et al., 2019). Spotted owls use mature forest for nesting, roosting, and foraging (Gutierrez et al., 1992; Moen & Gutiérrez, 1997), while woodrats are predominantly associated with younger, brushier forests and large oaks (Sakai & Noon, 1993; Williams et al., 1992), which are traditionally viewed as less suitable habitat for foraging owls (Atuo et al., 2019; Kramer, Jones, Whitmore, et al., 2021). Despite this purported mismatch between predator and prey habitat, in lower-elevation forests of the Sierra Nevada, USA, woodrats can compose up to 94% of spotted owl diet by weight (Williams et al., 1992). Sakai and Noon (1997) observed intermittent, short-distance movements into mature forests by woodrats occupying dense young forests within a patchy landscape, suggesting that forays across ecotonal boundaries may increase the vulnerability of woodrats to avian predation. Indeed, recent work has linked increasing forest heterogeneity at a home range scale to woodrat consumption (Hobart, Jones, et al., 2019) and documented frequent woodrat captures by owls foraging along edges between hardwood and coniferous-dominated forests (Zulla et al., 2022). In the Sierra Nevada, differences in management practices among landownership types has created landscapes that differ dramatically in forest composition and patch configuration (North et al., 2017), providing a gradient of heterogeneity to (1) examine the mechanisms driving increased woodrat consumption by spotted owls and (2) determine whether these mechanisms also confer benefits to woodrat populations at a landscape scale.

Herein, we hypothesized that heterogeneous landscapes featuring a mixture of early and late-successional habitat would create sources or spatial refuges for prey that benefit both predator and prey populations when predators and prey are associated with different habitats. We combined live trapping and monitoring of woodrat survival with direct observations of prey deliveries by spotted owls to test several predictions related to our central hypothesis. Specifically, we predicted (1) owl home ranges with greater habitat heterogeneity, in the form of a mosaic of vegetation types including mature forest, young forest, and open areas, would contain higher densities of woodrats than homogeneous home ranges consisting primarily of mature forest. We also predicted that (2) mortality rates of woodrats would be higher in mature forest and within homogeneous home ranges because of the lack of young forest refuges, but (3) a

functional response exists where owl predation rates on woodrats would be higher in heterogeneous than homogeneous home ranges. Finally, we predicted that (4) total biomass of prey delivered to owl nests would be greater in heterogeneous home ranges because of a greater consumption of large-bodied woodrats and, accordingly, the consumption of alternative, smaller-bodied prey would not reconcile this deficit in homogeneous home ranges.

METHODS

Study system

Our study primarily occurred on the western slope of the central Sierra Nevada in California in the USA, within and adjacent to the Eldorado Demography Study Area (EDSA; Figure 1), a long-term spotted owl monitoring site encompassing roughly 355 km² of the Eldorado National Forest (Jones et al., 2021). Elevation in the EDSA ranges from 366 to 2257 m, although we concentrated our woodrat trapping efforts within ~1000 to 1500 m, a range that can contain dense woodrat

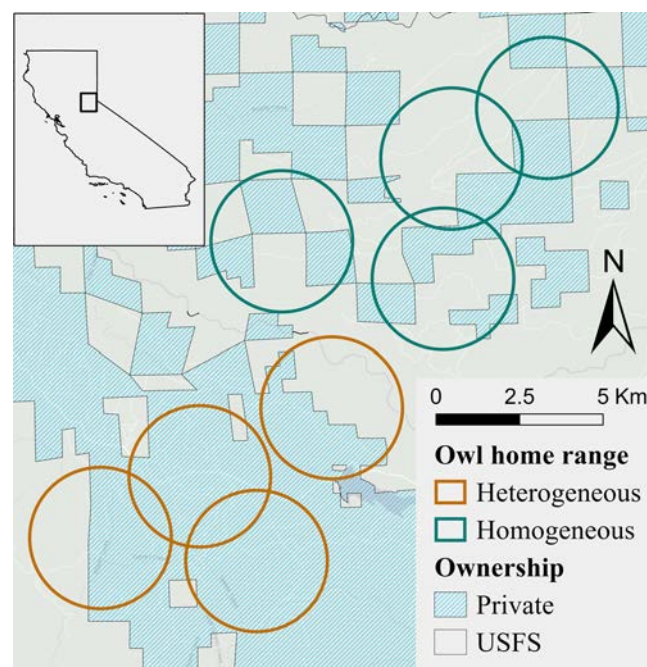


FIGURE 1 Locations of spotted owl (*Strix occidentalis*) home ranges within and adjacent to the Eldorado Demography Study Area (EDSA) in the central Sierra Nevada, California, USA, where dusky-footed woodrat (*Neotoma fuscipes*) abundance and survival (Predictions 1 and 2) were estimated in 2020 and 2021. Landscape composition is depicted by orange (heterogeneous) and teal (homogeneous) circles within private and public (USFS, United States Forest Service) land.

populations (Williams et al., 1992). Dominant conifer species included incense cedar (*Calocedrus decurrens*), ponderosa pine (*Pinus ponderosa*), sugar pine (*P. lambertiana*), Douglas fir (*Pseudotsuga menziesii*), and white fir (*Abies concolor*), while dominant hardwoods included California black oak (*Quercus kelloggii*) and tanoak (*Lithocarpus densiflorus*), the latter of which was patchily distributed throughout the study area in dense pockets (Fites-Kaufman et al., 2007).

Landownership in the EDSA was split between ~60% public land, primarily managed by the United States Forest Service (USFS), and ~40% private land, existing mostly as commercial timberlands. Differences in land use practices among ownership types in this region have created a landscape with distinct spatial variation in forest structure, age, and configuration. On USFS-managed lands, a century of fire suppression, coupled with selective logging of large trees, has created contiguous, spatially homogeneous stands of mature trees within public forests (Stephens et al., 2015). On privately owned lands, timber harvesting occurs more frequently, often with an emphasis on even-aged management that creates a mosaic of different stand types, including open clear cuts, young plantations interspersed with brushy pockets of saplings and tanoak, and patches of mature forest similar to those occurring on public lands (North et al., 2017). Forests on private lands are on average 30–40 years younger than those on public lands and may contain fewer stand features generally found in older forests, such as large snags and logs (North et al., 2017). Thus, private lands tend to contain forests with less vertical structure but more heterogeneity in forest ages, including young stands that can harbor dense woodrat populations (Sakai & Noon, 1993). Spotted owls nest and forage on both ownership types (Atuo et al., 2019; Hobart, Roberts, et al., 2019; Roberts et al., 2017).

Overview

To test our predictions about the effects of landscape heterogeneity on predator–prey interactions between spotted owls and woodrats we (1) used live-trapping and mark-recapture methods to estimate woodrat abundance (Prediction 1); (2) deployed very high frequency (VHF) collars on woodrats to monitor individual survival and identify causes of mortality (e.g., likely owl predation; Prediction 2); and (3) quantified consumption rates by monitoring woodrat and other prey deliveries to nests with video cameras within owl home ranges (Predictions 3 and 4). All three of these field methods were used in home ranges containing varying degrees of habitat heterogeneity.

Classifying landscape composition and configuration within spotted owl home ranges

We compared occupied spotted owl home ranges that were either highly homogeneous or heterogeneous in the proportional composition and configuration of open, young, and mature forest. To identify homogeneous or heterogeneous home ranges for woodrat sampling, we visually inspected aerial imagery from the National Agriculture Imagery Program (NAIP) at all known spotted owl home ranges ($n = 28$) within and immediately adjacent to the EDSA and identified those containing predominantly mature forest in large, contiguous stands versus those that had a more even mixture of open, young, and mature forest of differing patch sizes (Figure 2A,B).

For this subset of highly homogeneous and heterogeneous home ranges, we created circular buffers with a 2.12 km radius—an area equal to the median home range of all males tagged for a minimum of 25 days (14.12 km²) from previous studies (Atuo et al., 2019; Jones et al., 2016; Zulla et al., 2022)—around the most recent known nest or roost site. Next, within each buffered home range, we used NAIP imagery collected in 2018 and 2020 to manually digitize patches of relatively uniform vegetation conditions following protocols described in Tempel et al. (2014). We defined the three predominant forest structure classes based on canopy cover and size of dominant trees as follows: mature forest (>40% canopy cover and dominant trees >12 inches diameter at breast height [dbh]), young forest (>40% canopy cover and saplings or dominant trees <12 inches dbh), and open habitat (<40% canopy cover). Heterogeneous home ranges had more even representation of habitat types, estimated by Shannon's diversity index ($\hat{H} = 0.92$, range = 0.79–1.05; mean areas = 58.8% mature, 27.9% young, and 12.2% open) than homogeneous home ranges ($\hat{H} = 0.65$, range = 0.57–0.71; mean areas = 78.6% mature, 9.9% young, and 11.5% open).

For tests of woodrat abundance and survival (Predictions 1 and 2), we excluded home ranges that were far from other home ranges we considered sampling, above elevations with high woodrat densities (>1500 m) and below elevations where owls are commonly found in our study landscape (<1000 m), or predominantly within the King Fire footprint and likely confounded substantially by severe fire (Jones et al., 2016). From the remaining subset we then selected nine home ranges (five homogeneous, four heterogeneous) by prioritizing ones that were occupied at the time of woodrat sampling based on routine spotted owl surveys conducted as part of the EDSA (Jones et al., 2021), occurred at similar

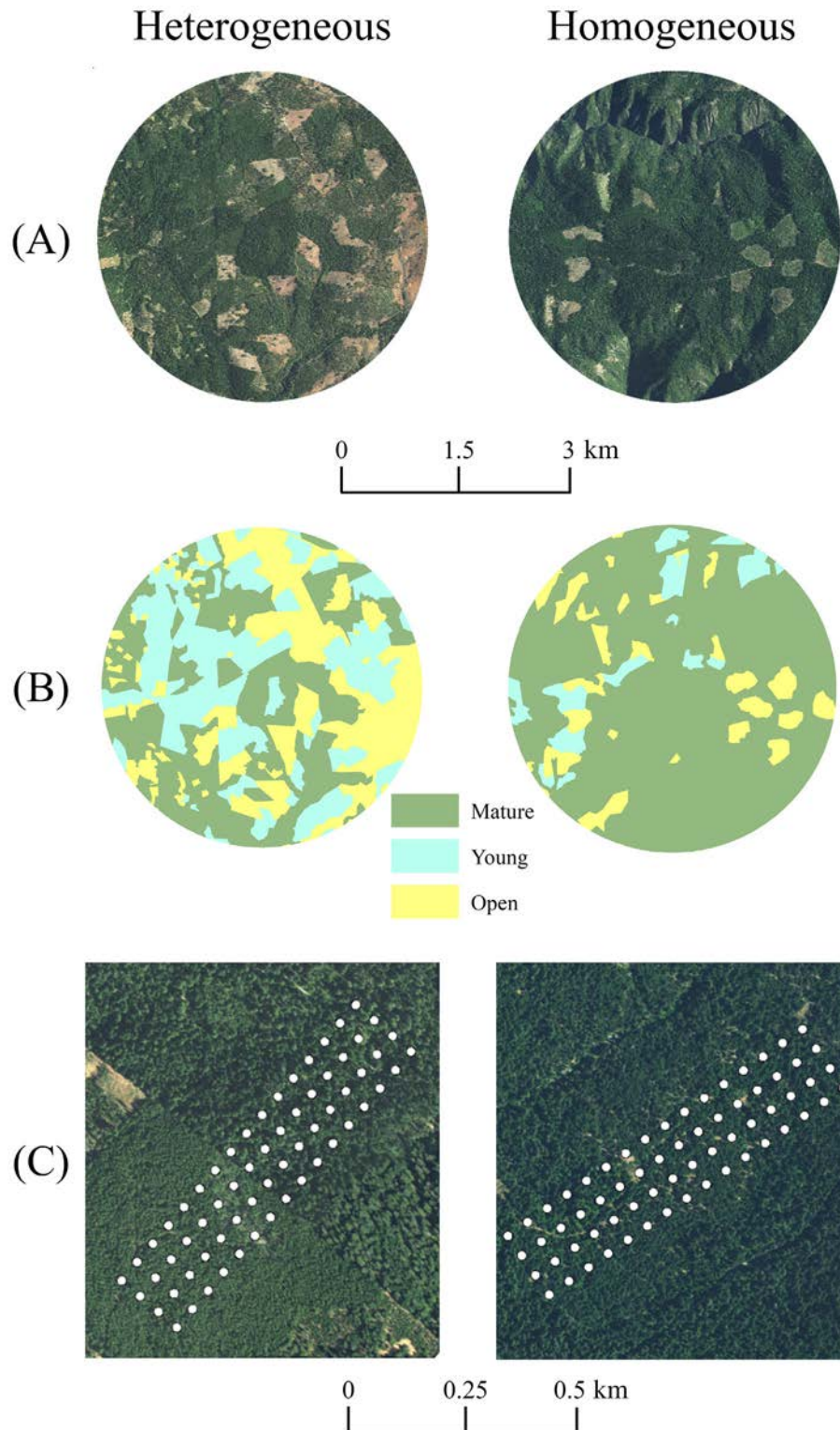


FIGURE 2 Examples of landscape composition (heterogeneous or homogeneous) within spotted owl (*Strix occidentalis*) home ranges surveyed in 2020 and 2021 in the central Sierra Nevada, California, USA. Differences are shown at the scale of a spotted owl home range with both (A) National Agriculture Imagery Program (NAIP) imagery and (B) habitat type (mature, young, and open), and (C) at the scale of a trapping grid visualized with NAIP imagery.

elevations (mean elevation range 1290–1372 m), and occurred in close proximity. For tests of prey delivery rates by owls (Predictions 3 and 4), we selected four of

these home ranges along with an additional 11 from the EDSA and Sierra Pacific Industries' Stirling Study Area (SSA) in the northern Sierra Nevada (Zulla et al., 2022).

Among these, home ranges had similar representation of habitat types compared to those from Predictions 1 and 2, with greater evenness in heterogeneous ($H = 0.99$, range = 0.82–1.05; mean areas = 54.3% mature, 27.9% young, and 17.8% open) than homogeneous home ranges ($H = 0.71$, range = 0.62–0.74; mean areas = 76.4% mature, 10.9% young, and 12.7% open).

Field methods and analysis

Prediction 1: Estimating woodrat abundance

To compare woodrat abundance within homogeneous and heterogeneous home ranges, in 2020 and 2021 we deployed grids of 64 traps (in 8×8 or 4×16 configuration) spaced at 50-m intervals among eight of the nine occupied spotted owl home ranges classified as homogeneous ($n = 4$) or heterogeneous ($n = 4$; Figure 1). Within homogeneous home ranges, we randomly placed grids within large stands of contiguous mature forest (Figure 2C). Within heterogeneous home ranges, we deployed trapping grids stratified by habitat—using ArcMap and NAIP imagery where, specifically, we created an algorithm to identify edge areas between young-mature and open-mature patches of a minimum size to center our trapping grids. We centered our trapping grids along habitat edges to ensure adequate representation of core and edge for each habitat type; variable patch size and distribution in heterogeneous home ranges posed challenges to sampling (e.g., uneven representation of habitat types) if we followed a truly random grid placement strategy (Figure 2B). As part of this process, we constrained grid locations such that they contained at least 30% each of mature forest and either young forest or open area (Figure 2C).

We deployed traps for six consecutive days following a paired approach in which two grids were sampled concurrently—one each within a heterogeneous and homogeneous home range. Within each home range, we deployed one ($n = 2$), two ($n = 2$), or four ($n = 4$) trapping grids. Trapping occurred from late spring through summer in 2020 and 2021. We captured woodrats in steel mesh traps (Model 105; Tomahawk Live Trap Company, Hazelhurst, Wisconsin, USA) baited with a mix of birdseed, dried fruit, and peanuts. All captured animals were ear punched and marked with a unique ear tag (Model 1005-1; National Band & Tag Company, Newport, KY, USA) or passive integrated transponder (PIT) tag (Avid Identification Systems, Norco, CA, USA). All captures were done with approval by the Institutional Animal Care and Use Committee of the University of Wisconsin, Madison (IACUC No. A006173-A01) and followed

guidelines from the American Society of Mammalogists (Sikes et al., 2019).

We estimated abundance using Huggins closed-capture models in the program MARK (White & Burnham, 1999). We modeled initial capture probability (p) and recapture probability (c) accounting for time (i.e., sampling occasion), sampling year, habitat type (open, young, mature), and home range configuration (heterogeneous or homogeneous). For model selection, we used Akaike's information criterion corrected for small sample size (AIC_c) and AIC_c weights (w) to select the best-supported model and assessed significance using 95% CIs. If a competitive model contained one or more uninformative parameters (i.e., parameter CIs overlapped zero), we dropped this model from consideration (Arnold, 2010). We then used our top model to derive woodrat abundance for each habitat type.

To estimate relative densities by habitat type, we applied these abundance estimates to the effective trapping area (ETA) surveyed (Gerber & Parmenter, 2015). We estimated ETA (in square kilometers) following Parmenter et al. (2003); in this, we buffered all grids by 50 m, equal to half of the estimated mean for maximum nightly distance moved by woodrats, then summed the total area of each habitat type captured across all buffered grids. Then we calculated density estimates for each habitat type by dividing the model-derived abundance estimates by their respective ETA (Schwemm et al., 2018). Given that dispersal from patches of adjacent young forest may facilitate increased woodrat densities (Sakai & Noon, 1993, 1997), we considered mature forest in heterogeneous and homogeneous home ranges as two separate habitat classes. We obtained estimates for woodrat abundance within homogeneous ($\hat{N}_H$) and heterogeneous ($\hat{N}_E$) home ranges by scaling up our density estimates relative to the area of open (A_O), young (A_Y), and mature (A_M) forest within each home range (Appendix S1: Section S1). We calculated SE values for density and abundance using the Delta method (Powell, 2007), which allowed us to estimate the variance of a parameter derived from multiple variables, each with its own variances. We also performed statistical comparisons of abundance between homogeneous and heterogeneous home ranges using a two-sample Welch's t -test.

Prediction 2: Estimating woodrat survival

To test Prediction 2, we monitored survival with radio transmitters and assessed cause-specific mortality. We selected a subsample of the woodrats caught within seven of the eight occupied spotted owl home ranges (three homogeneous, four heterogeneous) during our

mark-recapture surveys from Prediction 1, along with other individuals trapped opportunistically among these and one additional homogeneous home range, for survival monitoring. In 2020 and 2021, we fit woodrats weighing above 120 g with VHF collars (Lotek Model TW-5, 10 g; Lotek Wireless Inc., Newmarket, Ontario, Canada or Telenax Model TXE-116C, 6 g; Titley Scientific, Columbia, Missouri, USA) equipped with onboard activity sensors, which allowed us to detect mortality events shortly after they occurred. Within 2 days of collar deployment, we tracked individual woodrats to their nests (hereafter “middens”) and recorded relevant information about each area. We assigned habitat designations (open, young, mature) for all collared individuals based on where the midden was located, not where they were trapped—although these were typically the same habitat type.

We initiated VHF monitoring in 2020 in the week of 14 June and in 2021 in the week of 11 May. We located collared woodrats one to two times per week and recorded status (alive, dead, missing/collar failure) on each occasion from the first capture until death, disappearance, or the end of the study (17 October 2020 or 11 September 2021). We also performed monthly midden checks—repeating triangulation of collared woodrats to middens—to ensure that an individual had not permanently dispersed during our monitoring period. If a signal for a woodrat collar disappeared, we set traps outside of its midden for several days. In all but one incident, the source of the lost signal was a dead collar battery—in these cases, the individual was recaptured alive, the collar removed, and monitoring ended.

Once an inactive signal was detected, we immediately recovered the collar. We recorded images and took detailed notes for each mortality event, including location, habitat type, distance to midden, and state of collar, to assess cause of mortality. Avian predation was considered the cause of death if the collar was recovered with minor damage under a spotted owl nest tree or perch site with whitewash and/or viscera in the vicinity; while other raptor species were present in our study area, we attributed avian predation to spotted owls given that all sites were owl-occupied, mortalities occurred at night, and all recovered collars were found in close proximity to active spotted owl nest sites. Additionally, woodrats are the most common spotted owl prey and are rarely consumed by other predators of a similar size class (e.g., red-tailed hawk, *Buteo jamaicensis*). Mammalian predation was considered the cause of death if the collar was recovered in more open, brushy habitat absent any roosting or perching trees, with considerable damage and teeth marks to the collar. Finally, if the collar was tracked to a midden with a mortality signal active, we set traps for

several days to ensure that the collar was not malfunctioning and the individual was not alive—after which it was determined to be a mortality of unknown or of natural cause (e.g., age, nutritional deficiency, disease) and not a predation event.

We estimated weekly woodrat survival rates by constructing known-fate models in the program MARK (White & Burnham, 1999), with a staggered entry design to allow introduction of individuals throughout the study (Pollock et al., 1989). We analyzed two sets of known-fate models, one considering all mortality events and one only including mortalities that were attributed to avian (likely spotted owl) predation. In 2020, we constructed encounter histories from 14 June until 17 October; in 2021, we constructed encounter histories from 9 May until 11 September. We set Sunday as the start of each sampling week and introduced covariates relative to habitat type, home range composition, month, year, and distance to owl nest tree or territory center and considered a categorical effect relative to each unique home range.

Prediction 3: Estimating woodrat consumption rates by owls

We directly observed prey deliveries to dependent young by nesting spotted owls within home ranges classified as either homogeneous or heterogeneous. We used Global Positioning System (GPS) tagging and nest-video monitoring data collected and described previously by Zulla et al. (2022). Briefly, in 2019 and 2020, breeding spotted owls were located as part of ongoing work within the EDSA and SSA (Hobart, Roberts, et al., 2019; Roberts et al., 2017; Zulla et al., 2022), and 15 nesting males were captured and GPS tagged (five in 2019, 10 in 2020). Infrared video cameras (AXIS Q1786-LE 4; Axis Communications AB, Lund, Sweden) were placed at the nest sites of these individuals, secured to an adjacent tree with a clear view of the nest. These cameras continuously recorded high-quality video throughout the nocturnal foraging period (20:00–06:30 pacific daylight time). All video footage was reviewed, and prey deliveries to the nest were identified to species whenever possible. We detected 26 larger-bodied prey deliveries over the course of monitoring that could not be identified to species; these were split relatively evenly among homogeneous and heterogeneous sites, and we do not believe that excluding these from our count of woodrat deliveries compromised any results. We estimated woodrat delivery rates (in number delivered per hour) and scaled these to monthly estimates with bootstrapped CIs. We conducted a two-sample Welch's *t*-test to determine differences in mean monthly woodrat delivery rates between homogeneous and heterogeneous home ranges.

We corroborated the previously described estimates of monthly woodrat consumption rates in homogeneous and heterogeneous home ranges by multiplying per-capita mortality rates scaled to monthly values (Prediction 2) with woodrat abundance estimates for each home range within our landscape composition categories (Prediction 1). We calculated SE and 95% CI for these values using the Delta method (Powell, 2007). We then conducted a two-sample Welch's *t*-test to test for differences in monthly woodrat consumption rates between homogeneous and heterogeneous home ranges. We corroborated these estimated mortality rates with those derived from nest camera data by conducting a one-way ANOVA with two factors: estimation method (nest camera or known-fate estimates) and landscape composition (heterogeneous or homogeneous). This allowed us to determine whether the number of monthly woodrat mortalities differed between our methods of estimation.

Prediction 4: Estimating biomass delivery rates by owls

To estimate total biomass delivery rates (in grams per unit time), we used nest video data described in Prediction 3 and considered all prey deliveries. To convert number of prey items into biomass rates, we used mean values for body mass of each prey item collected and described in Zulla et al. (2022). Briefly, mean values for mass of woodrats and Humboldt flying squirrels (*Glaucomys oregonensis*) were estimated using regurgitated pellets collected from previous studies in the EDSA. Skull and mandible measurements of skeletons from these pellets were compared to those of museum specimens for which masses were available, and predictive relationships between mass and skull measurements were quantified to determine estimates of body mass for each skeleton collected from pellets. The estimated mean body mass of woodrats was 187.4 g (range 110.9–271.2 g), while that of flying squirrels was 98.8 g (range 80.2–117.2 g). Other prey species were assigned a mass based on the midpoint of mass ranges in the literature (e.g., mouse 20 g; Reid, 2006). Finally, if the species of a prey delivery could not be determined, then it was assigned to a size class (extra small: 5.3 g, small: 47.5 g, medium: 175 g, large: 205 g), with the corresponding mass derived from the average mass of species within this size class.

We summed deliveries of all species or size classes and converted these into biomass values, then standardized them to biomass delivery rates (in grams delivered per hour) and scaled these to monthly estimates. We also

conducted two-sample Welch's *t*-tests to determine whether there were differences in delivery rates of each prey group and total biomass delivery between homogeneous and heterogeneous home ranges.

Results

Prediction 1: Higher woodrat abundance within heterogeneous home ranges

Over the two field seasons, we deployed 22 grids of 64 traps each among eight spotted owl home ranges (four heterogeneous, four homogeneous) for a total of 8448 trap nights and captured 236 unique individuals a total of 460 times. Our most supported mark-recapture model for woodrat abundance suggested a behavioral response to capture, as $p = 0.12$ (95% CI: 0.07, 0.20) and $c = 0.33$ (95% CI: 0.30, 0.37), with neither parameter varying as a function of sampling year, habitat type, or landscape composition. Several other models occurred within 2 AIC_c, yet all included uninformative parameters (Arnold, 2010) so were deemed noncompetitive (Table 1).

Woodrat density was greatest in young forest (215.3 woodrats/km²; 95% CI: 156.0, 359.0) and mature forest in heterogeneous home ranges (134.2 woodrats/km²; 95% CI: 97.9, 220.0), followed by mature forest in homogeneous home ranges (57.8 woodrats/km²; 95% CI: 42.0, 95.7), with the lowest densities in open area (9.5 woodrats/km²; 95% CI: 5.8, 31.2; Figure 3). Extrapolating woodrat density estimates relative to the area of each habitat type within owl home ranges, woodrat abundance was ~2.5 times higher ($t_6 = 14.92$, $p < 0.001$) in heterogeneous home ranges ($\hat{N}_H = 1805.0$ woodrats; range: 1662.3–1897.8) than homogeneous home ranges ($\hat{N}_O = 727.3$ woodrats; range: 648.9–817.9).

TABLE 1 Top Huggins closed-capture models for estimating dusky-footed woodrat (*Neotoma fuscipes*) abundance in 2020 and 2021 in the central Sierra Nevada, California, USA.

Covariate(s)	AIC _c	ΔAIC _c	w	k
$p(\cdot), c(\cdot)$	1535.607	0.000	0.260	2
$p(\text{year}), c(\cdot)$	1536.610	1.003	0.158	3
$p(\cdot), c(t)$	1536.775	1.168	0.145	6
$p(\cdot), c(\text{year})$	1537.439	1.831	0.104	3
$p(t) = c(t)$	1537.517	1.909	0.100	6

Note: Information includes model covariates for initial capture probability (p) and recapture probability (c), ranked by AIC_c (Akaike's information criterion adjusted for small sample size) and compared by ΔAIC_c (difference in AIC_c between a model and the top-ranked model), w (model weight), and k (number of parameters).

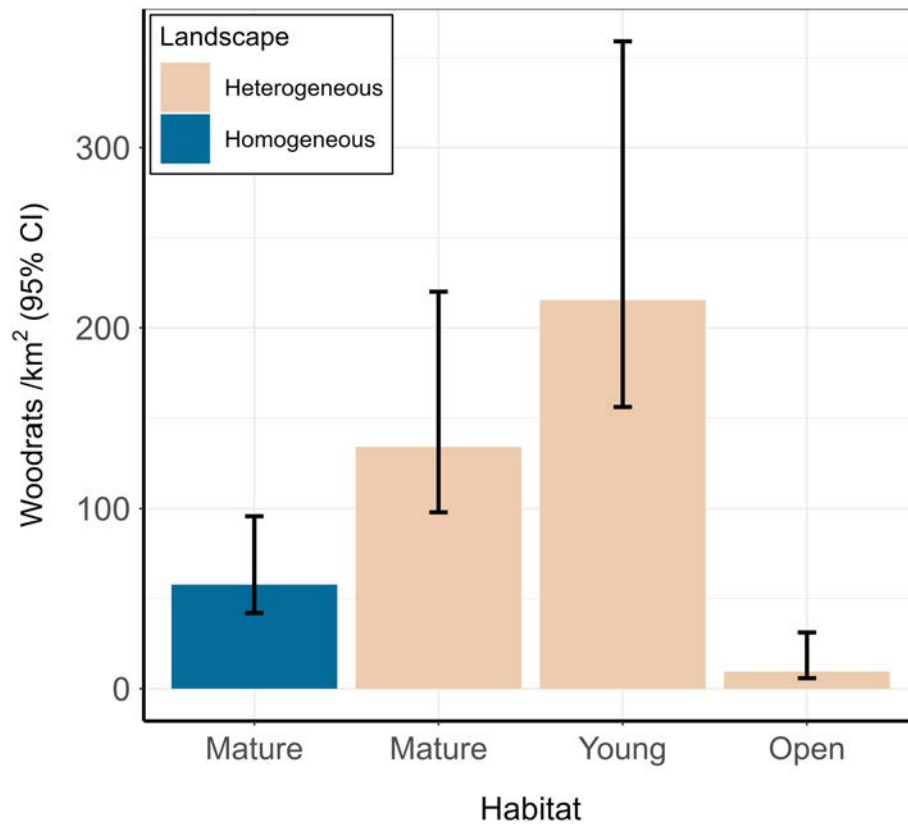


FIGURE 3 Estimated density ($\pm 95\%$ CI) of dusky-footed woodrats (*Neotoma fuscipes*) in 2020 and 2021 within habitat types in the central Sierra Nevada, California, USA. Density is shown as number of woodrats per square kilometer in open habitat, young forest, and mature forest within home ranges classified as heterogeneous and homogeneous.

Prediction 2: Higher woodrat mortality within mature forests and homogeneous home ranges

We radio-collared and monitored 108 woodrats (35 in 2020, 73 in 2021) within eight owl home ranges (four heterogeneous, four homogeneous) and compiled a total of 1030 weekly monitoring records. Collars were deployed evenly among three of the four habitat classes (37 mature-homogeneous, 36 mature-heterogeneous, 35 young). Woodrats were not collared in open areas given the low densities that occurred in this vegetation type. We observed minimal dispersal over the survey period. During monthly checks, only two individuals moved to a different midden with an average dispersal distance of 90 m, and neither of these individuals dispersed to a different habitat type. We confirmed 12 mortalities over the course of our study: three from avian (and presumably spotted owl) predation, three from mammalian predation, and six from nonpredation events.

The top model for woodrat survival contained only an intercept, indicating that woodrat survival rates did not vary by landscape composition, among habitat types, or year. Models including covariates for sampling year and habitat type were within 2 AIC_c yet involved

TABLE 2 Top known-fate survival models for estimating dusky-footed woodrat (*Neotoma fuscipes*) survival in 2020 and 2021 in the central Sierra Nevada, California, USA.

Covariate(s)	AIC_c	ΔAIC_c	w	k
Null	132.721	0	0.319	1
Year	133.942	1.221	0.173	2
Habitat	134.241	1.520	0.149	2
Landscape	134.725	2.004	0.117	2
Year + Habitat	135.419	2.697	0.082	3

Note: Information includes model covariates, ranked by AIC_c (Akaike's information criterion adjusted for small sample size) and compared by ΔAIC_c (difference in AIC_c between a model and the top-ranked model), w (model weight), and k (number of parameters).

uninformative parameters (Arnold, 2010), so they were deemed noncompetitive (Table 2). Weekly woodrat survival relative to all mortality sources was low ($\hat{s} = 0.988$; 95% CI: 0.980, 0.993), while weekly survival relative to avian (likely spotted owl) predation alone was even lower ($\hat{s} = 0.997$; 95% CI: 0.991, 0.999). While we did not detect an effect of habitat on survival rates, all three mortalities from avian predation occurred within mature forest (two mature-heterogeneous, one mature-homogeneous).

Prediction 3: Greater woodrat consumption by owls in heterogeneous home ranges

We monitored 15 nesting owl pairs over 115 days for 1173.3 total monitoring hours. One camera was removed from analysis due to limited deployment duration (10.5 h). We confirmed 306 prey delivery events and identified 243 deliveries to species. Of these, we identified 93 individual deliveries of woodrats (i.e., 30.4% of all deliveries of known species) to owl nestlings. From the video-based nest delivery data we estimated a consumption rate of 22.8 woodrats per month (95% CI: 13.5, 34.5) across all home ranges, with greater monthly consumption in heterogeneous ($\bar{x} = 32.4$ woodrats/month; 95% CI: 19.2, 48.8) versus homogeneous ($\bar{x} = 13.3$ woodrats/month; 95% CI: 5.2, 25.4) home ranges ($t_{12} = 1.85$, $p = 0.09$; Figure 4), significant at the $\alpha = 0.1$ but not 0.05 level. Based on our combined data from Predictions 1 and 2, we estimated an average mortality rate relative to avian (likely spotted owl) predation of 20.2 woodrats per month (95% CI: 14.1, 26.4) across all home ranges, with a greater number of monthly mortalities in

heterogeneous ($\bar{x} = 28.8$ woodrats/month; 95% CI: 27.2, 30.0) versus homogeneous ($\bar{x} = 11.6$ woodrats/month; 95% CI: 10.2, 13.0) home ranges ($t_6 = 14.92$, $p < 0.001$; Figure 4). This corroborated estimates from nest camera data, as there were no significant differences in woodrat consumption rates in homogeneous or heterogeneous home ranges between estimation methods (ANOVA: $p = 0.71$).

Prediction 4: Greater biomass delivery by owls within heterogeneous home ranges

In addition to woodrats, we confirmed deliveries of 90 flying squirrels, 30 *Peromyscus* spp., four voles, two pocket gophers, two moles, one bird, and one bat among the 306 confirmed deliveries. Another 63 deliveries were not identified to species but were grouped into size class to allow for biomass estimates; of these, nine were extra small, 19 were small, nine were medium, and 26 were large. The remaining 20 prey deliveries were not categorized into size classes. While woodrat consumption was much greater among spotted owls occupying

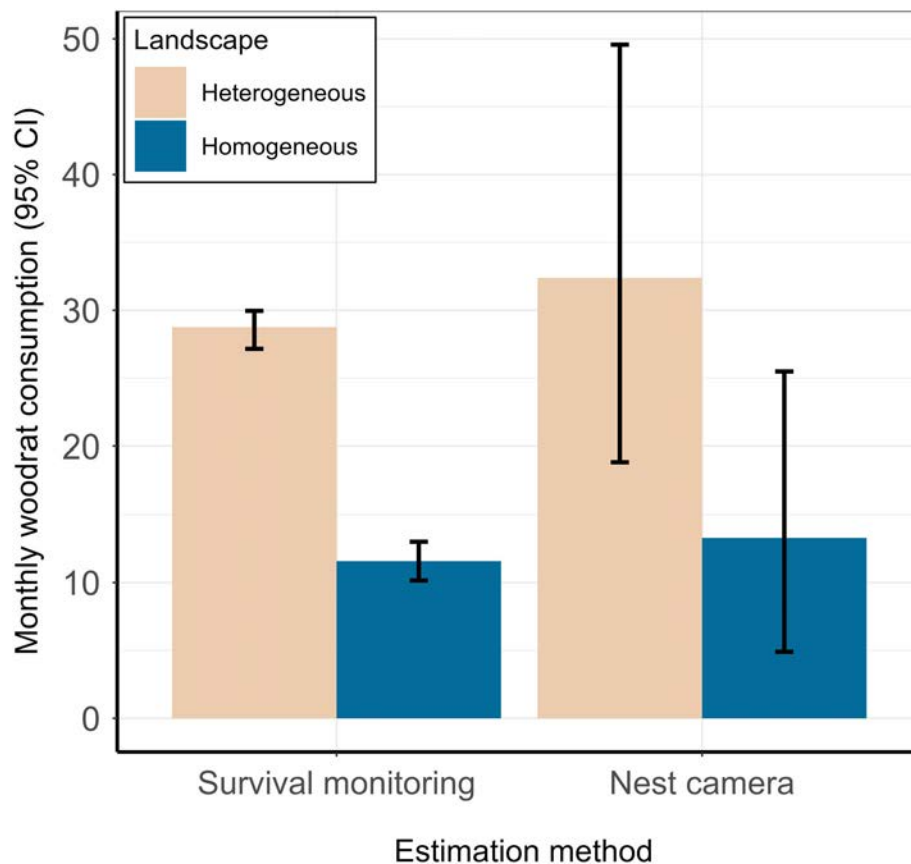


FIGURE 4 Estimated monthly consumption rate ($\pm 95\%$ CI) of dusky-footed woodrats (*Neotoma fuscipes*) by spotted owls (*Strix occidentalis*) within the central and northern Sierra Nevada, California, USA, derived from monitoring and mark-recapture data (survival monitoring) or nest camera data (nest camera) within home ranges classified as heterogeneous or homogeneous.

heterogeneous home ranges (see preceding discussion), we found no effect of landscape composition on the delivery frequency of flying squirrels ($t_{12} = 0.14$, $p = 0.89$) or all other alternative prey combined ($t_{12} = 0.80$, $p = 0.44$; Figure 5A). Accordingly, flying squirrel biomass was similar in heterogeneous ($\bar{x} = 2705.9$ g/month) versus homogeneous ($\bar{x} = 2553.6$ g/month) home ranges. Further, while spotted owls consumed an additional 1000 g/month of other prey in homogeneous ($\bar{x} = 3176.1$ g/month) versus heterogeneous ($\bar{x} = 2139.6$ g/month) home ranges (Figure 5B), this difference was not enough to compensate for the 2.5 times greater consumption of woodrat biomass in heterogeneous ($\bar{x} = 6055.6$ g/month) versus homogeneous ($\bar{x} = 2485.8$ g/month) home ranges. Specifically, owls delivered total biomass at a rate 1.3 times greater (2685.6 more g/month) in heterogeneous ($\bar{x} = 10,901.1$ g/month) versus homogeneous ($\bar{x} = 8215.5$ g/month) home ranges (Figure 5B).

DISCUSSION

We demonstrated that landscape-scale heterogeneity in vegetation types including young forest refuges increased the abundance and availability of woodrats that, in turn, provided energetic and potentially reproductive benefits to mature forest-associated spotted owls, thus providing strong empirical support for the hypothesis that prey refuges can benefit predators in heterogeneous landscapes. While previous theoretical and laboratory-based research suggested that landscape heterogeneity including patches of prey refuges could profoundly affect predator-prey dynamics, these approaches typically involved highly simplified conditions, were used at the patch rather than landscape scale, or failed to account for alternative prey (Juliano et al., 2022; Ryall & Fahrig, 2006). Thus, our findings provide some of the first evidence from natural systems that promoting landscape heterogeneity may

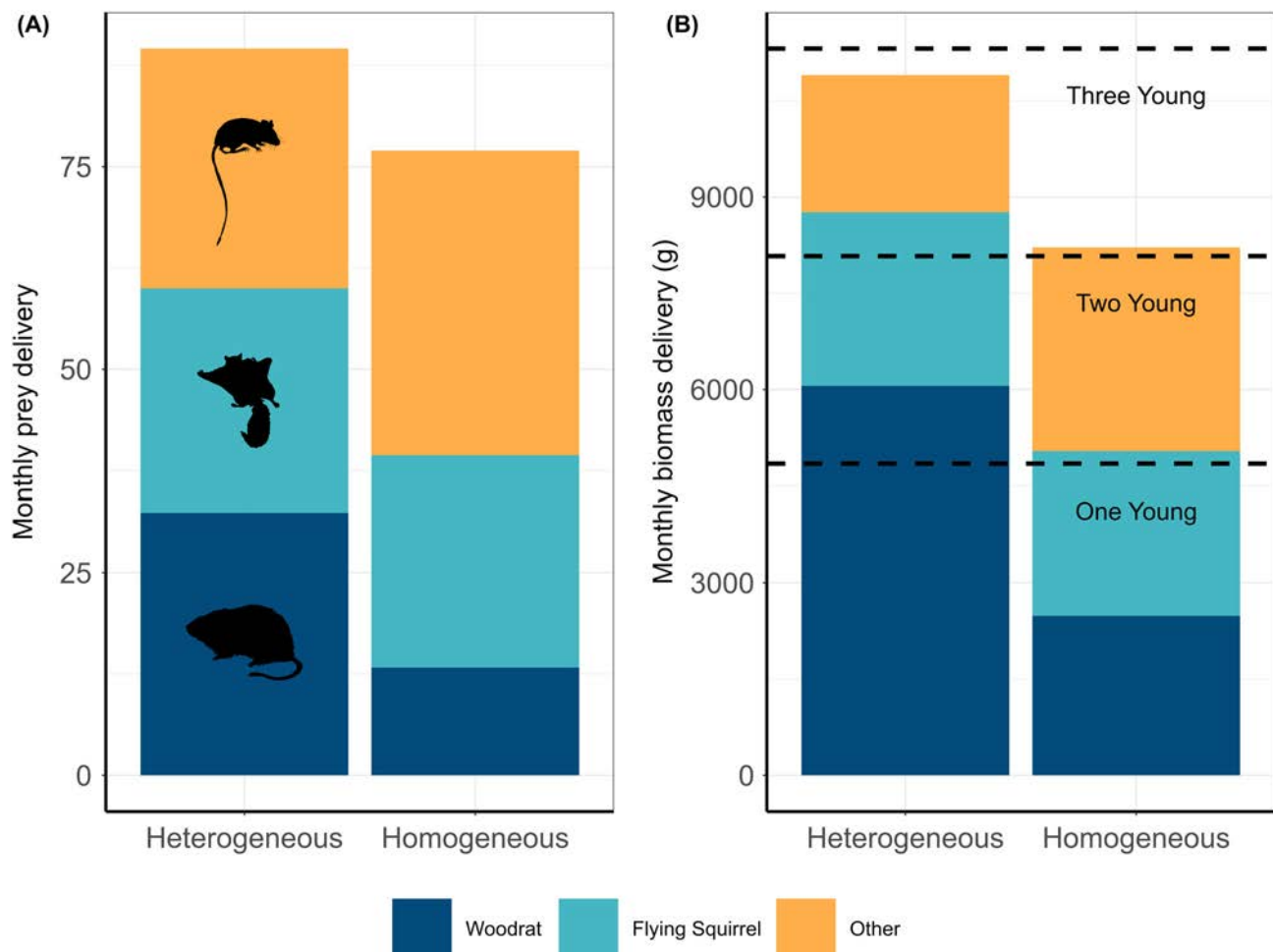


FIGURE 5 Estimated monthly prey delivery rate by prey species (A) and biomass (B) in 2019 and 2020 by spotted owls (*Strix occidentalis*) within heterogeneous and homogeneous home ranges within the central and northern Sierra Nevada, California, USA. Horizontal dashed lines in (B) represent the estimated metabolic cost to produce and raise one, two, or three young for a nesting owl pair, derived from Ward Jr. et al. (1998) and Weathers (1996).

provide co-benefits to both predator and prey populations and constitute an effective strategy for conserving endangered predators.

Young forests promote woodrat abundance within heterogeneous landscapes

As predicted, woodrat abundance was ~2.5 times greater in heterogeneous than homogeneous spotted owl home ranges, in large part because of the greater woodrat densities in young forests that were more prevalent in heterogeneous home ranges. While sample sizes of spotted owl home ranges were modest in our abundance and prey delivery analyses, the effects of landscape composition on these measures were large and occurred in directions consistent with our a priori understanding of the system—such that we do not believe limited sample size compromised our inferences. The finding that woodrat densities in young forests were considerably greater than in mature forests was consistent with previous studies (Sakai & Noon, 1993; Ward Jr et al., 1998), as were low densities in open areas with little vegetation cover (Cranford, 1977). Young forest likely confers benefits to woodrat populations by providing higher-quality food resources owing to a greater diversity and abundance of flora (Carraway & Verts, 1991; Sakai & Noon, 1993), a more stable microclimate (Atsatt & Ingram, 1983), structures and materials required for nest building (Innes et al., 2007), and cover that reduces predator risk (Sakai & Noon, 1997). In particular, while black oak acorns represent a preferred food item (Innes et al., 2007), woodrats consume a variety of fruits, nuts, and fibrous woody plants—many of which occur in greater densities within young forest and are not subject to inconsistent mast production (Carraway & Verts, 1991; McEachern et al., 2006). High woodrat densities in young forest, whether the result of resource availability or reduced predation, may have supported woodrat populations in nearby mature forests as evidenced by the 2.3 times greater densities we estimated for mature forests within heterogeneous compared to homogeneous home ranges (Figure 3). Indeed, high densities and associated intraspecific competition in young forest patches may lead to increased dispersal from these source populations that recruit into lower-density mature forest patches (Hansen et al., 2019; Sakai & Noon, 1997), a process expected to be weaker in homogeneous spotted owl home ranges containing less young forest.

Counter to our predictions that woodrat survival rates would be greater in young forests and heterogeneous (prey-dense) home ranges, we observed no difference in survival among vegetation or landscape types, either overall or from presumed spotted owl predation. This result

contrasts with a previous study that found lower survival within mature forest patches, likely due to higher predation rates from spotted owls (Sakai & Noon, 1997). However, mortality rates were uniformly very low, both overall and from spotted owl predation, which may have limited our ability to detect differences in survival rates among vegetation or landscape types statistically. Of note, all presumed spotted owl predation events observed in this study occurred in mature forest: one in mature homogeneous and two in mature heterogeneous—similar to observations by Sakai and Noon (1997). As such, the balance of evidence indicates that young forests, to a degree, act as woodrat refuges from spotted owl predation. However, young forests almost certainly harbored relatively high woodrat densities primarily because they provided greater resource availability given the marked difference in densities yet similar predation rates among habitat types. Spotted owl predation exerted little to no top-down pressure on woodrat populations given the very low estimated per-capita predation rates, even in mature forests—suggesting that high densities in young forests are driven as much, and likely more, by bottom-up processes.

Landscape heterogeneity promotes woodrat consumption by spotted owls

Spotted owls consumed more woodrats in heterogeneous than homogeneous landscapes, presumably because of greater woodrat abundance—with nest video monitoring and population-based approaches yielding very similar estimates of woodrat consumption rates. This finding supports previous analyses via stable isotopes that the proportion of woodrats present in spotted owl diets increases with forest heterogeneity (Hobart, Jones, et al., 2019). Spotted owls in our study exhibited a type I functional response (i.e., prey consumption rate increases linearly with prey density; Holling, 1959) given they consumed 2.5 times more woodrats in heterogeneous home ranges, which themselves contained a 2.5 times greater abundance than homogeneous territories. The 1:1 relationship between woodrat consumption and abundance suggests that spotted owls are consuming more woodrats in heterogeneous home ranges because of higher encounter rates rather than kill rates. Regardless of the mechanism, the linear functional response indicates that vegetation management promoting woodrat populations can, under appropriate conditions, lead to direct increases in woodrat acquisition by spotted owls.

As expected, lower delivery rates of woodrats by spotted owls to their nests in homogeneous home ranges containing fewer woodrats reduced overall biomass delivery rates (Figure 5B). Further, owls in homogeneous

home ranges only partially reconciled the deficit of decreased woodrat deliveries with alternative prey (Figure 5A). Thus, the “reduction” in mature forest spotted owl habitat in heterogeneous landscapes did not come at a cost to, but rather benefited, spotted owl prey acquisition. Spotted owls likely attempt to maximize energy gain by selecting prey that most efficiently balance foraging costs with the benefits of prey consumption (Sih, 2005; Stephens & Krebs, 1986). Reliance on smaller and less dense prey, such as flying squirrels, or very small species, such as mice, may incur costs, including increased energetic expenditures associated with prey searching or reduced biomass delivery rates (Moorhouse-Gann et al., 2020; Ruiz-Olmo & Jiménez, 2009). In contrast, consuming a greater proportion of larger-bodied and densely distributed prey such as woodrats can reduce these costs (McNab, 1963) or increase biomass delivery rates, with benefits for occupancy, space use, and even population growth (Coulson et al., 2006; Hobart, Roberts, et al., 2019; Wendland, 1984).

To explore potential fitness outcomes associated with increased biomass delivery rates in heterogeneous home ranges, we estimated the energetic cost of a nesting spotted owl pair to produce and raise one, two, or three young and converted this into monthly prey biomass values based on Ward Jr et al. (1998) and Weathers (1996) (Appendix S1: Section S2). Based on these calculations, we estimated that spotted owls GPS-tagged in homogeneous landscapes captured and delivered enough biomass to produce and raise approximately two young, whereas owls in heterogeneous landscapes met the energetic costs of raising approximately three young (Figure 5B). While we were not able to assess whether greater prey biomass delivered to nests translated directly to fitness benefits in this study population given our sample size and the uncertainty surrounding estimates drawn from a number of variables, food supplementation has increased reproductive performance in many avian species, including owls, in controlled experiments (Korpimäki, 1992; Ruffino et al., 2014). Thus, we consider it likely that prior observations of higher spotted owl reproduction in heterogeneous home ranges (Franklin et al., 2000) and home ranges containing more young forest and hardwoods (Hobart, Roberts, et al., 2019) were the result of greater woodrat abundance and consumption by owls, as suggested by these authors.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

Spotted owls depend on mature forests for nesting (Moen & Gutiérrez, 1997; North et al., 2000) and often

forage within forests characterized by large trees (Zulla et al., 2022). Nevertheless, our results suggest that promoting landscape heterogeneity could benefit spotted owl populations in parts of their range where woodrats are important prey. Heterogeneity is a natural feature of many dry forest ecosystems occupied by spotted owls and was maintained historically by frequent and predominantly low- to moderate-severity fires and smaller high-severity burned areas resulting from natural and Indigenous sources (Hoffman et al., 2021; McLauchlan et al., 2020). These forests, then, were typically characterized by larger stands of comparatively open but large-tree-dominated forests interspersed with smaller patches of early successional shrub and young forest (Boisramé et al., 2017) that presumably harbored dense woodrat populations (Innes et al., 2007; Sakai & Noon, 1993). However, more than a century of fire suppression coupled with the historic selective logging of large trees has created denser, more homogeneous forests with fewer early successional patches and large trees (North et al., 2017). While our landscape classification did not include old-growth forest as a standalone category, our results suggest that the homogenization of these forests has reduced the abundance of woodrats and their consumption by spotted owls—and come at a cost to overall prey acquisition and potentially reproductive success. This conclusion is supported by a constellation of previous studies indicating that spotted owls (1) forage and capture woodrats at the edge of young and mature forests (Kramer, Jones, Kane, et al., 2021; Sakai & Noon, 1997; Zulla et al., 2022); (2) consume a greater proportion of woodrats in more heterogeneous landscapes based on stable isotope analyses (Hobart, Jones, et al., 2019); (3) have smaller home ranges, higher territory occupancy rates, and higher densities in areas where they consume more woodrats (Hobart, Jones, et al., 2019; Zabel et al., 1995); and (4) can have higher reproductive rates in heterogeneous landscapes (Franklin et al., 2000), including those that contain a relatively high proportion of young forest with hardwoods (Hobart, Roberts, et al., 2019).

As such, our findings, in conjunction with those of previous studies, indicate that promoting landscape heterogeneity characterized by a mosaic of mature and young forests could help ameliorate the population declines observed in some areas by enhancing prey availability (Conner et al., 2016; Tempel et al., 2014). This condition could be achieved through active management that incorporates fire use and timber harvest strategies that mirror the fine-scale forest loss and recruitment events typically supported by historical disturbance regimes (Collins et al., 2017). Such strategies could continuously create small patches of open habitat that regenerate into future young forest following planting or

natural reseeding, emulating a natural mosaic of vegetation types. By mimicking historical processes of disturbance-prone forests, including those in western North America, the “managed dynamics” approach to conservation can maintain critical wildlife habitat (Gaines et al., 2022; Steel et al., 2022), although it requires continuous action to balance successional changes within regenerating patches (Steel et al., 2022). Our work demonstrating the benefits of heterogeneity to spotted owls, mediated by woodrat availability, was conducted in landscapes containing, in addition to national forests, privately owned lands managed for commercial timber production that yield a relatively high proportion of such young forests in patches tens of acres in size. While national forests are increasingly managed with an emphasis on fuel reduction intended to restore lower-severity fire regimes, this strategy can produce stands of younger forests in small, severely burned patches only if small high-severity patches are acknowledged and planned for as a desired outcome. Thus, the current emphasis on the restoration of historical fire regimes and historical forest structure (e.g., individual trees, clumps, and openings) from active harvest and burning strategies is likely to benefit spotted owl populations by creating high-density woodrat refuges adjacent to mature forest, while also reducing the risk of megafires that render large areas unsuitable for spotted owl foraging (Jones et al., 2016, 2020). Our work provides yet further evidence that the conservation of spotted owls and promotion of forest ecosystem resilience are compatible rather than conflicting objectives (Jones et al., 2022)—a perception that has constrained forest restoration in these highly vulnerable ecosystems (Collins et al., 2010).

We suggest that our findings have implications for species and ecosystems beyond the forests of western North America as historical and contemporary land-use practices have homogenized forests worldwide (Collins et al., 2017; Sapkota et al., 2021; Schulte et al., 2007). Human activities, including timber extraction, agricultural intensification, afforestation, and severe fires, have created ecological patterns without historical equivalent across all forest biomes (Seastedt et al., 2008). These departures from historical landscape conditions can alter the availability, predictability, and distribution of resources (Ullmann et al., 2018) and are increasingly recognized as a global threat to biodiversity and ecosystem function, particularly among species adapted to naturally complex ecosystems (Anile et al., 2019; Riley et al., 2003). For predators, landscape simplification can cause declines in prey diversity and abundance (Benedek & Sîrbu, 2018; Cramer & Willig, 2002), with consequences for behavior, space use, and demography (Parsons et al., 2022). However, despite the fact that

species at higher trophic levels may be most impacted by landscape-scale changes such as homogenization due to space and resource needs (Ripple et al., 2014), these effects have often been overlooked in studies of predators inhabiting human-altered environments (Ryall & Fahrig, 2006).

Here, we provide empirical evidence demonstrating the mechanisms whereby landscape-level processes alter prey availability to predators and explore a trophic-driven fitness consequence of landscape simplification. We recommend the promotion of management strategies that preserve and restore historical heterogeneity and also highlight the importance of considering spatial scale, habitat associations, and predator mobility in future studies on predator–prey interactions. There is a growing drive to understand and incorporate ecological complexity within conventional restoration approaches (Bullock et al., 2022), and our results show that understanding the role of landscape heterogeneity in predator–prey dynamics can benefit predator conservation worldwide.

AUTHOR CONTRIBUTIONS

Corbin C. Kuntze, M. Zachariah Peery, Jonathan N. Pauli, Ceeanna J. Zulla, Sarah C. Sawyer, Brian P. Dotters, Kevin N. Roberts, and John J. Keane conceived the ideas and designed the methodology. Corbin C. Kuntze and Ceeanna J. Zulla collected the data. Corbin C. Kuntze, M. Zachariah Peery, and Jonathan N. Pauli analyzed the data. Corbin C. Kuntze and M. Zachariah Peery led the writing of the manuscript, with key input from Jonathan N. Pauli. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Kuntze et al., 2023a) are available in Dryad at <https://doi.org/10.5061/dryad.4mw6m90g5>. Code (Kuntze et al., 2023b) is available in Zenodo at <https://doi.org/10.5281/zenodo.8011794>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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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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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-

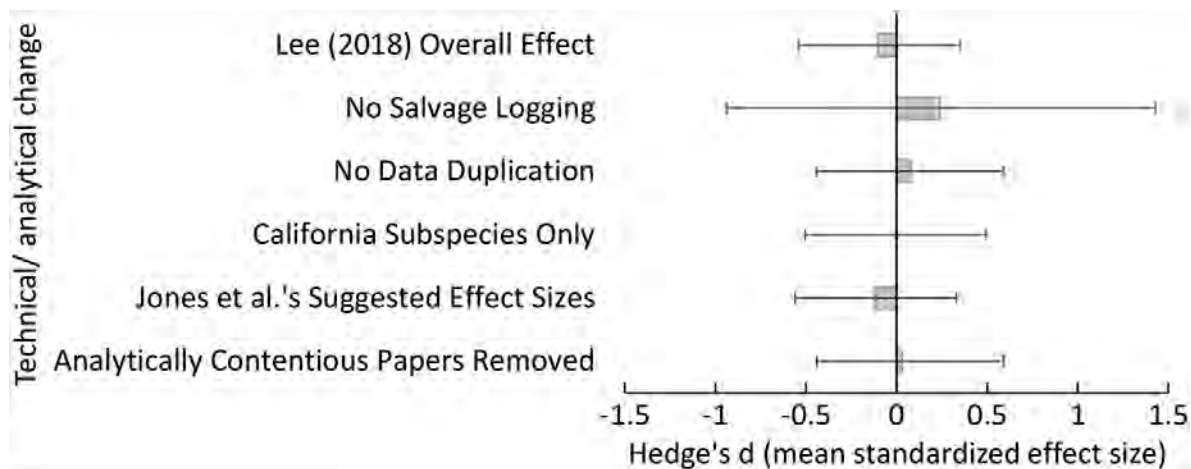


Fig. 1. Results from reanalyses of data used in Lee (2018) meta-analysis of spotted owl responses to mixed-severity forest fire, as suggested in Jones et al. (2020). Whiskers indicate the 95% confidence interval. Jones et al.'s speculations that various changes in data would alter results were not empirically 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

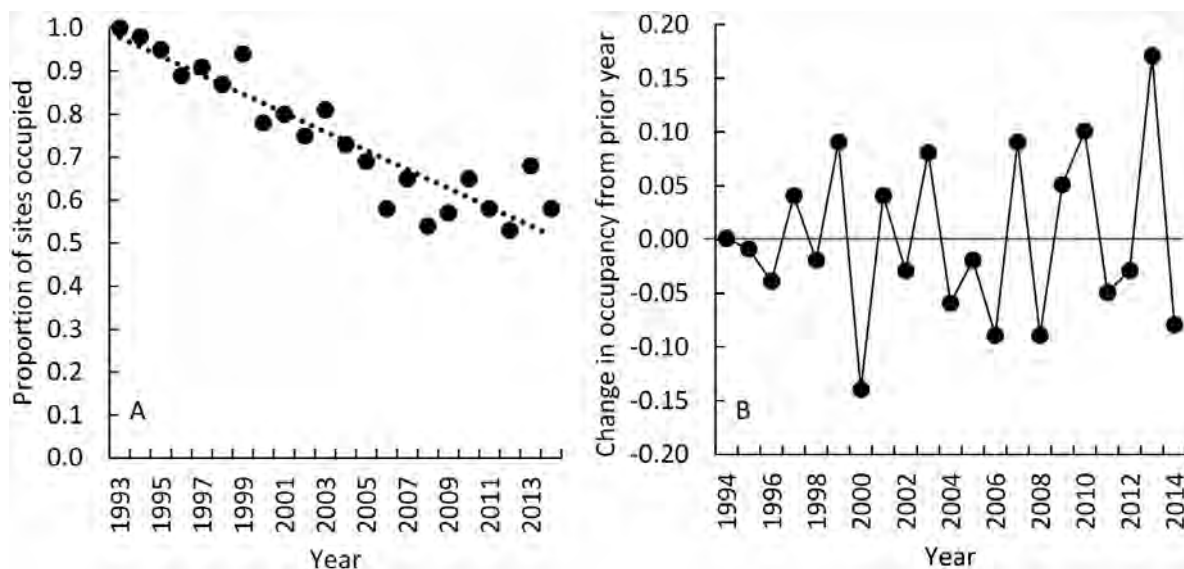


Fig. 2. (A) Annual estimates of spotted owl site occupancy (ψ) in Eldorado, California study area 1993–2014 (data from Jones et al. 2016: Fig. 3e). The dotted line represents a regression line fitted to the time series ($y = -0.02x + 1.0$). (B) Change in spotted owl site occupancy probability from year $t - 1$ 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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Noisy neighbors and reticent residents: Distinguishing resident from non-resident individuals to improve passive acoustic monitoring

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ABSTRACT

Passive acoustic monitoring (PAM) is an increasingly common method for studying populations of vocally active species. However, the detection of individuals not resident to a site may obfuscate inferences about occurrence and population change. Here, we provide a framework for distinguishing resident from non-resident individuals to estimate territory—rather than site—occupancy in PAM programs by leveraging datasets on vocal behavior and acoustic detections for spotted owls (*Strix occidentalis*) in the Sierra Nevada, California, USA. Based on acoustic/GPS tags, the extent over which individuals typically vocalized (the “vocal home range”) was small relative to space use, such that the likelihood of double counting resident territory-holders across multiple survey sites was low. However, comparing passive acoustic detections to known resident owl locations revealed that detections occurred at PAM survey sites known to be unoccupied, possibly because of the presence of non-territorial individuals. Strict thresholds that required acoustic detections over multiple survey periods successfully removed all detections of non-resident individuals but increased the probability of not detecting resident individuals. Conversely, relatively liberal thresholds that minimized the probability of missing resident individuals increased the probability of detecting non-residents. Thus, a tradeoff exists between error types, with optimal threshold criteria dependent on conservation objectives. Our study highlights the importance of examining patterns in individual vocal behavior and acoustic detections to minimize inferential errors in PAM. It also provides a generalizable framework that can be tailored according to specific conservation objectives to strengthen inferences from PAM as it becomes standard practice in conservation science.

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1. Introduction

Population monitoring is central to species conservation programs worldwide, yet the monitoring of rare and cryptic species over large spatial and long temporal scales can be logistically challenging and costly. An increasingly common and effective alternative when traditional monitoring techniques are not practical is passive acoustic monitoring (PAM) (Sugai et al., 2019). This method uses autonomous recording units (ARUs) to record animal sounds, allowing for surveys of vocally active species across broad spatial and temporal scales with comparatively little effort (Gibb et al., 2019; Shonfield and Bayne, 2017). Passive acoustic monitoring can also yield detection/non-detection data well-suited for occupancy modeling and the estimation of population trends, with sufficient sampling density to yield large sample sizes that provide high statistical power to detect even modest changes in occupancy over space and time (Wood et al., 2019a).

Passive acoustic programs typically use grid-based sampling designs to estimate site occupancy probabilities based on patterns of detections at individual survey sites, however such survey sites do not necessarily reflect meaningful biological units. Consequently, site-based acoustic detections (i.e., site occupancy) can be misleading if they are assumed to represent resident territory-holders (i.e., territory occupancy). Under such assumptions, false positive detections can be introduced through ecological processes—as opposed to through the sampling process (e.g., misidentification of the target species)—when non-resident animals without defended territories are recorded in sampling locations that are truly unoccupied (Sutherland et al., 2013). False positive detections can also occur when the spatial extent over which a resident territory-holder produces vocalizations (i.e., the “vocal home range”) is larger than a single sampling unit, resulting in individuals being double counted across multiple survey sites assumed to be independent. Importantly, the potential for double counting wide-ranging resident individuals is rarely quantified in occupancy programs (Berigan et al., 2019). Therefore, both non-resident and double counting false positive detections can inflate occupancy estimates and compromise the ability to detect changes in the breeding or territorial component of a population (Berigan et al., 2019; Sutherland et al., 2013).

One approach for reducing false positives is to characterize patterns of acoustic detection and establish thresholds indicative of territory occupancy beyond the detection/non-detection binary (Wood et al., 2020). Such criteria could include some minimum number of acoustic detections recorded over a sampling period, the detection of vocalizations indicative of breeding activities, or the detection of individuals of both sexes—depending on the life history of the focal species. Survey sites with acoustic detections that met the specific threshold could then be considered indicative of occupied territories, allowing for site occupancy to more accurately reflect territory occupancy. However, overly strict thresholds could also increase the frequency of false negatives (treating truly occupied sites as unoccupied), which reduce statistical power to detect population change within an occupancy framework (Popescu et al., 2012; Wood et al., 2019a). These tradeoffs between false positives and negatives are also important to consider for other PAM conservation goals, including the identification of occupied territories or breeding areas for management—a particularly important objective given the promise PAM provides for surveying rare and cryptic species at broad spatial scales. In this context, false negative errors are especially detrimental because locating a high proportion of resident territory-holders can be critical for ensuring effective, population-level conservation measures. Thus, strict thresholds that minimize false positives or liberal thresholds that minimize false negatives could both lead to undesirable conservation outcomes. Variation in focal species’ vocal behavior may influence false positive and negative errors, yet for most species this behavior is poorly understood. Therefore, improved understanding of patterns in individual vocal behavior and acoustic detections is crucial for evaluating and minimizing tradeoffs between error types, resulting in more rigorous PAM sampling designs that yield stronger inferences regarding territory occupancy and population change.

Here, we assessed tradeoffs between false positive and false negative errors of spotted owls (*Strix occidentalis*)—one of the most well-studied species in western North America (see below)—to improve inferences from regional-scale, PAM-based survey programs. Specifically, we: 1) assessed the likelihood of false positives generated by double counting resident territory-holders with large vocal home ranges using data from acoustic/GPS tags, 2) assessed patterns of passive acoustic detections at sites known to be occupied and unoccupied by resident spotted owls, and 3) developed thresholds based on those patterns in acoustic detections to balance tradeoffs between false positive and negative errors. These analyses directly benefit PAM-based conservation and management programs for the spotted owl, and are broadly relevant to PAM-based surveys of numerous territorial species (Wood et al., 2019b).

2. Methods

2.1. Study species

The spotted owl provides excellent opportunities for illustrating and overcoming some of the challenges that complicate PAM inferences as it is a territorial species and the subject of concurrent demographic and PAM-based studies, providing a valuable opportunity to evaluate vocalization patterns and acoustic detections in relation to territory occupancy. Population monitoring for this species is transitioning from long-term, yet spatially limited, mark-recapture studies (Dugger et al., 2016; Jones et al., 2018; Tempel et al., 2017) to regional-scale, PAM-based survey programs (Duchac et al., 2020; Wood et al., 2019a). Because spotted owls display high territory fidelity, traditional vocal lure-based surveys of unmarked individuals assume detections within known territories represent occupancy by established residents (Gutiérrez et al., 2017). However, recent GPS tagging studies demonstrate that resident spotted owls regularly use multiple territories within a single breeding season for foraging and other activities (Berigan et al., 2019; Blakey et al., 2019), potentially resulting in the double counting of individuals which can upwardly bias occupancy estimates (Berigan et al., 2019). The extent to which double counting may likewise affect PAM-based surveys is unknown. Accounting for such false positives can improve occupancy estimation, as well as conservation and forest management for the spotted owl. Locating occupied territories is imperative to mitigate potential near-term impacts to this old-forest-reliant species from management activities, without

constraining activities—such as fire-reducing fuels treatments—in areas that are truly unoccupied. Therefore, developing criteria that minimize and balance tradeoffs between false positive and negative errors in PAM programs is crucial for both spotted owl occupancy estimation and forest management objectives.

2.2. Data Collection

2.2.1. Acoustic/GPS tagging and data processing

To estimate vocal home range size for individual spotted owls, we deployed acoustic/GPS tags (Vesper 3.2 tag, manufactured by ASD, Haifa, Israel; encapsulated in epoxy by Lotek, Wareham, UK) on 17 resident California spotted owls (*S. o. occidentalis*) in the Sierra Nevada, California, from May–July, 2019 and 2020. Acoustic/GPS tags weighed 11.6 g and were mounted on the rectrices of resident owls captured by trained field crews. Tags recorded both audio and location data, with GPS locations recorded at one-minute intervals with a median error of 29 m. Audio was recorded continuously from approximately 1900 to 0500 PST, with a delayed start at 2100 PST on the first night to account for disturbance from capture. Tags included a high-sensitivity ultrasonic MEMS microphone to record audio with an 8 kHz sample rate, and data were stored on-board in the Waveform audio file format. Tag batteries enabled up to five nights of data collection. Audio data was manually reviewed in Raven Pro 2.0 (Center for Conservation Bioacoustics, Cornell Lab of Ornithology) and all spotted owl “four-note” vocalizations—a long-range territorial call unique to this species (Forsman et al., 1984) used to indicate presence in PAM programs—were identified and linked to corresponding minute-by-minute GPS locations.

2.2.2. Locating resident spotted owls

To assess PAM survey site occupancy by resident spotted owls, we identified activity centers (the locations to which marked individuals return after foraging bouts, e.g. a nest or roost site) for all resident owls within the 2200 km² Lassen Demographic Study Area (LDSA), California, the site of a long-term mark-recapture study of California spotted owls (Franklin et al., 2004) (Fig. 1). We located activity centers as a routine part of demographic surveying following standard protocols (Franklin et al., 2004), with additional

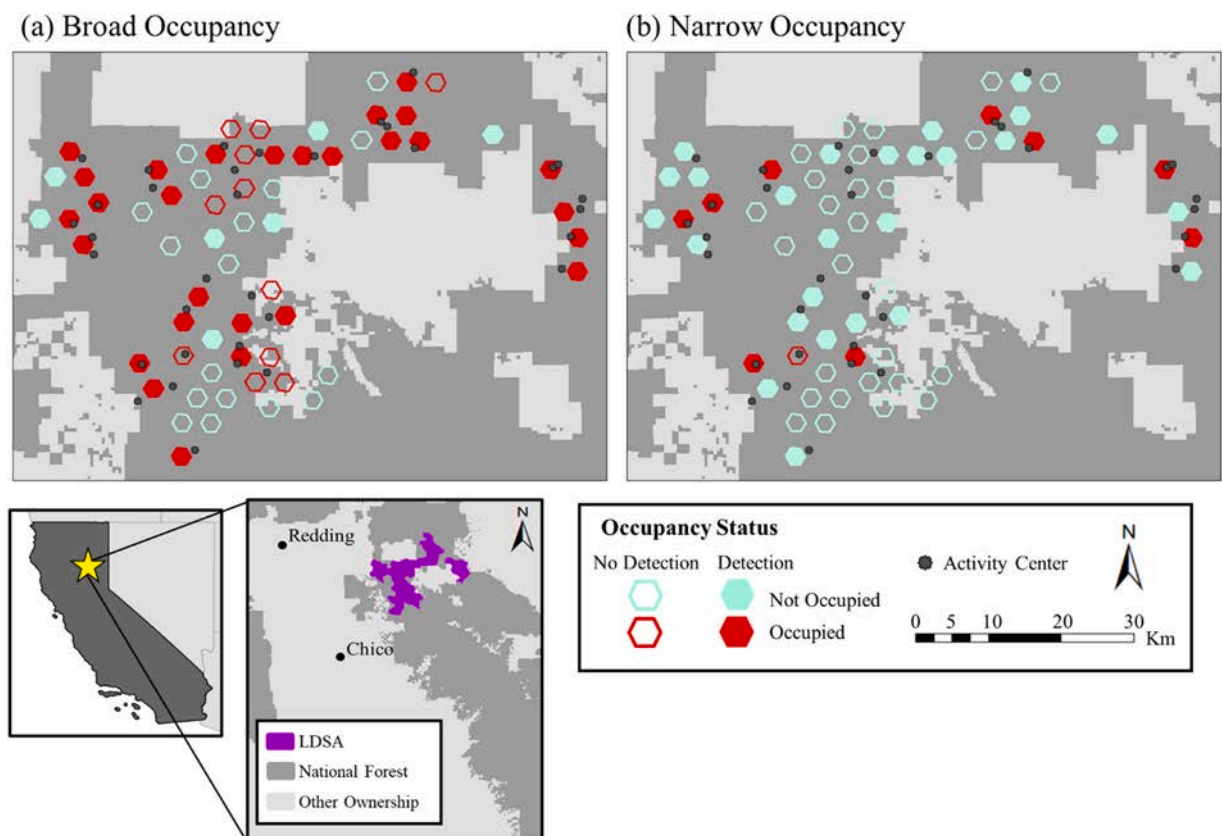


Fig. 1. Resident spotted owl activity centers and occupancy status of passive acoustic survey sites in 2018. Solid hexagons indicate survey sites where acoustic detections were obtained, while outlined hexagons indicate sites with no acoustic detections. Two definitions of occupancy were examined, where sites were defined as occupied if a spotted owl activity center was located (a) within the site or within an adjacent, unsurveyed site (“broad occupancy”) or (b) solely within the survey site (“narrow occupancy”). All passive acoustic surveys were conducted within the Lassen Demographic Study Area (LDSA), shown in purple. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

activity centers within 4 km of the LDSA provided by adjacent landowners. We considered owls residents if they were detected on two or more occasions separated by ≥ 1 week and detections occurred ≤ 800 m of one another, or if they were marked individuals re-sighted within the same territory as the year prior. We ascertained pair and breeding status using a standard four-mouse protocol (Franklin et al., 1996). For nesting birds, we defined activity centers as the nest tree location or the first observed juvenile location if a nest tree was not found. For non-nesting birds, we defined activity centers as the first daytime location at which the individual or pair was observed. Because we surveyed the entire demography area and survey season detection probabilities are effectively one, it is unlikely that resident owls went undetected (Tempel et al., 2016).

2.2.3. Passive acoustic surveys and data processing

To assess passive acoustic detections at PAM sites in relation to the location of spotted owl activity centers, we conducted passive acoustic surveys from May–August of 2018 and 2019 throughout the LDSA (Fig. 1). Acoustic survey sites were 4 km² hexagonal grid cells, approximately the size of a spotted owl territory in this region (Jones et al., 2018), and were non-contiguous to reduce potential non-independence—although the effectiveness of this spacing is unknown and thus a question we addressed in this study. We included only acoustic survey sites ($n = 125$ sites across both years) for which we were confident that all nearby activity centers were located. We conducted two or three passive acoustic surveys per year at each site with surveys consisting of five-to-seven night deployments (i.e., secondary sampling periods) separated by ≥ 1 month. For each five-to-seven night deployment, we deployed two or three ARUs (Swift Recorder, Center for Conservation Bioacoustics, Cornell Lab of Ornithology) within a survey site without knowledge of owl occupancy history (Wood et al., 2019a). We typically deployed ARUs at acoustically advantageous locations such as ridgetops, with ARUs in the same cell separated by ≥ 500 m. We deployed ARUs in the same locations during different five-to-seven night deployments within years, but locations within survey sites differed between 2018 and 2019. Recording units had one omni-directional microphone and recorded continuously from 2000 to 0600 PST at a sample rate of 32 kHz and 16-bit resolution and gain of + 38 dB.

We analyzed audio data using the Template Detector feature of Raven Pro 2.0, which automatically identified potential spotted owl four-note vocalizations (see Wood et al., 2019a for further template detector details). We manually reviewed all template-identified four-note calls and classified calls as male or female based on frequency (Wood et al., 2020). Then, we manually reviewed audio data before and after a confirmed detection for additional four-note calls missed by the detector until 10 min had elapsed without spotted owl vocal activity.

2.3. Data Analysis

2.3.1. Objective 1: Assessing likelihood of double counting

To assess the likelihood of double counting resident spotted owls across multiple PAM survey sites, we used audio and spatial data obtained from the acoustic/GPS tags to estimate individual vocal home ranges (the area over which a spotted owl produced detectable four-note vocalizations over the tracking period) which we overlaid onto our PAM survey grid. Vocal home range size was calculated using the *ks* package (Duong, 2021) in the program R (Version 4.0.3, R Core Team, 2020) based on four-note vocalization locations using 95% fixed-kernel density estimators, considered one of the most accurate and unbiased methods of home range estimation (Seaman and Powell, 1996). We calculated the smoothing factor (h_{pi}) for each vocal home range using the “plug-in” method, considered an appropriate or even improved alternative to other smoothing methods (Gitzen et al., 2006; Walter et al., 2009). We then overlaid each vocal home range onto our existing PAM survey grid at 2000 randomly selected points. We then calculated the average proportion of times each vocal home range intersected more than one survey site. We treated this proportion as the probability of a false positive detection resulting from double counting a single individual at multiple survey sites over the tracking period. Finally, we estimated space use (the spatial extent covered by an owl over the tracking period) using all location points following the same methods as described above for comparison with vocal home range size.

2.3.2. Objective 2: Assessing detections at known occupied and unoccupied sites

To assess patterns of passive acoustic detections at known occupied and unoccupied PAM survey sites, we performed a logistic regression analysis in R to examine acoustic detections at survey sites in relation to the location of resident spotted owl activity centers. We used two alternative definitions of acoustic survey site occupancy as our dependent variable, where sites were considered occupied if a spotted owl activity center was located, more broadly, (i) within the site or within an adjacent, unsurveyed site (hereafter, “broad occupancy”) (Fig. 1a) or, more narrowly, (ii) solely within the survey site (hereafter, “narrow occupancy”) (Fig. 1b). The narrow occupancy definition is better suited for acoustic surveys intended to locate activity centers on the landscape, but we expected it to be relatively sensitive to false positives arising from activity centers located outside of but immediately adjacent to survey sites; thus, we also examined broad occupancy to account for such false positives. Independent variables for these analyses included three metrics of acoustic detection frequency: detection visits (proportion of 2–3 total secondary sampling periods with an acoustic detection), detection nights (proportion of total survey nights with an acoustic detection) and call rate (total number of detected calls divided by the number of survey nights). We also included whether or not a female spotted owl was detected at a site as a covariate because female owls vocalize less often and thus their detection may be more indicative of an activity center (Wood et al., 2020, 2019c).

We constructed logistic regression models using all possible additive combinations of the four (linear) independent variables, resulting in 15 models. We then created four sets of these models (i.e., 60 total models for each of the two definitions of occupancy) by implementing temporal limitations on when acoustic detection were obtained, accounting for both time of night (either from the full night or only the dusk/dawn time period before 2200 or after 0400 PST) and time of year (either from the full season or only the early May–July season). We considered these temporal limitations because spotted owls increase their vocal activity and are more likely to be

found near their activity center during dusk and dawn (Gutiérrez et al., 2017; Wood et al., 2019c), and also exhibit more wide-ranging behavior in late summer (Forsman et al., 1984), thus we expected dusk/dawn and early season temporal limitations to aid in identifying occupied sites. We ranked models with Akaike's Information Criterion corrected for small sample size (AIC_c) using the MuMIn package (Barton, 2020), and considered all models within 2 AIC_c of the top model to be competitive (Burnham and Anderson, 2002). We also examined summed Akaike model weights ($0 \leq \sum w \leq 1$) and 85% confidence intervals for each covariate in order to assess the relative importance of each variable (Arnold, 2010). We assessed multicollinearity for all models by calculating the variance inflation factor (VIF) using the car package (Fox and Weisberg, 2019), with no models having $VIF > 10$. We assessed model fit for top ranked models with McFadden's adjusted pseudo- R^2 (McFadden, 1973) using the blorr package (Hebbali, 2020).

2.3.3. Objective 3: Estimating and balancing false positive and false negative errors

To determine the effect of thresholds on false positive (i.e., Type I) and false negative (i.e., Type II) error rates, we examined a range of threshold values for the most supported temporal limitations and acoustic detection metrics identified in our logistic regression analyses. We calculated the false positive error rate as the proportion of acoustic survey sites that met the criteria of a given threshold but were truly unoccupied based on the location of spotted owl activity centers, and the false negative error rate was calculated as the proportion of acoustic surveys sites that failed to meet the criteria of a given threshold but were truly occupied. We first calculated false positive and negative error rates under a "relaxed" threshold where a single acoustic detection was treated as an indication of occupancy by a resident spotted owl. This relaxed threshold is equivalent to detection/non-detection binary data typically used in occupancy modeling and represents our current criteria for defining occupancy by resident owls in our PAM program. We then examined how a range of stricter thresholds based on supported temporal limitations (e.g., detections must occur during the dusk/dawn time period) and acoustic detection metrics (e.g., > 10 survey nights with acoustic detections) affected error rates relative to the relaxed threshold. Exploring a range of thresholds for supported detection metrics provided an explicit means to examine and balance tradeoffs between false positive and negative errors to best meet conservation objectives.

3. Results

3.1. Objective 1: Assessing likelihood of double counting

Acoustic/GPS tags recorded for an average of 40.55 h (range: 28.00–46.65), resulting in an overall tracking period of approximately three to five nights, which aligns reasonably well with the five-to-seven-night secondary sampling periods of our passive acoustic surveys. On average, 1853 GPS locations (range: 1066–2394) and 40 four-note vocalization locations (range: 0–177) were

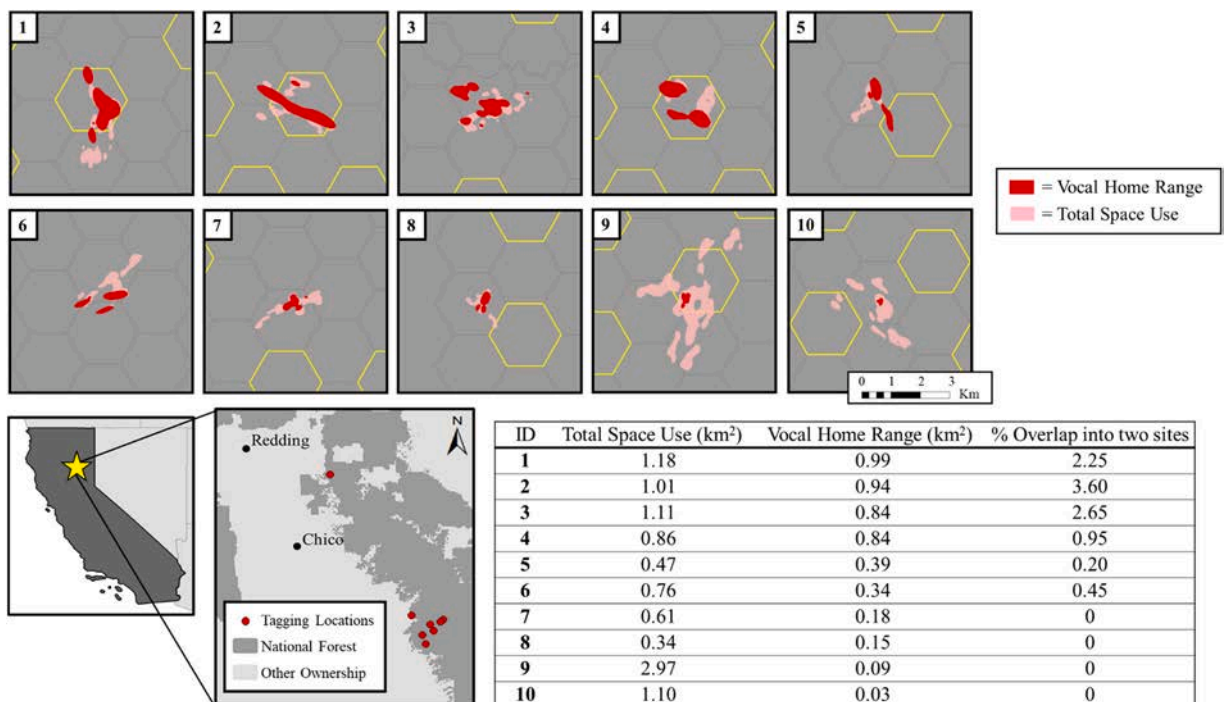


Fig. 2. Map of space use and vocal home ranges for individual spotted owls estimated using the 95% kernel density method. Passive acoustic survey sites are outlined in yellow, with all maps shown at the same scale. Tagging locations throughout the Sierra Nevada are also shown, along with total space use and vocal home range size in square kilometers as well as the percent likelihood of vocal home range overlap into two survey sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recorded per individual over the tracking period. Of our 17 tagged spotted owls, we estimated vocal home ranges for ten owls with ≥ 15 four-note vocalization locations—a threshold considered sufficient for reliable kernel estimation (Anich et al., 2009). The remaining seven spotted owls produced four-note vocalizations at zero to eight locations, all in very close proximity, and were therefore assigned a vocal home range size of zero. Mean vocal home range size was 0.28 km^2 (range: 0.00–0.99, $n = 17$) and mean total space use was 1.12 km^2 (range: 0.34–2.97, $n = 17$) (Fig. 2). Thus, mean vocal home range size was 33% (range: 0–97%, $n = 17$) of mean space use. While vocal home ranges varied in size and shape, when overlaid onto our existing PAM survey grid at 2000 random locations, a single vocal home range overlapped multiple survey sites only 0.6% of the time on average (range: 0–3.6%, $n = 17$) and never overlapped more than two sites.

3.2. Objective 2: Assessing detections at known occupied and unoccupied sites

Under broad occupancy, all competitive models included the covariate of detection visits utilizing detections from the dusk/dawn time period across the full season; this covariate also had the highest summed Akaike weight (Table 1a). The probability of a site being occupied increased with detection visits ($\beta = 6.65$, 85% CI: 4.30–9.90) based on the top model (adjusted pseudo- $R^2 = 0.17$) (Fig. 3a). Female detection and call rate from the dusk/dawn time period across the full season were also present in some competitive models, but these covariates were always non-significant with p-values $> 0.05\%$ and 85% confidence intervals that overlapped zero. Under narrow occupancy, the top model included the covariate of detection visits from the full night across the early season; this covariate had the highest summed Akaike weight as well (Table 1b). The probability of a site being occupied increased with detection visits ($\beta = 4.22$, 85% CI: 3.05–5.58) based on the top model (adjusted pseudo- $R^2 = 0.29$) (Fig. 3b). No other models were competitive and thus other covariates were not considered informative.

3.3. Objective 3: Estimating and balancing false positive and false negative errors

When occupancy was defined broadly, acoustic detections were recorded at 45 of 74 (61%) occupied sites with activity centers within or adjacent to the site, and at 10 of 51 (20%) unoccupied sites with no activity centers in the area. When occupancy was defined narrowly, acoustic detections were recorded at 15 of 17 (88%) occupied sites containing activity centers, and at 40 of 108 (37%) unoccupied sites not containing activity centers. Thus, using a relaxed threshold where a single acoustic detection was considered an indication of occupancy (e.g., detection/non-detection) resulted in a false positive error rate of 0.20 and a false negative error rate of 0.39 under broad occupancy (Fig. 4a), and a false positive error rate of 0.37 and a false negative error rate of 0.12 under narrow occupancy (Fig. 4b). These relaxed thresholds represent the current error rates observed in our PAM program.

To explore the effect of stricter thresholds on false positive and negative errors in relation to the relaxed threshold, we estimated error rates across a range of threshold values for our most supported covariates. For broad occupancy, we examined thresholds in detection visits (proportion of 2–3 total secondary sampling periods with a detection) from the dusk/dawn time period across the full season. An intermediate threshold requiring only a temporal limitation—where detections during the dusk/dawn time period were

Table 1

Summed Akaike weights (Σw) for model covariates for two separate analyses of survey site occupancy, where sites were defined as occupied if a spotted owl activity center was located (a) within the site or within an adjacent, unsurveyed site (“Broad Occupancy”) or (b) solely within the survey site (“Narrow Occupancy”).

Time of Night	Time of Year	Model Covariate ^a	Σw	
			(a) Broad Occupancy	(b) Narrow Occupancy
Full Night	Full Season	Detection Visits	0.02	0.03
		Female Detected	0.01	0.00
		Call Rate	0.00	0.01
		Detection Nights	0.00	0.01
	Early Season	Detection Visits	0.04	0.78
		Female Detected	0.04	0.20
		Call Rate	0.01	0.20
		Detection Nights	0.01	0.20
	Full Season	Detection Visits	0.85	0.01
		Female Detected	0.52	0.00
		Call Rate	0.27	0.00
		Detection Nights	0.26	0.00
Dusk/Dawn	Full Season	Detection Visits	0.07	0.15
		Female Detected	0.04	0.04
		Call Rate	0.02	0.04
		Detection Nights	0.02	0.04

Four sets of model covariates were examined based on the time of night (either from the full night or only the dusk/dawn time period) and time of year (either from the full season or only the early May–July season) in which acoustic detections were obtained. The largest cumulative weight for each analysis is bolded below.

^a Covariates were defined as follows: Detection Visits – proportion of 2–3 total secondary sampling periods with an acoustic detection; Detection Nights – proportion of total survey nights with an acoustic detection; Call Rate – total number of detected calls divided by the number of survey nights; Female Detected – whether or not a female spotted owl was detected.

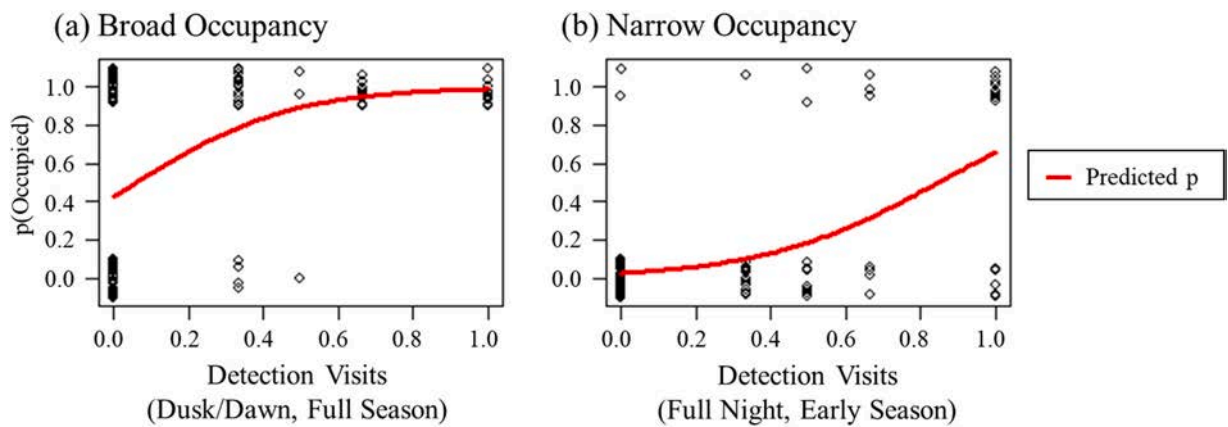


Fig. 3. The relationship between the probability (p) of a site being occupied by a spotted owl and the most supported model covariate, where sites were defined as occupied if a spotted owl activity center was located (a) within the site or within an adjacent, unsurveyed site (“broad occupancy”) or (b) solely within the survey site (“narrow occupancy”). Under broad occupancy, the most supported covariate was detection visits from the dusk/dawn time period across the full season. Under narrow occupancy, the most supported covariate was detection visits from the full night across the early season. Points are jittered for clarity.

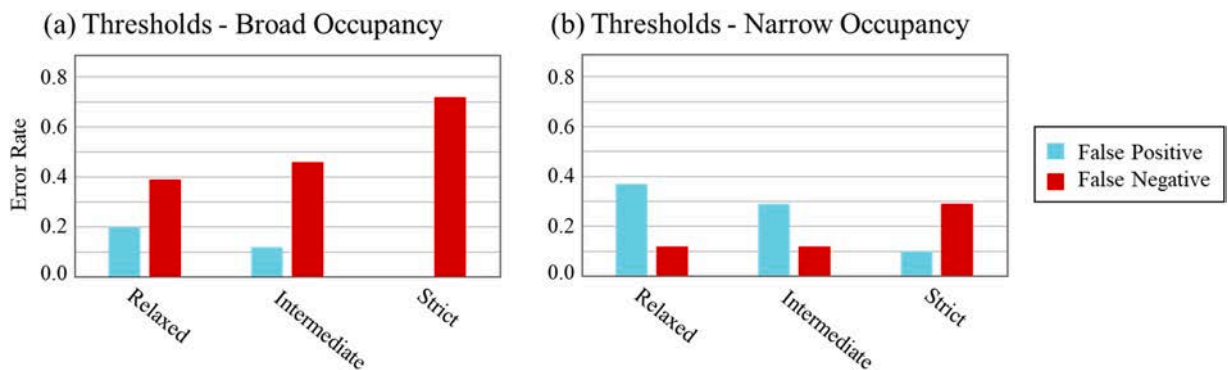


Fig. 4. False positive and negative error rates under relaxed, intermediate, and strict acoustic detection thresholds, where sites were defined as occupied if a spotted owl activity center was located (a) within the site or within an adjacent, unsurveyed site (“broad occupancy”) or (b) solely within the survey site (“narrow occupancy”). Relaxed thresholds considered any detection an indication of occupancy; intermediate thresholds required a temporal limitation (broad occupancy: detections must occur during dusk/dawn to indicate occupancy; narrow occupancy: detections must occur during the early season); strict thresholds required a temporal limitation along with detections to occur across two secondary sampling periods to indicate occupancy.

considered an indication of occupancy—reduced the false positive error rate from 0.20 to 0.12 and increased the false negative error rate from 0.39 to 0.46 (Fig. 4a). A strict threshold requiring a temporal limitation plus specific detection criteria—where detections during the dusk/dawn time period across more than one secondary sampling period (i.e., a detection visit threshold ≥ 0.667) were considered an indication of occupancy—reduced the false positive error rate to zero. This strict threshold also increased the false negative error rate to 0.72 (Fig. 4a). However, it is important to note that this observed high rate of false negative error resulted in part from how occupancy was defined, as a single activity center could cause multiple adjacent survey sites to be classified as “occupied” but—as reported above—the resident owl at that activity center was unlikely to be detected at more than one site. Thus, a high number of “occupied” sites never recorded an acoustic detection, influencing the observed false negative error rate.

For narrow occupancy, we examined error rates across a range of detection visit thresholds from the full night across the early season. An intermediate threshold requiring only a temporal limitation—where detections during the early season were considered an indication of occupancy—reduced the false positive error rate from 0.37 to 0.29 and resulted in no increase to the false negative error rate of 0.12 (Fig. 4b). A strict threshold requiring a temporal limitation plus specific detection criteria—where detections during the early season across more than one secondary sampling period (i.e., a detection visit threshold ≥ 0.667) were considered an indication of occupancy—further reduced the false positive error rate to 0.10, but also increased the false negative error rate to 0.29.

4. Discussion

False positive errors resulting from the detection of individuals not resident to a site are increasingly recognized as potential biases

in occupancy and population trend estimation (Berigan et al., 2019; Sutherland et al., 2013), yet their impact on PAM programs is rarely evaluated. Our study system presented a valuable opportunity to utilize high-resolution acoustic/GPS tagging data and concurrent PAM and mark-recapture occupancy survey data to assess the extent to which acoustic detections reflect resident individuals and thus territory occupancy. In doing so, our study provides a generalized framework for identifying and minimizing false positive, as well as false negative, errors that could help designate and estimate territory occupancy, thereby improving inferences from PAM programs.

Our study reinforced that passive acoustic surveys are an effective means of detecting spotted owls and other territorial species (Darras et al., 2018; Duchac et al., 2020; Wood et al., 2019a), but also demonstrated that false positive error rates in PAM programs can be high. False positive detections occurred despite small vocal home ranges, which were always smaller than total space use and rarely ($< 1\%$) spanned two survey sites and never overlapped > 2 sites. Thus, our non-contiguous survey grid design appeared to mitigate double counting errors as intended, although we acknowledge that tagged individuals were only tracked for the approximate duration of one secondary sampling period (< 1 week) and that shifts in owl activity centers over the summer could have caused some false positive detections. Nevertheless, we consider it unlikely that double counting errors were the primary source of false positives, which we consider more likely the result of sporadic detections of non-resident (“floater”) individuals. Indeed, our active, nighttime spotted owl surveys detected unmarked owls that appeared to be floater individuals at six sites in 2018 and 2019 that were not detected nesting or roosting at the site during follow-up dusk/dawn surveys. Reducing the likelihood of detecting floater individuals a priori as part of PAM sampling design development will be challenging, but opportunities exist for culling such detections as part of the post-data collection process (see below).

A clear tradeoff exists between false positive and negative errors, with important implications for design and analysis of PAM programs. Strict thresholds in acoustic detection metrics reduced false positive errors but also increased false negative errors; conversely, more relaxed thresholds that reduced false negative errors came at the cost of increased false positives.

Notably, when we defined occupancy broadly, false positive detections at unoccupied sites were eliminated under a strict threshold requiring detections over multiple survey visits, although false negative errors were high (0.72) (Fig. 4a). By eliminating false positives, this strict threshold could minimize occupancy inflation in our PAM program, potentially leading to more accurate population monitoring for the spotted owl. But the high false negative error rate could also potentially reduce statistical power to detect population change (Popescu et al., 2012; Wood et al., 2019a), resulting in more years of survey effort required to reliably estimate change. Additional work involving statistical power analyses would be required to identify detection thresholds that reduced bias and precision in estimates of trends in occupancy and thus populations. It is also important to recognize that, under our broad definition of occupancy, an “occupied” site can have multiple occupied territories adjacent to the surveyed site (Fig. 1a). Conversely, a single occupied territory can cause more than one survey site to be considered “occupied” (Fig. 1a). Both of these situations could decouple occupancy and abundance when occupancy is defined broadly, in which case the narrow definition (and associated detection thresholds) might be more appropriate.

The trade-off between false positive and negative errors persisted when occupancy was defined narrowly, but false positive error rates were significantly higher and false negative error rates were significantly lower under this definition. Notably, false negative error rates did not increase between relaxed and intermediate thresholds (0.12) and remained relatively low under a strict threshold (0.29) (Fig. 4b). While false positive error rates decreased with increasingly stringent thresholds, false positives still persisted even under a strict threshold (Fig. 4b), illustrating the difficulty of differentiating when acoustic detections at a site represent an activity center within the site itself versus an activity center in an adjacent area.

The aforementioned tradeoffs between false positive and negative errors indicate that (i) different acoustic detection thresholds (relaxed versus strict) and (ii) different definitions of occupancy (broad versus narrow) will likely be needed to meet specific conservation goals. For example, when occupancy inflation is considered detrimental to population monitoring—and false negatives can be accommodated by modeling detection probabilities in an occupancy framework—defining occupancy broadly and adopting relatively strict detection thresholds are likely to strengthen inferences from PAM programs. In contrast, using relaxed detection thresholds, defining occupancy narrowly, and surveying all sites of interest may be required when the objective is to locate specific occupied sites for conservation and the consequences of not detecting resident individuals are considered high. Such an approach, however, could result in wasted conservation resources given likely high false positive error rates. In the case of spotted owls in our sampling area, under a false positive error rate of 0.39 when occupancy is defined narrowly, relaxed detection criteria are used, and all potential sites ($n = 63$) in one year are surveyed would result in the designation of 25 unoccupied sites as occupied. These sites, then, would need to be visited with active surveys to ascertain that they are truly unoccupied and thus increase the effort and cost of such follow-up surveys. Nevertheless, the framework presented here can help quantify such tradeoffs explicitly and thus facilitate decisions about how to best invest conservation resources and meet specific conservation objectives.

4.1. Conclusions

Our study indicates that several strategies could reduce false positive detections in PAM programs during survey design, post-survey data processing, and data analysis. First, survey sites can be spaced at distances unlikely to be acoustically defended by a territorial individual, decisions facilitated considerably by high-resolution information on vocalization patterns provided by acoustic/GPS tags. Our survey grid design was based on considerable a priori knowledge of spotted owl space use to minimize double counting (Berigan et al., 2019; Blakey et al., 2019), yet still yielded frequent false positive detections, demonstrating the difficulty of accounting for all sources of false positive detections a priori—particularly those emerging from non-resident “floater” individuals. Second, adopting stringent acoustic detection thresholds can reduce false positive detections when they occur. In our study, the number of

secondary sampling periods in which individuals were detected, as well as the diurnal and seasonal timing of detections, was a strong predictor of spotted owl occupancy and was able to lower false positive error rates significantly. However, thresholds also involve a tradeoff where minimizing false positive errors increases false negative errors, potentially to levels that compromise the ability to meet other conservation objectives. If false negative error rates remain higher than desired even under more relaxed thresholds, longer sampling periods could help to increase the likelihood of detection. However, this strategy could also increase false positive error rates by providing more opportunities for double counting or non-resident detections—again highlighting the need for careful attention to the design of PAM programs and the analysis of acoustic survey data. Finally, occupancy models that explicitly estimate false positive error rates and account for false positive detections can also reduce biases in occupancy estimates (Berigan et al., 2019), but these models require the estimation of additional parameters and, notably, model performance when false positive error rates are high has yet to be determined. Accordingly, all three approaches may be necessary to reduce the effects of false positive detections and draw strong inferences from PAM programs as they continue to emerge as a standard approach for monitoring vocally active species in conservation. With rigorous population monitoring vital to the conservation and management of taxa around the world, our results allow PAM to offer an increasingly effective monitoring framework across broad spatial and temporal scales.

CRediT authorship contribution statement

Authors CMW, RJG, and MZP conceived of the study; DSR, CMW, and MZP designed the analysis; SAW, WJB, JJK, SCS, PAS, KGK and NK collected the data; DSR, AR, and KGK processed the acoustic data; HK supported the acoustic analyses and study conception; HAK assisted with spatial analyses; DSR conducted the formal analysis and wrote the manuscript. All authors provided critical feedback and gave final approval for publication.

Statement of Compliance

Work conducted as part of this study was authorized by federal banding permit #23865 and California state scientific collecting permit S-193180001-19324-001. All animal handling was conducted in accordance with an approved IACUC protocol A005367 from the University of Wisconsin.

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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ARTICLE

Mega-disturbances cause rapid decline of mature conifer forest habitat in California

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Abstract

Mature forests provide important wildlife habitat and support critical ecosystem functions globally. Within the dry conifer forests of the western United States, past management and fire exclusion have contributed to forest conditions that are susceptible to increasingly severe wildfire and drought. We evaluated declines in conifer forest cover in the southern Sierra Nevada of California during a decade of record disturbance by using spatially comprehensive forest structure estimates, wildfire perimeter data, and the eDaRT forest disturbance tracking algorithm. Primarily due to the combination of wildfires, drought, and drought-associated beetle epidemics, 30% of the region's conifer forest extent transitioned to nonforest vegetation during 2011–2020. In total, 50% of mature forest habitat and 85% of high density mature forests either transitioned to lower density forest or nonforest vegetation types. California spotted owl protected activity centers (PAC) experienced greater canopy cover decline (49% of 2011 cover) than non-PAC areas (42% decline). Areas with high initial canopy cover and without tall trees were most vulnerable to canopy cover declines, likely explaining the disproportionate declines of mature forest habitat and within PACs. Drought and beetle attack caused greater cumulative declines than areas where drought and wildfire mortality overlapped, and both types of natural disturbance far outpaced declines attributable to mechanical activities. Drought mortality that disproportionately affects large conifers is particularly problematic to mature forest specialist species reliant on large trees. However, patches of degraded forests within wildfire perimeters were larger with greater core area than those outside burned areas, and remnant forest habitats were more fragmented within burned perimeters than those affected by drought and beetle mortality alone. The percentage of mature forest that survived and potentially benefited from lower severity wildfire increased over time as the total extent of mature forest declined. These areas provide some opportunity for improved resilience to future disturbances, but strategic management interventions are likely also necessary to

mitigate worsening mega-disturbances. Remaining dry mature forest habitat in California may be susceptible to complete loss in the coming decades without a rapid transition from a conservation paradigm that attempts to maintain static conditions to one that manages for sustainable disturbance dynamics.

KEYWORDS

climate change, drought, fisher, forest conservation, forest disturbance, habitat loss, spotted owl, wildfire

INTRODUCTION

Mature forests characterized by large, old trees are essential ecosystems that support biodiversity conservation and ecological function globally (Lindenmayer & Laurance, 2017). Additionally, these forests provide high levels of terrestrial carbon storage (Stephenson et al., 2014) that when managed in accordance with their natural disturbance regime, can be strong carbon sinks (Liang et al., 2018). Mature forests in the western USA, particularly those composed of tall, old trees and complex understories, support numerous species of conservation concern including the spotted owl (*Strix occidentalis*) and fisher (*Pekania pennanti*) (North et al., 2017; Purcell et al., 2009). Conserving the habitat for these species while also managing to reduce wildfire hazard has been a major objective of dry forest management for decades (Stephens et al., 2019; Thompson et al., 2011). Historically, mature forest patches characterized by large fire-resistant trees and varying densities made up a substantial component of the landscape vegetation mosaic (Hessburg et al., 2015; Lydersen & Collins, 2018) and were maintained by frequent, low-to-moderate severity fire ignited by lightning and Indigenous peoples (Anderson, 2013; van Wagtenonk et al., 2018).

Through a combination of past logging and increasingly severe ecological disturbances, mature forests around the world are in decline (Lindenmayer et al., 2012). In the western USA, past timber harvesting that focused on large-tree removal is primarily responsible for the limited contemporary extent of mature forest habitat (Collins et al., 2017). Further, widespread fire suppression and exclusion of Indigenous burning during the 20th and 21st centuries has allowed small fire-sensitive trees and shrubs to replace the previously extracted large fire-resistant trees (Bernal et al., 2022; Knapp et al., 2013; Taylor, 2004). These changes to forest structure and flammability plus a warming climate have led to increasingly severe disturbance cycles that may pose an existential threat to spatially limited, remnant mature forests (Figure 1; Steel et al., 2015; Stephens et al., 2018). Patch size of forest loss due to severe wildfire is also increasing, whereas unburned refugia within fire perimeters are becoming more

fragmented and sustained in smaller patches (Steel et al., 2018), which can lead to slow or unsuccessful re-establishment of conifer species dependent on live seed trees (Welch et al., 2016). Forest densification can also lead to extensive tree mortality during drought due to a combination of elevated water stress and associated beetle attack (Fettig et al., 2019). This is particularly impactful for mature forests when beetle species preferentially select large host trees, such as sugar pine (*Pinus lambertiana*) and ponderosa pine (*P. ponderosa*) in the Sierra Nevada (Stephenson et al., 2019).

These recent and increasingly extensive losses of mature forests threaten the persistence of wildlife species that require a mosaic of seral stages, including stands of large trees and multilayered canopies. Interiors of large high severity burn patches constitute poor habitat for mature forest specialists and support lower biodiversity for at least some taxa (Jones et al., 2020; Steel, Fogg, et al., 2022). Even black-backed woodpeckers, long held up as an example of fire-dependent species in dry western forests (Hutto, 2008; Odion & Hanson, 2013), have recently been shown to be sensitive to fire patch size with large, homogenous high severity patches creating sink habitats for juveniles (Stillman et al., 2019, 2021). Further, the loss of fire refugia limits the capacity of many species to recolonize the postfire landscape (Cunningham et al., 2003; Thompson et al., 2021; Vanbianchi et al., 2017).

Several factors have led to documented or likely declines in populations of mature forest-dependent species in the western USA, including the California spotted owl and the West Coast population of fishers, with projected further loss of habitat posing a grave threat to these populations (Aubry et al., 2013; Gutiérrez et al., 2017; USFWS, 2020). The southern Sierra Nevada in particular supports populations at risk of climate-related shifts in drought and wildfire patterns, including the federally endangered Southern Sierra Nevada Distinct Population Segment of fishers. The region's complex topography and elevation range also provides potential climate refugia for these species, if such habitats avoid catastrophic disturbance. Policies adopted to protect remnant patches of mature forest habitat have been in place for several

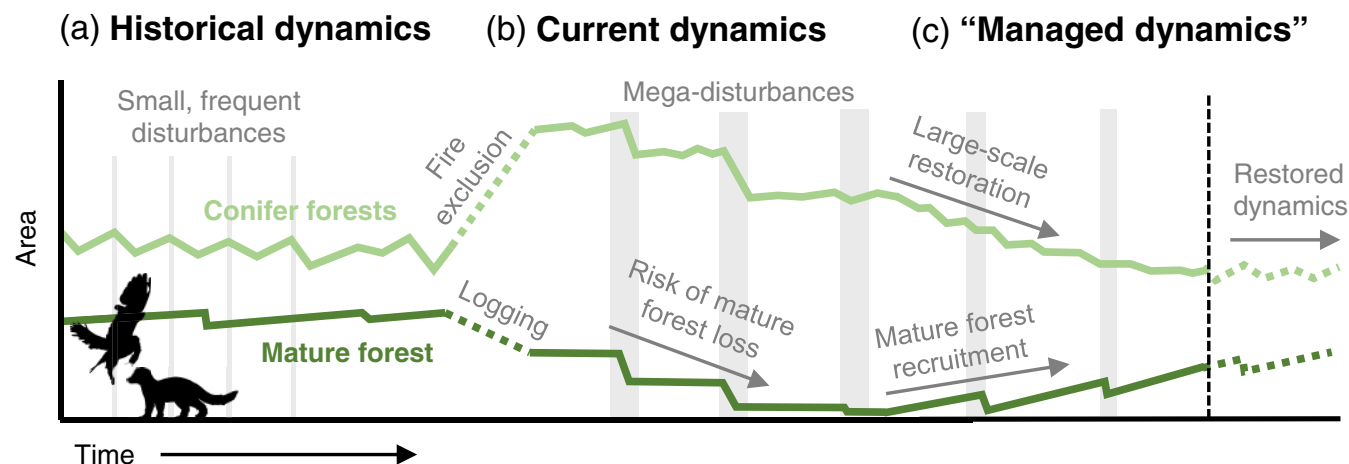


FIGURE 1 Conceptual figure showing trends in areas of conifer forests and of mature forest habitat under regimes of (a) historic, (b) current, and (c) potential future dynamics (achieved via “managed dynamics”). The late 2010s and early 2020s have been characterized by compounding mega-disturbances and extensive declines of mature forest habitat. Future managed dynamics include the restoration of small, frequent, low intensity disturbances that can help stabilize and perhaps reverse these recent trends. Vertical gray bars represent hypothetical disturbance events, with thicker bars indicating greater size/severity.

decades (Gutiérrez et al., 2017). Implementing such policies has led to land management designations such as spotted owl protected activity centers (PACs) in the Sierra Nevada National Forest Plans, and late-successional reserves in the Northwest Forest Plan. Spotted owl PACs are a roughly 120-ha land allocation designated wherever territorial owls are found in the Sierra Nevada portion of the California spotted owl range and delineated to include the best habitat (i.e., multistory, large-tree, and dense canopy cover habitat). Late-successional reserves are land allocations, representing 30% of the federal land within the range of northern spotted owls, designed to serve as habitat for late-successional- and old-growth-related species. Although these policies have effectively ended the harvest of large, old trees on United States Forest Service lands, they also limit other management activities (e.g., thinning from below, prescribed fire) making restoration of these disturbance-adapted forests more difficult (Collins et al., 2010). Furthermore, these policies implicitly assume that “protected” habitat areas can be preserved, more or less in their current form, in perpetuity (USDA, 2019). Recent disturbance trends in western forests create a test of this assumption and of the efficacy of a static approach to habitat conservation in disturbance-prone systems. Results from the Pacific Northwest suggest that in dynamic, disturbance-dependent forests, this assumption is not well supported (Davis et al., In Press). Under climate change, a static approach to mature forest conservation may be even less effective in drier and warmer regions such as the southern Sierra Nevada.

In this paper, we describe the change in the extent of mature conifer forests in the southern Sierra Nevada of

California during 2011–2020, a decade and ecoregion characterized by compounding severe wildfires and drought follow prolonged fire exclusion. The primary objectives of this analysis are to: (1) quantify the decline of conifer forest cover and of mature forest habitat due to drought (and associated beetle attack) and wildfire between 2011 and 2020; (2) test the assumption that static areas of restricted management will conserve mature forest habitat over time by examining whether rates of decline differed within versus outside of spotted owl protected areas; (3) compare the spatial pattern of drought/beetle-caused mortality with wildfire effects to better understand their differential impacts on mature forest habitat and the species that depend on it; and (4) assess whether and where forests have survived recent wildfires, potentially improving their resilience to future severe disturbance. Finally, considering the overall magnitude and extent of these disturbances, we discuss a potential shift in approach toward managing habitat for sensitive species, from one dominated by mega-disturbances toward a restoration of smaller, frequent disturbances necessary for the persistence of mature forests in fire- and drought-adapted ecosystems (Figure 1).

METHODS

Study area

Our study area is defined by the southern Sierra Nevada ranging approximately from 35° to 39° latitude and –121° to –117° longitude (Figure 2). We focus on forests

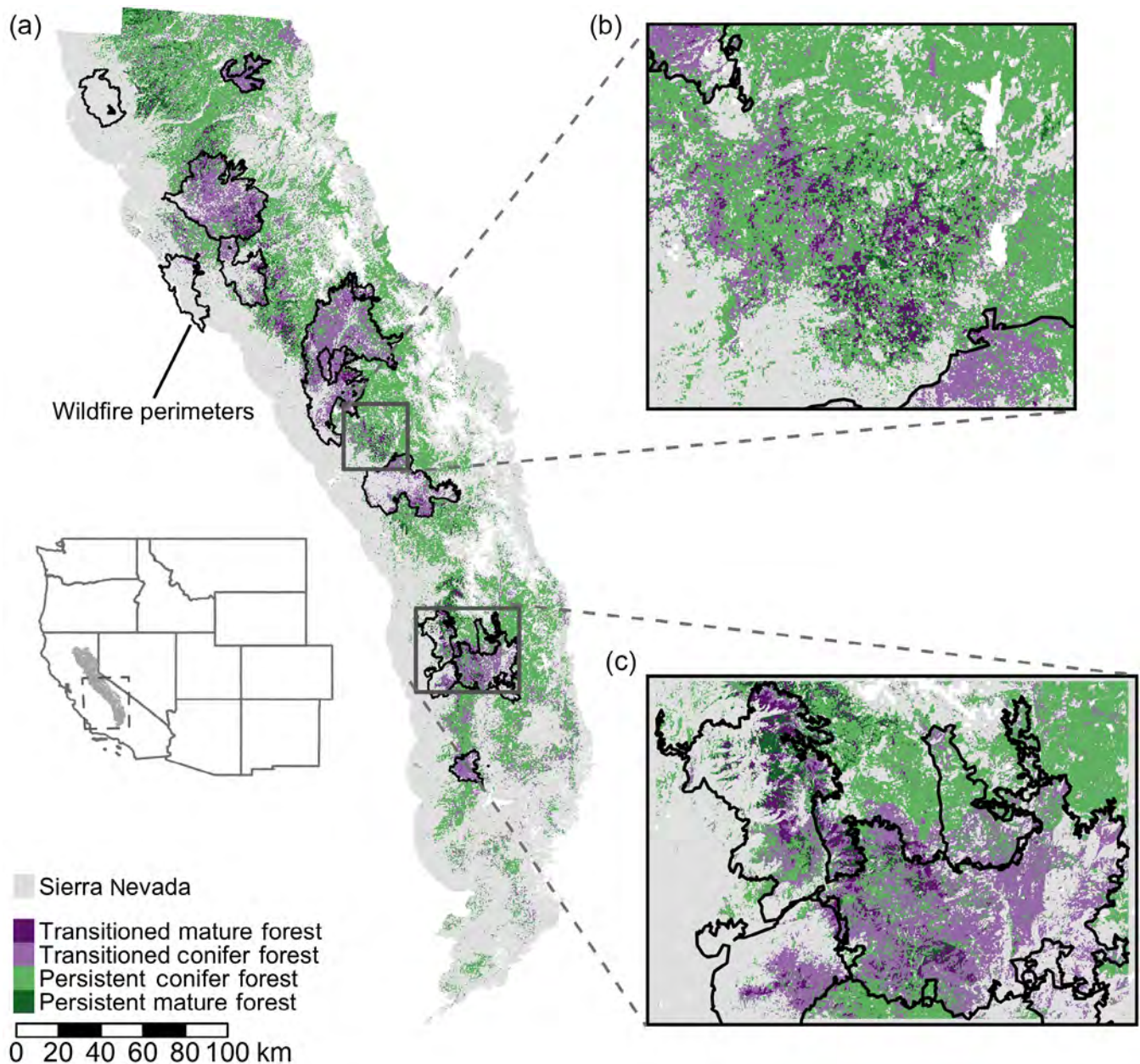


FIGURE 2 Map of forest and mature forest habitat transitions due to drought and wildfire mortality between 2011 and 2020. (a) Areas of conifer forest persistence and transitions in the southern Sierra Nevada. (b) An example of the spatial pattern of transition where drought and beetle infestation led to relatively small, but widely dispersed, patches of mortality. (c) An example of where the combination of drought and wildfire led to larger and more aggregated patches of mortality (i.e., within the 2020 Castle fire). Forests and mature forest (moderate and high density) habitats were considered to have experienced transition if canopy cover had declined below 25% and 40%, respectively. Areas initially considered mature were further limited to forests where the average height of the tallest trees exceeded 30 m. Black polygons show the perimeters of medium to large (≥ 5000 ha) wildfires during the study period and areas in the Sierra Nevada not dominated by conifer species are shown in gray.

that were conifer dominated as of 2011. Hardwood-dominated forests are also an important habitat for mature forest specialists (Aubry et al., 2013; Green et al., 2019; North et al., 2000). However, we limit our analysis to conifer-dominated forests because the tree mortality data used (described below) have not yet been

calibrated for nonconifer cover types. At lower elevations, conifer forests are dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), and incense cedar (*Calocedrus decurrens*), transitioning to a mixed-conifer community at mid elevations that also includes sugar pine (*Pinus lambertiana*), Douglas-fir

(*Pseudotsuga menziesii*), giant sequoia (*Sequoiadendron giganteum*), and California black oak (*Quercus kelloggii*) (Mayer & Laudenslayer, 1988; North et al., 2016). At higher elevations, Jeffrey pine (*Pinus jeffreyi*), red fir (*A. magnifica*), lodgepole pine (*Pinus contorta* var. *murrayana*), and western white pine (*Pinus monticola*) become dominant (Mayer & Laudenslayer, 1988; North et al., 2016). The southern Sierra Nevada has a Mediterranean-type climate where most precipitation occurs between November and May followed by an annual dry period broken up by sporadic summer thunderstorms (North et al., 2016).

Prior to Euro-American colonization, fire return intervals were short, especially in ponderosa pine and mixed-conifer forests (Safford & Stevens, 2017). Fire severity in these forests was predominantly low to moderate, resulting in the survival of most mature fire-resistant trees (Safford & Stevens, 2017). Return intervals were longer and the share of high severity effects (i.e., >95% vegetation mortality; Miller et al., 2009) were somewhat higher in higher elevation red fir and subalpine forest (Meyer & North, 2019). Due to 20th and 21st centuries fire suppression and exclusion, contemporary return intervals are much longer than their historic reference, although fire frequency and severity have both increased markedly in recent decades due to fuel accumulation, human ignitions, and climate change (Steel et al., 2015; Westerling, 2016; Williams et al., in revision). Severe drought was not uncommon in this region during the last two millennia (Swetnam, 1993). However, the most recent drought (2012–2016) may have been the most severe event in the last 1200+ years (Robeson, 2015).

Data and analysis

We used F^3 data of canopy cover and large-tree height to map conifer forest and mature conifer forest cover as of 2011 (Huang et al., 2018). The F^3 product integrates Forest Inventory and Analysis (FIA) field data with landscape and vegetation succession models to generate spatially contiguous estimates of stand structure, which has been validated for Sierra Nevada forests (Huang et al., 2018). We defined conifer forests as areas with a minimum of 25% canopy cover dominated by conifer species. This threshold is consistent with the USDA's vegetation classification system in which tree-dominated vegetation with a minimum height of 5 m and 25%–100% canopy closure is considered forest or woodland (Brewer et al., 2005). Here, 10%–25% tree canopy cover can be considered sparse woodland or savanna vegetation. We defined mature forests as a subset of conifer forests in which the average height of the 40 largest diameter trees

within the area equivalent to a FIA plot (0.4 ha) is at least 30 m. Cover of tall trees is particularly valuable for mature forest specialists such as the spotted owl (North et al., 2017). We further classified mature forests into subgroups using the F^3 data and following the California Wildlife Habitat Relationships classification of moderate density (40%–59% canopy cover) and high density ($\geq 60\%$ canopy cover) forests, which support various life history requisites (foraging, nesting/denning) and demographic parameters (reproduction, survival) of mature forest wildlife (Table 1). For example, 56%–61% cover may be optimal for fisher resting sites (Purcell et al., 2009) and California spotted owls tend to occupy nest sites with >70% canopy cover (Tempel et al., 2016). Forests characterized by tall trees, but <40% canopy cover may be considered low density mature forests. This forest type only covered 1076 ha in 2011, which constituted 1% of mature forest extent and 0.1% of overall conifer forest extent. The savanna and low density mature forest subclasses were not analyzed independently here as our focus was on species associated with higher canopy covers.

Estimates of live canopy cover decline (at 30 m resolution) were obtained from the Ecosystem Disturbance and Recovery Tracker (eDaRT), an image analysis system that processes all usable historic Landsat imagery (normally at the 8- or 16-day step). The eDaRT algorithm statistically models normal (e.g., phenology driven) variability in multiple vegetation indices across the image time series, and tracks model residuals through time to detect disturbance events as anomalous changes in the residuals' trajectories, relative to a recent baseline (Koltunov et al., 2015, 2020). For detected disturbances, the algorithm estimates the resulting loss of live tree canopy cover (as pixel area fraction) using the eDaRT Mortality Magnitude Index (MMI). In this paper, we used the MMI values integrated on an annual basis between 2011 and 2020 (detailed description

TABLE 1 Conifer forest classification definitions.

Classification	Canopy cover range (%)	Large-tree height minimum (m)
Nonforest	0–25	None
Sparse woodland/savanna ^a	10–25	5
Conifer forest	25–100	5
Mature forest	40–100	30
Low density ^a	25–40	30
Moderate density	40–60	30
High density	60–100	30

Note: Classifications are hierarchical with mature forests being a subset of conifer forest and mature forests further subdivided into density classes.

^aThe savanna and low density mature subclasses are not explicitly analyzed.

in Appendix S1). Conifer forests and mature forests are considered to have transitioned to a different vegetation class if live canopy cover drops below their minimum canopy cover thresholds. Although increases in live canopy cover did occur in some instances over this time period, this new cover was predominated by seedling to sapling size trees following large-tree mortality events (Young et al., 2020). Thus, only declines in canopy cover were considered here.

The current eDaRT version does not directly differentiate the cause of detected disturbances (e.g., fire vs. drought and beetle infestation), thus necessitating additional analyses to attribute detected disturbance to tree mortality. Specifically, we assumed eDaRT-detected reduction in canopy within wildfire perimeters of a given year to be attributable to a combination of wildfire and underlying drought conditions, and within management areas to be a combination of timber harvest or fuels reduction treatments and drought conditions. To delineate burned areas for each study year, we used California's interagency fire perimeter database (available at <https://frap.fire.ca.gov/frap-projects/fire-perimeters/>; FRAP, 2022). To delineate areas managed for timber harvest or fuels reduction treatments we used the Knight et al. (2022) dataset that combined spatially explicit activities data from the California Department of Forestry and Fire Protection (CalFire) and the United States Forest Service (FACTS database); and crosswalked these activities by treatment type and intensity. Knight et al. (2022) also refined the spatial and temporal accuracy of the combined data using satellite imagery and the Continuous Change Detection and Classification algorithm. While these data include a wide range of activity types, we limited our assessment to activity types that can significantly reduce live canopy cover at the Landsat pixel scale (e.g., clear-cuts and thinning). This dataset does not include activities on National Parks land, where mechanical tree removal is minimal and at the time of writing does not include 2020 activities. Canopy declines in areas and years in which no fire or management activity occurred were attributed to drought and associated beetle kill only. This assumption likely resulted in a slight overestimate of drought mortality in 2020 when management activity data were not available.

Spotted owl PAC polygons were obtained from a United States Forest Service geospatial dataset and included a total of 651 PACs in our study area, 96% of which were established before 2011. A regular grid of non-PAC sample points was generated across our study area but limited to Forest Service lands and outside established PACs. Grid spacing (3.9 km) was set to allow an equal number of non-PAC points (651) within the 2011 extent of conifer forests. Sample points were

buffered to create non-PAC areas equal to the mean size of study area PACs (128 ha). The 2011 canopy cover, 2011 average large-tree height, and relative decline in canopy cover between 2011 and 2020 were summarized for each PAC, all non-PAC Forest Service lands, and for each non-PAC sample area. Relative canopy cover declines were calculated as the percentage of 2011 canopy cover that was lost between 2011 and 2020. Mean values within each PAC and non-PAC area were used for statistical comparison. To assess whether forest habitats within PACs were successfully preserved despite regional disturbances we modeled relative decline in cover as a function of sample class (PAC or non-PAC). Separately, we modeled relative decline in cover as a function of 2011 canopy cover and 2011 average large-tree height. Structural and PAC class variables were not combined in the same model to avoid statistical confounding as PAC delineation is determined largely by forest structural characteristics (USDA, 2004). We fitted generalized linear models using a beta error structure with a logit-link because relative canopy cover decline is a proportion bounded between zero and one. Models were fitted using the *BRMs* package in program R (Bürkner, 2017; R Core Team, 2021).

We compared landscape pattern within and outside burned areas to contrast the effect of the combined impacts of wildfire and drought/beetles with areas only affected by drought and beetle attack. Patches of all forest and mature forest that transitioned to lower density classes between 2011 and 2020 were assessed for size and core area. Area ≥ 90 m (3 pixels) from nontransitioned edge was defined as core area, which approximated distance estimates of when conifer seed dispersal and habitat use of some forest-associated species become minimal (i.e., 100 m; Jones et al., 2020; Kramer et al., 2021). Additionally, to assess the degree of fragmentation due to each combination of disturbances, we calculated the aggregation index of forest cover prior to the disturbances in question (2011), as well as within and outside of burned areas at the end of our study period in 2020. Assessments of landscape pattern were conducted for each forest class. We focused this analysis on drought and wildfire patterns only because the extent of mechanical management activities during our study period was relatively minimal (see “Results”).

To assess the degree to which forests survived a recent fire and potentially experienced partial restoration of the historic fire regime, we calculated years since the last fire for all areas remaining as forest and mature forest each year. Forested pixels were considered to have experienced recent fire if years since the last fire were equal to or less than twice the mean reference return interval for a given forest type (e.g., $\leq 2 \times 11$ years for dry mixed conifer) according to the California fire return interval departure

dataset (Safford & Van de Water, 2014). This measure has been used in previous work as an indication of uncharacteristically high fuel accumulation (North et al., 2012) and consequently greater vulnerability to severe fire (Steel et al., 2015). Spatial analyses were performed primarily using the *sf*, *terra*, and *landscape metrics* packages in the R statistical environment (Hesselbarth et al., 2019; Hijmans, 2022; Pebesma, 2018; R Core Team, 2021).

RESULTS

Conifer forest cover decline

As of 2011, there were a total of 1,407,597 hectares of conifer forest in our southern Sierra Nevada study region. 96,810 ha of these forests were classified as either moderate density (41,175 ha) or high density (55,634 ha) mature forest habitat (Table 2). Between 2011 and 2020, canopy cover across 30% of conifer forests declined below 25%, constituting a change to either sparse woodland/savanna vegetation or, in many cases, a transition to nontree-dominated vegetation (Figures 2 and 3). During this period, 50% of moderate or high density mature forest habitat saw canopy cover decline below 40%, constituting a transition to lower density forest (22% of the original extent) or nonforest vegetation (28% of the original extent). Within the mature forest classification, higher density areas experienced more extensive declines, with 85% of this subclass falling below the 60% canopy cover definition of high density. The moderate density mature forests experienced little net change, with much of its declining area compensated by transitions from the high density mature forest group (Table 2; Figure 3).

Spotted owl PACs saw rates of decline across conifer forest classes similar to the study area overall, with the exception of moderate density mature forests, which saw a net increase of 13% due to transitions from the high density class (Table 2). However, because of how they were delineated, PACs generally were biased toward containing denser forests than the study area as a whole, resulting in differences in the average rates of canopy cover decline. In 2011, PACs were characterized by a mean canopy cover of 56%, mean large-tree height of 24 m, and 20% of their conifer forest area were categorized as mature forest of moderate or high density. In contrast, all conifer forests in our study area in 2011 were characterized by a mean canopy cover of 36%, mean large-tree height of 13 m, and 7% were categorized as mature forest of moderate or high density. By 2020, the mean absolute decline in canopy cover was greater inside PACs (26%) compared with all conifer forests in the study area (16%).

Statistical comparisons of PAC and non-PAC areas within Forest Service lands confirmed that the decline in relative canopy cover (percent of 2011 canopy cover) was greater in PACs and also showed clear effects of initial forest structure, with greater decline within areas characterized by higher 2011 canopy cover and less decline in areas characterized by greater 2011 large-tree height (Figure 4). Models predict the average PAC lost 49% (95% prediction interval [PI] = 46, 51) of its 2011 canopy cover by 2020, whereas non-PAC areas lost 42% (PI = 40, 44; Figure 4a). In both PAC and non-PAC areas, areas that had higher canopy cover in 2011 were more susceptible to percentage canopy cover loss and vegetation class transition than areas with lower canopy cover (Figure 4b). For example, mean predicted declines at our density class

TABLE 2 Hectares (percentage of 2011 area) of conifer forests and forest class change between 2011 and 2020 for the full study area and spotted owl protected activity centers (PACs).

Extent	Class	2011	2020	Transition to nonforest	Net change
Study area	All forests	1,407,597	988,601 (70%)	418,996 (30%)	−418,996 (−30%)
	Mature forests ^a	96,810	48,385 (50%)	26,675 (28%)	−48,425 (−50%)
	Mod density	41,175	39,957 (96%)	11,409 (28%)	−1218 (−3%)
	High density	55,634	8427 (15%)	15,265 (27%)	−47,207 (−85%)
Protected activity centers	All forests	76,819	49,936 (65%)	26,883 (35%)	−26,883 (−35%)
	Mature forests ^a	15,072	7568 (50%)	4194 (28%)	−7504 (−50%)
	Mod density	5233	5889 (113%)	1690 (32%)	655 (13%)
	High density	9838	1679 (17%)	2503 (25%)	−8159 (−83%)

Note: Conifer-dominated areas with >25% live canopy cover are considered forests. Within that class, mature forests are defined by a mean tall tree height of >30 m further nested within the mature forest class are moderate density (40%–60% canopy cover) and high density (>60% canopy cover) mature forests. Forests density classes either transitioned to nonforest (canopy cover dropped below 25%) or to a lower density class (e.g., a decline from 70% to 50% cover constitutes a transition from high density mature forest to the moderate density class).

^aIncludes mature forests with >40% 2011 canopy cover (i.e., excludes low density mature forests).

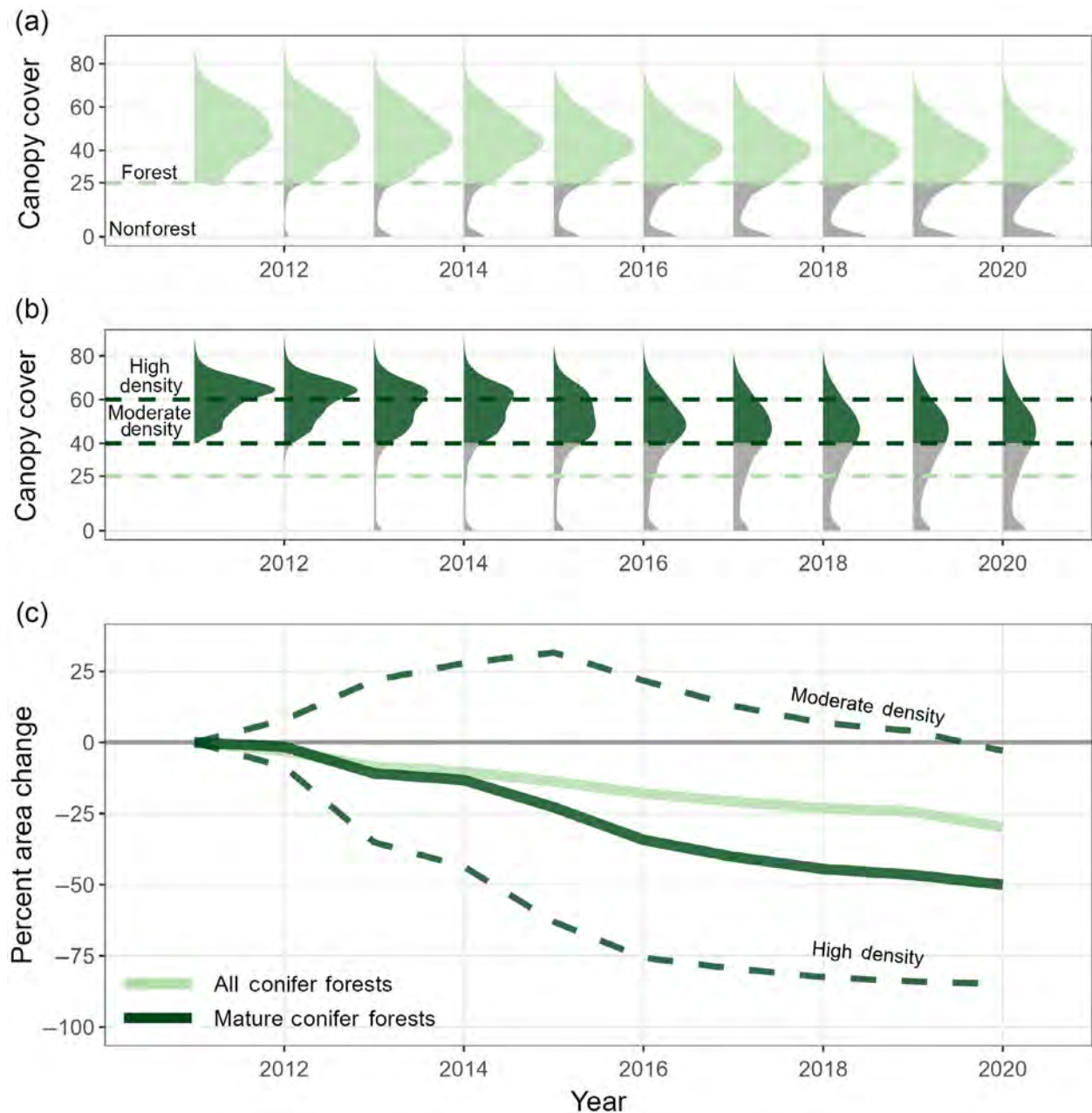


FIGURE 3 Change in conifer forest habitat between 2011 and 2020 in the southern Sierra Nevada. Annual density distribution of canopy cover for (a) all conifer forests (>25% canopy cover), and (b) moderate and high density mature conifer forests (>40% canopy cover and >30 m mean height of tallest trees). Gray portions of density distributions illustrate the area of transition since 2011 of each forest class. (c) Change in area of all conifer forests and mature conifer forests relative to 2011. Mature forest subclasses are shown as dashed lines in (c) and illustrate the initial increase in moderate density mature forests (40%–60% canopy cover) due to transitions from declining high density mature forests (>60% cover).

thresholds of 25%, 40% and 60% canopy cover were 31% (PI = 27, 34), 39% (PI = 37, 41), and 51% (PI = 49, 53), respectively (Figure 4b). The effect of large-tree height on relative canopy cover decline was negative, albeit with a smaller effect size, indicating the presence of large, tall trees had a moderating effect on disturbance. For example, a forest with a mean large-tree height of 15 m was

predicted to experience a 55% (PI = 49, 61) relative canopy cover decline, whereas a mean large-tree height of 30 m was expected to result in a relative canopy cover decline of 52% (PI = 47, 57; Figure 4c) when controlling for 2011 canopy cover. Model uncertainty was low (95% credible intervals did not include zero) for all effect estimates (Appendix S1: Table S1).

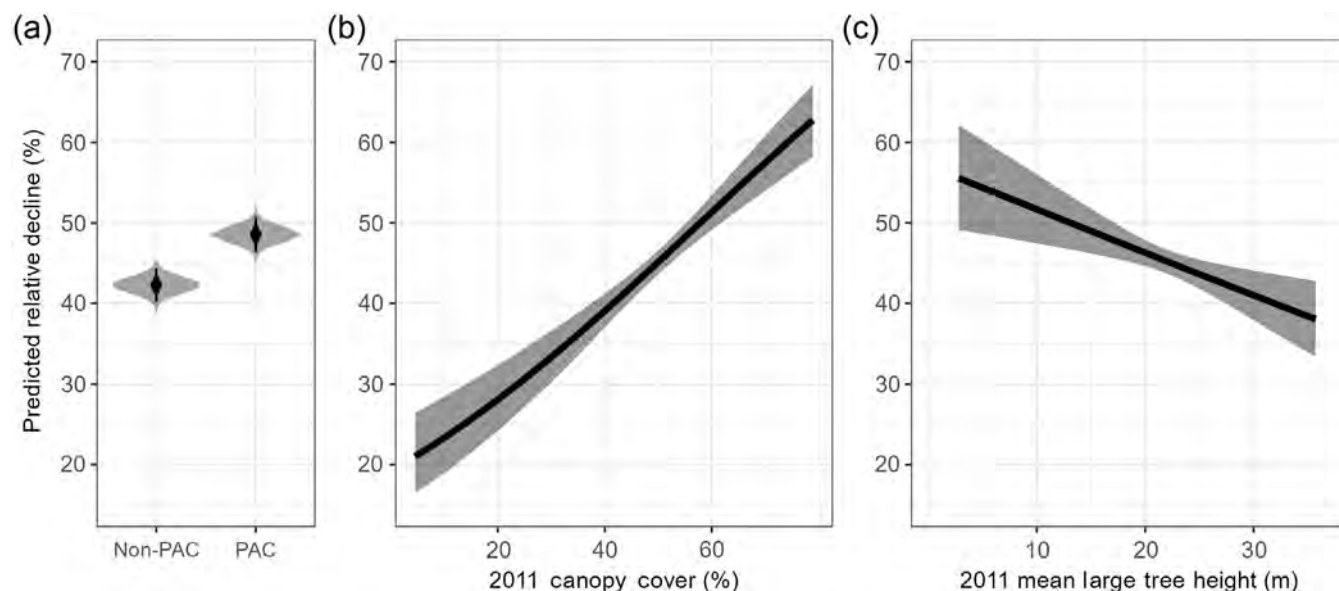


FIGURE 4 Expected relative canopy cover declines between 2011 and 2020 as predicted by (a) spotted owl protected activity center (PAC) class, (b) 2011 canopy cover, and (c) 2011 mean large-tree height. Relative canopy cover declines are calculated as the percentage of 2011 canopy cover that was lost between 2011 and 2020. The effects of 2011 canopy cover and height are fitted using data from both PAC and non-PAC sample areas. Points and vertical lines represent the mean estimate and 90% credible intervals in (a). Black lines and grey bands represent the mean estimate and 90% credible intervals in (b) and (c). Tabulated model coefficients can be found in Appendix S1: Table S1.

Wildfire and drought patterns

Because drought conditions were ubiquitous during large parts of our study period, we compared three types of interacting forest disturbances: (1) drought and associated beetle infestation (jointly referred to as “drought”) in the absence of other disturbances, (2) the combination of wildfire plus drought, and (3) the combination of mechanical management activities (e.g., timber harvest and thinning) plus drought. A greater cumulative area of forests was converted to nonforest due to drought alone (213,000 ha; 51% of total area transitioned) than when wildfires were also a contributing factor (190,000 ha; 45%), or when mechanical activities were a contributing factor (16,000 ha; 4%). The differential was even greater in the case of moderate and dense mature forests where transitions to nonforest or a lower density class were more attributable to drought alone (32,000 ha; 66%), than to the combination of wildfire and drought (15,000 ha; 31%) or mechanical activities and drought (2000 ha; 4%).

For all forest classes, patch and core size of transitioned areas were greater within burned forest than those that were not burned during 2011–2020 (Figure 2; Table 3). Distributions of disturbed patch sizes were highly skewed with relatively few large patches accounting for a disproportionate amount of the area of transitioned forest. The largest transitioned forest patch (68,389 ha) and contiguous core area (25,186 ha) of transitioned forest were found within burned areas during

this period. Likewise, the largest patch size (1119 ha) and contiguous core area (326 ha) of transitioned moderate and high density mature forest habitat occurred within fire perimeters (Table 3). These differences in spatial pattern of interacting drought and wildfire resulted in greater forest fragmentation than areas affected by drought alone as measured by the aggregation index. Low aggregation index values approaching 0 represent greater fragmentation and high values approaching 100 represent greater aggregation. For all forests, the aggregation index declined from 93 in 2011 to 88 in unburned areas and to 75 in burned areas by 2020. Similarly, the aggregation index for mature forests declined from 85 in 2011 to 75 in unburned forests and 64 in burned forests (Table 4).

There was a clear temporal pattern of forest mortality attributable to drought and beetle infestation alone with a 2016 peak in forest cover decline corresponding to the last year of the 2012–2016 drought. Transitions due to the combination of wildfire and drought were less consistent and corresponded with individual large wildfire events (e.g., the 2013 Rim Fire and the 2020 Creek and Castle Fires). Transitions attributable to mechanical activities and drought were consistently limited between 2012 and 2019 (Figure 5a).

As of 2011, a large majority of the conifer forests and mature forests in the southern Sierra Nevada had not experienced a wildfire in at least twice their reference fire return interval. The absolute amount of forest

TABLE 3 Summary statistics of disturbance patch size and core area size created by drought/beetles and wildfire between 2011 and 2020.

Metric	Class	Disturbance	N	Mean	Q50	Q95	Max
Area	Forest	Drought	233,874	0.66	0.18	1.89	2246.04
Area	Forest	Fire + Drought	36,953	7.15	0.18	3.77	68,372.36
Area	High density mature	Drought	11,467	2.25	0.27	5.84	1741.95
Area	High density mature	Fire + Drought	5694	3.74	0.36	9.52	827.43
Area	Mature forest	Drought	20,306	1.04	0.18	3.23	447.88
Area	Mature forest	Fire + Drought	9078	3.00	0.36	8.17	1115.57
Area	Moderate density mature	Drought	14,629	0.86	0.18	2.51	373.26
Area	Moderate density mature	Fire + Drought	6939	1.54	0.27	4.49	970.91
Core	Forest	Drought	1268	2.36	0.54	7.54	342.46
Core	Forest	Fire + Drought	671	116.43	0.81	93.79	25,179.57
Core	High density mature	Drought	375	6.15	0.63	24.90	653.32
Core	High density mature	Fire + Drought	322	10.15	1.39	41.56	295.41
Core	Mature forest	Drought	278	2.51	0.36	11.57	67.88
Core	Mature forest	Fire + Drought	400	8.41	0.99	32.24	326.03
Core	Moderate density mature	Drought	124	2.68	0.45	10.98	58.63
Core	Moderate density mature	Fire + Drought	156	5.40	0.72	19.64	292.45

Note: Patches without core area are included in the patch size (area) metric but excluded from the core area (core) metric. *N* represents the number of patches in each group, and all other summary statistics are in hectares. In most cases disturbed patches are small (i.e., 50th quantile <1 ha). Thus, we summarize the large end of data distributions (i.e., 95th quantile, and max) as these patches affect the greatest amount of area and are the most ecologically important.

TABLE 4 Aggregation index values prior to and following drought/beetles and wildfire in the southern Sierra Nevada during 2011–2020.

Class	Initial (2011)	Postdrought (2020)	Postdrought and wildfire (2020)
All forests	93	88	75
Mature forests	85	75	64
Moderate density mature	77	63	52
High density mature	83	61	46

Note: Index values range from 0 to 100, in which low values represent highly fragmented forest cover and high values represent highly aggregated forest cover.

that was within twice its reference return interval was largely stable across the study period, but the proportion of recently burned forest and recently burned mature forest increased due to an overall decline in forest cover (Figure 5b). Specifically, the percentage of recently burned conifer forests increased from 25% in 2011 to 33% in 2020, whereas recently burned mature forests increased from 7% to 20% during the same period.

DISCUSSION

Rapid decline of mature forest habitat

The 2010s was a decade characterized by severe and unprecedented ecological disturbance in California's conifer forests; one that portends a rapid reshaping of forested landscapes, the ecosystem services they provide, and their dependent wildlife communities. Here we documented a temporary or permanent conversion of 30% of the conifer forests and a transition of half of the moderate and high density mature forest habitat in the southern Sierra Nevada between 2011 and 2020 due to compounding megafires and a historic drought. Changes were particularly pronounced in dense mature forest habitat, which declined by 85% either by transitioning to lower density forest or through complete conversion to nonforest vegetation. Spotted owl PACs, also saw dramatic declines with a loss of 49% of their 2011 canopy cover. Worsening wildfire and climate trends are expected to continue or accelerate in the coming decades (Abatzoglou et al., 2021), making the continued decline of conifer forest extent likely and the complete loss of remaining moderate and high density mature forest habitats plausible (Stephens, Miller, et al., 2016; Westerling, 2016).

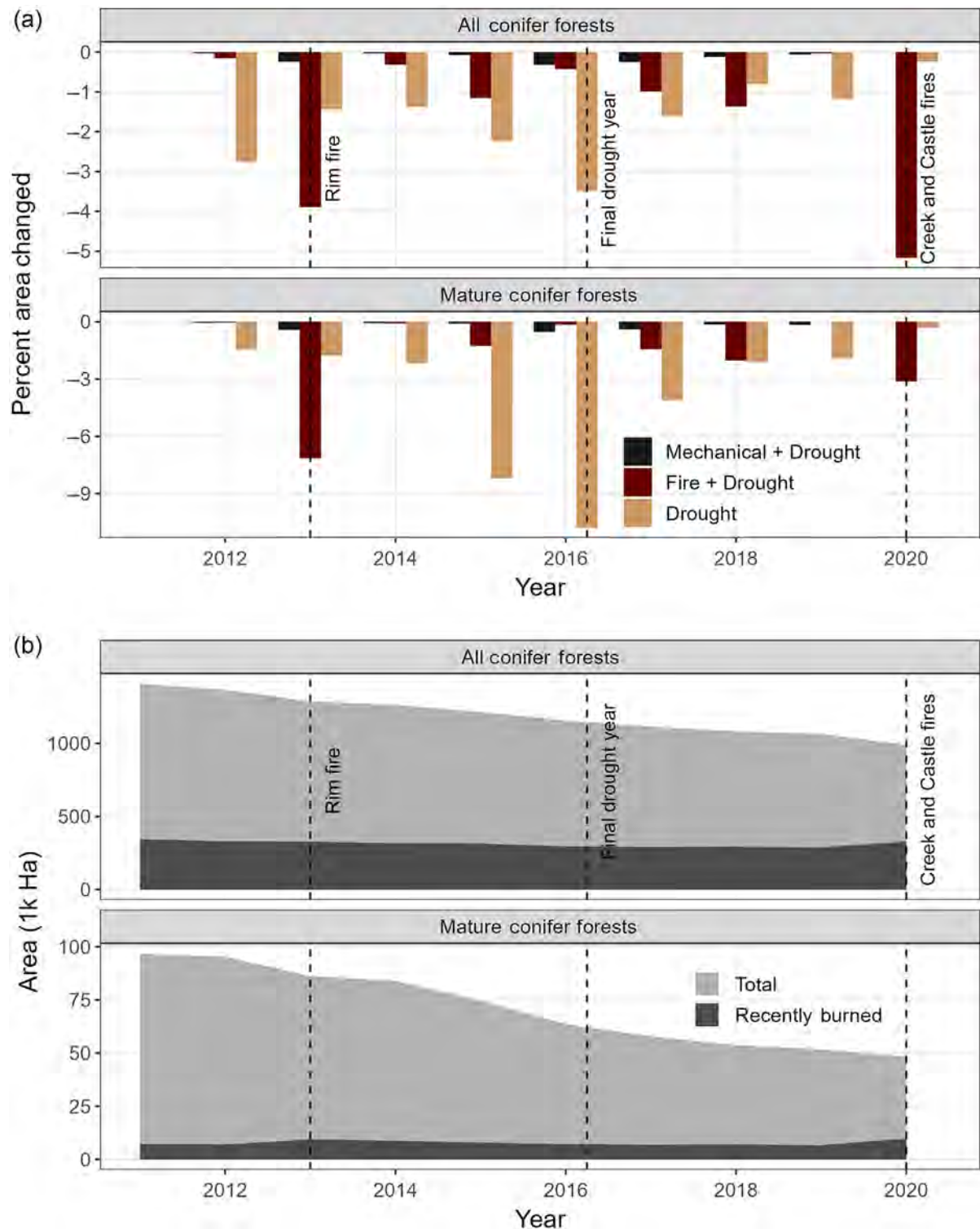


FIGURE 5 (a) All forest and mature forest area transitioned annually due to drought, a combination of drought and wildfire, or a combination of drought and mechanical management activities (timber harvest or thinning) from 2011 to 2020. (b) The total amount of area remaining as forest or mature forest as well as the amount of area that survived a recent burn (time since the last fire was less than twice the historic fire return interval). Conifer forests are defined by a minimum of 25% canopy cover. Mature forests are defined as having a minimum of 30 m average height of the tallest trees as of 2011 and maintaining at least 40% canopy cover. The timing of three large fires and the final year of the 2012–2016 drought are noted with vertical dashed lines. No mechanical activity data were available during 2020, potentially inflating the estimate of drought-only transitions for that year. Changes in mature forest density subclasses are shown in Appendix S1: Figure S1.

Megafires create large high severity patches that can be inaccessible or inhospitable to mature forest specialists, and as a result they tend to support lower wildlife species diversity overall (Jones et al., 2020; Steel, Fogg, et al., 2022). Further, large severe wildfires can increase fragmentation of limited mature forest habitat. Our results demonstrate that wildfire (in combination with drought) created distinctly larger contiguous patches of forest loss and increased forest fragmentation, whereas tree mortality from drought and beetle kill resulted in patchier and more fine-scale spatial patterns with relatively moderate increases in habitat fragmentation. In the Sierra Nevada, suitable fisher habitat is distributed in a north/south pattern limited by elevational bounds and periodically disrupted by bottlenecks that occur near large river canyons (Thompson et al., 2021). These bottlenecks, which are typically associated with isolated stretches of linkage habitat, may be comprised of lower quality habitat but are crucial for maintaining overall population connectivity and gene flow (Tucker et al., 2014). Since 2013, habitat within key linkage areas has been lost to high severity fire at nearly twice the rate of habitat outside key linkage areas (Thompson et al., 2021; USFWS, 2020), limiting population-scale connectivity and increasing the risk of genetic isolation (Tucker et al., 2014). The spotted owl is tolerant of, or even selects for, small high severity burned patches if mature stands survive in the nearby matrix, but they are intolerant of increasingly large high severity patches created by fires such as the 2013 Rim, 2020 Creek, and 2020 Castle fires in the southern Sierra Nevada (Jones et al., 2020; Kramer et al., 2021). A mosaic of burn severities consisting of predominantly low-to-moderate severity fire with small patches of high severity can create “pyrodiverse” landscapes that contain early seral habitat including shrublands and recently killed “snag forests” required by some species, while also promoting the persistence of key habitat structures for late seral-dependent species (Jones, Kramer, et al., 2021; Steel, Collins, et al., 2021). These disturbances also leave a network of residual habitat patches (i.e., fire refugia) that are critical to fisher re-colonization (Blomdahl, 2018; Thompson et al., 2021). Without these refugia, the potential exists for a community shift to more generalist species (Green et al., 2022).

Low-to-moderate severity fire can create habitat for some wildlife species and increase forest resistance to future severe disturbance (Steel, Foster, et al., 2021), but drought mortality has the potential to add flammable fuels to the system and increase the likelihood of future forest loss due to wildfire (Stephens et al., 2018, 2022). The 2012–2016 drought and associated beetle epidemics resulted in the mortality of more than 150 million trees in California’s Sierra Nevada (USDA, 2020), which was

disproportionately concentrated in large conifers (e.g., in >38 cm diameter ponderosa pine; Fettig et al., 2019). Fishers rely on large trees for resting and denning habitat (Green et al., 2019; Purcell et al., 2009), and spotted owl population declines have been linked to losses of large, old trees used for nesting (Jones et al., 2018). Thus, the mechanism of canopy cover decline in mature forests is also important. For example, shifts from high density to moderate density mature forests may be restorative when wildfire is the causal agent because it consumes fuel and generally kills smaller trees, leaving larger trees intact and further insulated from subsequent disturbance. Fuels reduction treatments that target fine fuels can have a similarly restorative effect, especially when including the use of prescribed or cultural fire (North et al., 2021). Additional research is needed to better understand how mature forest specialist species respond to wildfire and wildfire surrogates that reduce canopy cover below a known optimum, while maintaining important features such as large, tall conifers and restoring resilience to future disturbance (Jones, Keyser, et al., 2021). However, when canopy cover declines are attributable to drought and beetle attack (Appendix S1: Figure S1), there is likely to be a corrosive effect on habitat quality because large trees are preferentially killed and dead fuel is added to the system, increasing the vulnerability to subsequent wildfire effects.

Rapid loss in mature forest habitat in the southern Sierra Nevada and longer term trends in fire-related forest decline throughout California (Steel et al., 2018; Stevens et al., 2017) suggest that existing forest management paradigms may be inadequate for maintaining mature mixed-conifer forests under current and projected future disturbance dynamics (North et al., 2022). If these rates of decline continue, we are likely to see near total loss of southern Sierra Nevada mature conifer forests in the coming decades. This would be much more rapid than the time horizon of mature forest loss estimated by Stephens and colleagues (2016) (by 2089, or ~75 years). However, Stephens and colleagues (2016) did not consider drought-related mortality, and only analyzed fire activity up to 2014, which missed the record fire year of 2020 (Safford et al., 2022). It is worth noting that the extreme fire activity documented in California during 2020 was likely not a one-off anomaly; recent observations indicate similar, if not exacerbated, fire activity in 2021 (Shive et al., 2021). The region has also re-entered extreme drought (Williams et al., 2022) with implications for both drought and beetle mortality and severe wildfire. More optimistically, total loss of mature forests in this region could be delayed until midcentury if we enter a period of cooler, wetter years, if surviving mature forests within these fire footprints have gained resilience to future disturbances, or if recruitment

of mature hardwood species compensates for losses of large conifers. Hardwood species may become a greater component of the Sierra Nevada landscape as conifers decline (Restaino et al., 2019; Steel, Foster, et al., 2021). Oaks, especially California black oaks, are relatively resilient to both wildfire and drought, and are utilized by species such as the spotted owl and fisher (Aubry et al., 2013; Green et al., 2019; North et al., 2000). However, loss of mature forest habitat, on any likely timeline, is unsustainable given that the recruitment of conifer or hardwood mature forests takes many decades to centuries. Stephens et al. (2016) emphasized that policies prioritizing forest resilience over other resource concerns may be needed to meaningfully address the current backlog in forest management and shift the course from forest decline to sustainable disturbance dynamics. Indeed, our analysis showed that areas of higher canopy cover are more at risk of loss, and that large areas of relatively homogenous moderate and higher density forests, like PACs, are at risk of larger declines if resilience needs are not addressed. Recognizing the dynamic nature of habitat in these forests, and prioritizing the restoration of these dynamics over the attempted strict preservation of existing habitat, may help to minimize the impacts of these changes and maintain habitat functionality in the long term (Fabritius et al., 2017; Gaines et al., 2022; Stoetzel et al., 2020).

Management implications: Toward more sustainable disturbance dynamics

Landscapes are naturally dynamic in space and time, but society's approach for conserving landscapes often views them as static entities (Stoetzel et al., 2020). Habitat conservation typically involves cordoning off lands for full or partial protection from human activities, while at the same time allowing for fire suppression activities to preserve current structure. Conservation approaches that aim to keep ecosystems in stasis have been largely successful in conserving biodiversity and threatened species worldwide (Gray et al., 2016) by preventing threats to habitats such as infrastructure development and natural resource extraction (Barber et al., 2014). These approaches are heavily informed by conservation objectives in more naturally static ecosystems (e.g., Barber et al., 2014) as opposed to those adapted to frequent low intensity disturbance. Such "static" conservation approaches are heavily embedded in existing wildlife and ecosystem conservation policy (Leopold et al., 2018), as well as land management plans (e.g., USDA, 2004) in North America. Yet recent disturbance patterns and their cumulative impacts have demonstrated that efforts to resist change are often falling short in

dynamic ecosystems, such that achieving the specific conservation objectives and possibly the intent outlined in policy documents may no longer be feasible in disturbance-prone areas (Davis et al., *In Press*). In fact, continued attempts to resist change may be counterproductive when a hands-off approach (but continued fire suppression) creates a higher likelihood of rapid, transformational, and undesirable changes in the form of large-scale type conversion and habitat loss from disturbance (Rissman et al., 2018). In our study region, spotted owl PACs are often managed using a static conservation approach but our analysis shows that they have recently experienced more declines in canopy cover (49% relative to 2011) than outside of their borders (4%). This observation suggests that conservation of habitat for old-forest-dependent species may require a more dynamic approach that increases the resilience to disturbance, while maintaining valuable habitat features such as large, tall trees.

As an alternative to the static approach to habitat conservation currently in practice, a landscape conservation paradigm that recognizes and incorporates ecological system dynamics (Gaines et al., 2022; Hessburg et al., 2021) may prove to be better suited for disturbance-prone forests. Collectively, we refer to this as the "managed dynamics" paradigm (Figures 1 and 6). Although the overall goal of this alternative approach is similar to that of a more traditional static paradigm, i.e., to conserve a particular landscape feature (in this case, mature forests), the managed dynamics paradigm strives for something closer to a dynamic equilibrium (*sensu* Bonnicksen & Stone, 1982) of habitat loss and recruitment. In Sierra Nevada dry forests that historically were highly dynamic, patches of mature forest were periodically lost or degraded but were balanced by continual successional changes supported by a frequent low severity disturbance regime (Miller & Safford, 2017). Moving away from a "static" conservation paradigm in favor of a "dynamic" one does not prescribe eliminating protected areas or habitat preserves; nor would it involve removal of large trees, which our analysis shows supported forest resilience during the last decade. Rather it suggests that greater active management is necessary (e.g., through fire use and ecologically based thinning; *sensu* North et al., 2021) with an eye for emulating fine-scale heterogeneity and forest resilience likely supported by historic disturbance regimes (Jones, Keyser, et al., 2021). Further, management tactics and tools may need to be similarly dynamic and allowed to shift when objectives are not being met, or when needs have changed (e.g., Spies et al., 2018; Wood et al., 2018).

Managing for sustainable dynamics also embraces the positive role of humans in actively managing ecosystems. For millennia, Indigenous peoples of western North America burned vast areas of land to increase access to natural

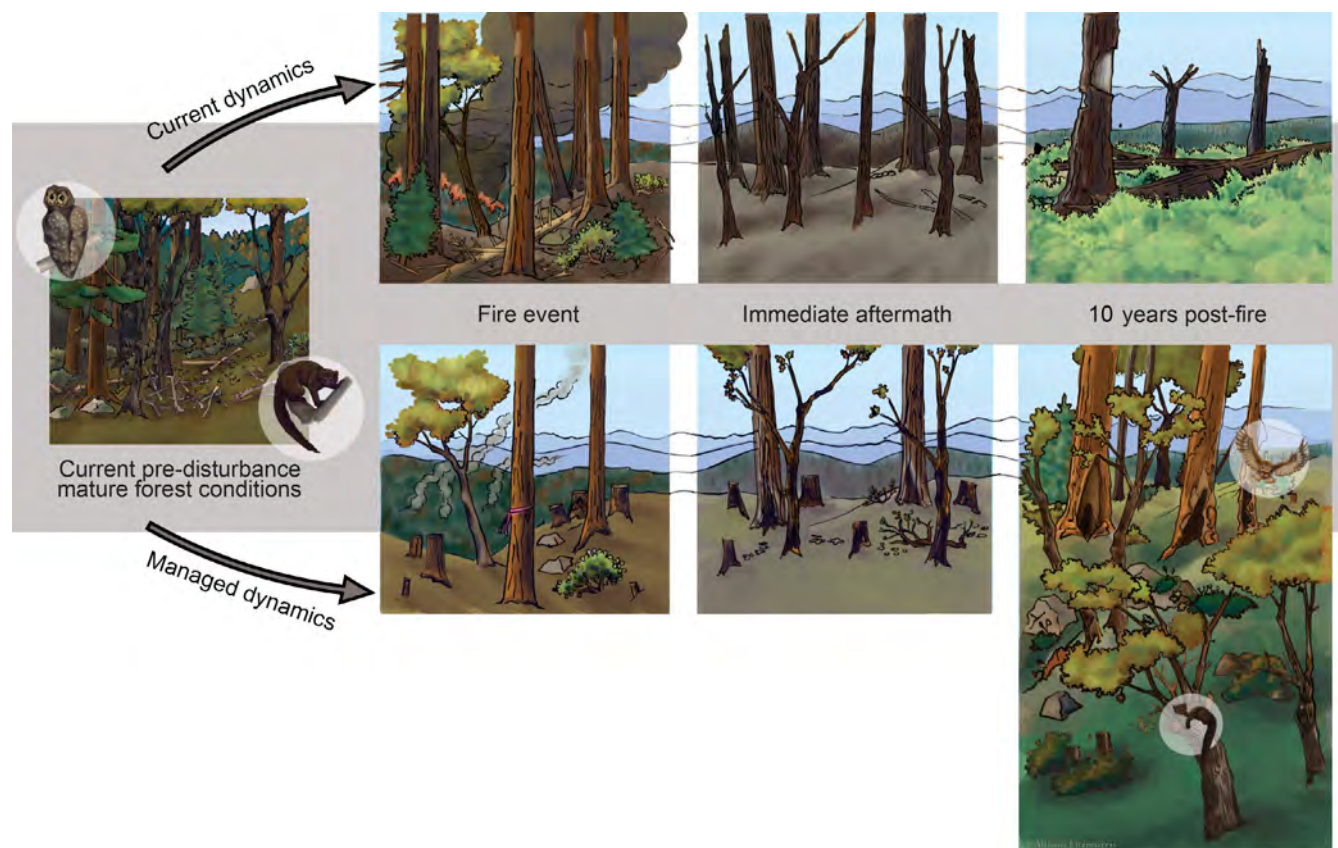


FIGURE 6 Illustration of two approaches to management in seasonally dry disturbance-prone California forests. Attempts to avoid and exclude all disturbance has led to mega-disturbances and transitions from mature forests conditions (top scenario), while managing for sustainable disturbance dynamics can maintain forest resilience and wildlife habitat (bottom scenario).

resources (Anderson, 2013; Hoffman et al., 2021). Indigenous burning as part of historic fire regimes also produced other ecosystem benefits such as increased forest resilience to subsequent disturbances (Eisenberg et al., 2019), enhanced biodiversity (Hoffman et al., 2021), and mutual protection for cultural and ecological resources (Slaton et al., 2019). A major part of implementing a managed dynamics paradigm in the Sierra Nevada includes increasing support for Indigenous fire use, as well as state and federally supported and ecologically driven management. Specific management actions would likely include leveraging areas of low-to-moderate severity effects within unplanned wildfires as well as active fuels reductions across large landscapes with prescribed and managed fire in a “pyrosilviculture” framework (North et al., 2021). Such an approach would be expected to result in reduced forest conversion to nonforest, increased water supply, more stable carbon storage, reduced competitive stress, as well as both protection and promotion of growing conditions for large, old trees (Figure 6; Stephens et al., 2020, 2021; North et al., 2022).

A managed dynamics paradigm is not without its challenges. Implementing forest treatments and restorative actions is generally difficult due to insufficient funding

and staffing, perceived and realized risks of employing prescribed, cultural, and managed wildfire, as well as other political and societal concerns (North et al., 2021; Schultz et al., 2019). Perhaps foremost among these obstacles when sensitive wildlife habitat is of concern is that a managed dynamics approach appears at odds with the precautionary principle, which has governed land management and wildlife conservation for decades (e.g., Kriebel et al., 2001). The precautionary principle “imposes a burden of proof on those who create potential risks, and it requires the regulation of activities, even if it cannot be shown that those activities are likely to produce significant harms” (Sunstein, 2002). In the Sierra Nevada, the principle has led to resistance of managing disturbance dynamics because management activities such as fuels reduction and thinning have been perceived to pose a risk to spotted owls and fishers via habitat alteration (Tempel et al., 2015). Indeed, many past management practices have had negative impacts on old-forest habitat features, including harvesting of the largest trees and removal of damaged trees that contain cavities or provide platforms for nesting and denning. Yet under current conditions characterized by rapid change, decision “paralysis”

(Sunstein, 2002) precipitated by the precautionary principle may lead to far greater harm to spotted owls and fishers via complete loss of mature forest habitat (Hessburg et al., 2021). For example, an estimated 10%–14% of the global population of giant sequoia were lost in 2020 alone due to high severity wildfire within the southern Sierra Nevada with additional losses to giant sequoia groves incurred from two large wildfires in 2021 (Shive et al., 2021). Many of the affected giant sequoia groves had largely gone untreated (i.e., no large-scale fuels reduction activities have occurred) and there is concern that increased restrictions for the southern Sierra fisher population may add an additional barrier to restoration efforts. Yet avoidance of action is a management decision, and our analysis shows that a hands-off approach is increasingly failing to preserve mature forests. Thus, we suggest that the managed dynamics paradigm is compatible with an interpretation of the precautionary principle that explicitly recognizes the risk of inaction. For example, as described in Wood et al. (2020), the precautionary principle could posit that management actions should be taken despite uncertainties if the cost of inaction is high.

CONCLUSION

Shifting disturbance patterns pose stark challenges to forest management and conservation. This has become particularly evident during the past decade in the southern Sierra Nevada of California, where compounding megafires and unprecedented drought have rapidly eroded already limited mature forest habitat. Although this period of forest degradation appears exceptional at present, continued climate change and the lingering legacy of fire exclusion and suppression make continued mega-disturbances likely. Indeed, drought conditions returned to the region in 2019 and persist through the time of writing in 2022. To forestall continued loss and fragmentation of habitat critical to mature forest specialist species a shift from a static, preservationist paradigm of habitat conservation to one striving for sustainable disturbance dynamics is likely to be necessary in fire- and drought-prone forests. Encouragingly, some recent forest policy appears to be moving toward a recognition of the need for managing for desirable dynamics. For example, recent management strategies for both Sierra Nevada fishers and California spotted owls recognized the shortcomings of the static approach of identifying “protected” habitat areas with limited management allowed (USDA, 2019). These new strategies call for a more dynamic approach to providing this habitat over time and space, while also incorporating the likelihood of disturbance.

A broadscale shift in forest conservation paradigm faces challenges, but given the rapid rate of forest degradation and future outlook, an equally rapid adaptation of management approach is likely to be needed to maintain and restore mature forests in the coming decades.

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CONFLICT OF INTEREST

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code (Steel, Jones, et al., 2022a) is available in Zenodo at <https://doi.org/10.5281/zenodo.7044555>. Data (Steel, Jones, et al., 2022b) are available in Dryad at <https://doi.org/10.6078/D1W43V>. Additional publicly available data sets utilized for this research are as follows: California fire perimeter geospatial data (FRAP, 2022; <https://frap.fire.ca.gov/frap-projects/fire-perimeters/>) and the California fire return interval departure dataset (Safford & Van de Water, 2014; <https://www.fs.usda.gov/detail/r5/landmanagement/gis/?cid=stelprdb5327836>).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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Tall, heterogeneous forests improve prey capture, delivery to nestlings, and reproductive success for Spotted Owls in southern California

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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

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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

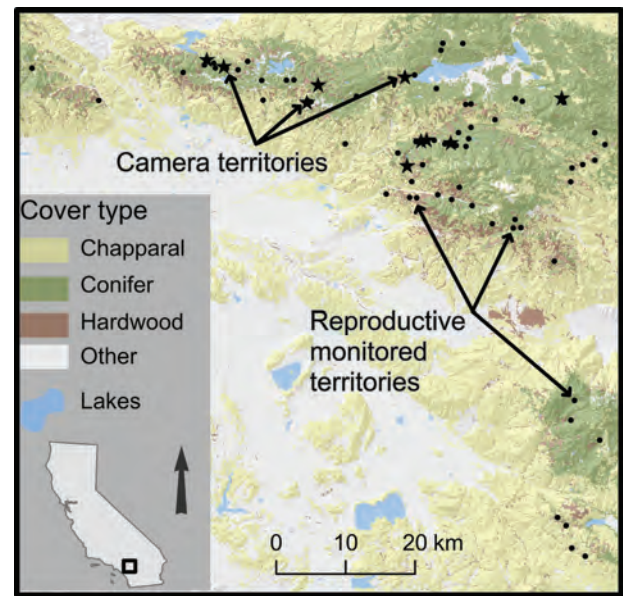


FIGURE 1. Map depicting 10 nest video camera locations for California Spotted Owl (*Strix occidentalis occidentalis*) hunting success and delivery rate analyses (black stars) as well as the 71 territories used in the reproductive success analysis (black circles) overlaid over dominant vegetation types. 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.

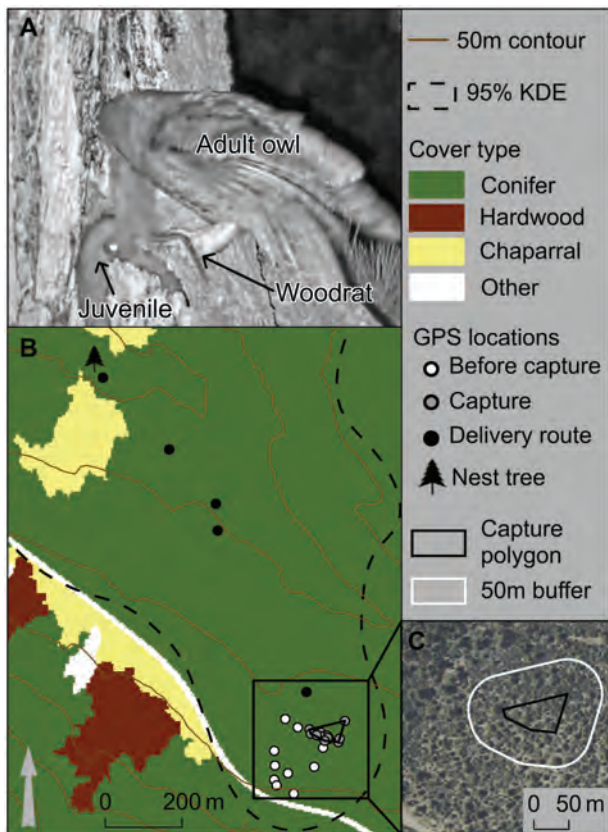


FIGURE 2. (A) Male delivering a woodrat to a juvenile on video camera. (B) Map of GPS points before (white), during (grey), and after (black) a successful hunt by a Spotted Owl as it returns to the nest with the prey, within the owl's 95% kernel density estimate (KDE). Note that the grey points in (B) 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

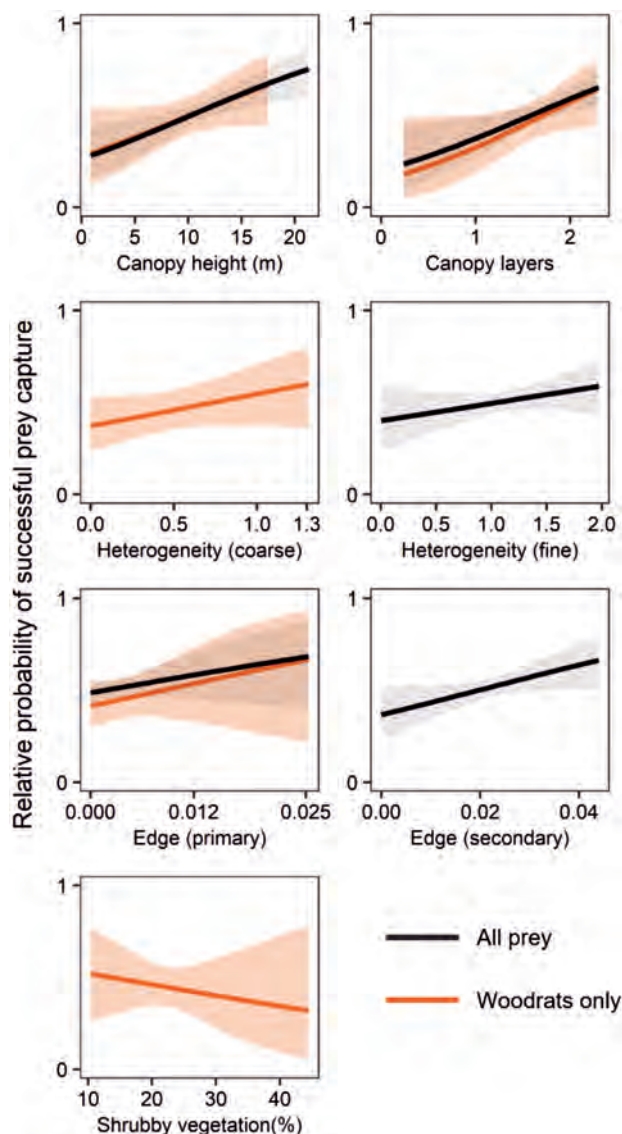


FIGURE 3. Averaged model predictions for relative probability of hunting success for all prey and woodrats only plotted against vegetation conditions for foraging Spotted Owls, with 95% confidence intervals shown as shaded areas. Heterogeneity metrics calculated as Shannon diversity of vegetation types 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

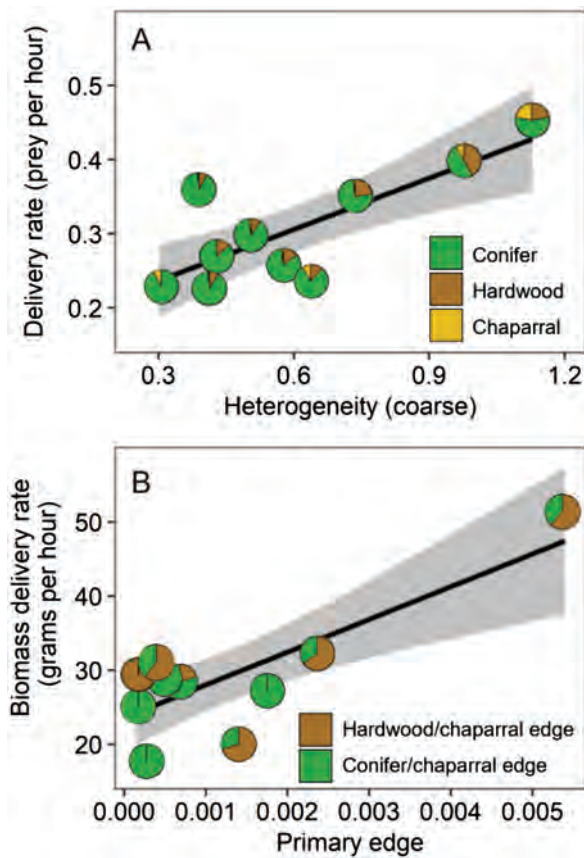


FIGURE 4. Prey delivery rate per hour (A) and prey biomass delivery rate (B) as functions of coarse vegetative heterogeneity (Shannon diversity of vegetation types) and primary edge (edge density of chaparral-forest edge), respectively. Each point represents an owl territory, with points in (A) displayed 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,

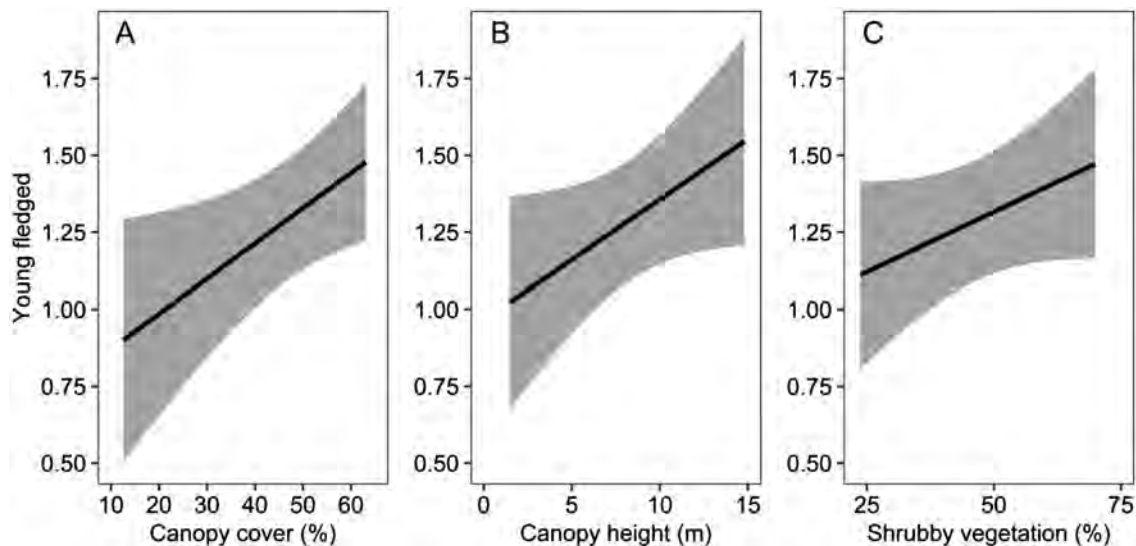


FIGURE 5. Averaged model predictions of number of young fledged plotted against (A) mean percent canopy cover, (B) mean canopy height, and (C) mean shrubby vegetation density within the territory, with shaded 95% confidence intervals.

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

Home Range and Habitat Selection of Spotted Owls in the Central Sierra Nevada

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ABSTRACT We studied home range and habitat selection of radio-marked adult California spotted owls (*Strix occidentalis occidentalis*) randomly selected from among the breeding population of owls in the central Sierra Nevada, California from June to October 2006. The most parsimonious home-range estimate for our data was 555 ha (SE = 100 ha). Home-range size was positively correlated with the number of vegetation patches in the home range (habitat heterogeneity). We used resource selection ratios to examine selection of vegetation types by owls within our study area. Owl home ranges contained a high proportion of mature conifer forest, relative to its availability, although the confidence interval for this estimate overlapped one. We also used resource selection functions (RSF) to examine owl foraging habitat selection. Relative probability of selection of foraging habitat was correlated with vegetation classes, patch size, and their interaction. Owls showed highest selection rates for large patches (>10 ha) of pole-sized coniferous forest. Our results suggested that spotted owls in the central Sierra Nevada used habitat that contained a high proportion of mature conifer forest at the home-range scale, but at a finer scale (foraging site selection) owls used other vegetation classes interspersed among mature forest patches, consistent with our hypothesis that spotted owls may use other forest types besides old growth and mature forests when foraging. Our study provides an unbiased estimate of habitat use by spotted owls in the central Sierra Nevada. Our results suggest that forest managers continue to protect remaining mature and old-growth forests in the central Sierra Nevada because owl home ranges contain high proportions of these habitats. However, our results also showed that owls used younger stands as foraging habitat so that landscape heterogeneity, with respect to cover types, may be an important consideration for management but we did not attempt to relate our findings to fitness of owls. Thus management for some level of landscape heterogeneity for the benefit of owls should proceed with caution or under an adaptive management framework. © 2011 The Wildlife Society.

KEY WORDS California spotted owls, radio-telemetry, random sampling design, resource selection function, Sierra Nevada, *Strix occidentalis occidentalis*.

Management of California spotted owls (*Strix occidentalis occidentalis*) has been predicated on identifying and protecting their primary habitat (Verner et al. 1992, U. S. Forest Service 2004). Their management has been controversial because there is incomplete knowledge of their habitat and home-range use patterns. For example, much effort has been devoted to identifying California spotted owl nest and roost habitat selection patterns (Bias and Gutiérrez 1992, LaHaye et al. 1997, Moen and Gutiérrez 1997, Bond et al. 2004, Chatfield 2005), but much less effort has been directed toward understanding their foraging habitat (Call et al. 1992, Zabel et al. 1992). Emphasizing nesting and roosting habitat selection for management may result in a limited view of habitat use by spotted owls because this subspecies appears to use a greater variety of habitats for

foraging than for nesting and roosting (Verner et al. 1992, Gutiérrez et al. 1995). Thus, we studied California spotted owl home range and foraging habitat selection using a random selection of owls within the central Sierra Nevada, California. Our main objectives were to 1) estimate home-range sizes of owls, 2) estimate habitat characteristics associated with differences in home-range size, 3) estimate second-order (home-range) habitat selection based on vegetation-class selection by owls relative to the entire study area, and 4) estimate third-order (foraging) habitat selection based on foraging locations of owls within their home range.

STUDY AREA

Our study area (3,188 km²) was located on the Eldorado and Tahoe national forests. The study area was characterized by cold, wet winters and hot, dry summers. Topography was mountainous and bisected by steep river drainages; elevation ranged from 233 m to 3,041 m. At lower elevations vegetation was Sierran mixed-conifer montane forests dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies*

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concolor), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), California black oak (*Quercus kelloggii*), and, at higher elevations, California red fir (*Abies magnifica*) forest was dominant (Küchler 1977). Vegetation was influenced by aspect, climate, fire, logging, livestock grazing, edaphic conditions, and elevation, which resulted in a diverse pattern of forest types (Verner et al. 1992, Skinner and Chang 1996).

METHODS

The owls we used were randomly selected from all known owl territories ($n = 146$) in the central Sierra Nevada as part of an experiment on effects of logging on owls (R. J. Gutiérrez, University of Minnesota, unpublished data). This was a constrained random selection required by the design of the logging experiment (e.g., owl territories having recent, concurrent, or scheduled tree harvest during the study were excluded from sampling because harvest would have confounded experimental treatments; reasons such as legal constraints precluded sampling on some territories). Once owl territories met selection criteria we placed them in the sampling pool. Originally, we randomly selected 12 territories representing 24 owls (12 pairs) from this pool, which was the number of owls we considered feasible to monitor given available funding. We surveyed selected owl territories following methods described by Forsman (1983).

Owl Capture and Radio-Telemetry Monitoring

Once we located owls, we determined their sex by voice (Forsman et al. 1984), their age by plumage characteristics (Forsman 1981), and their pair status (Franklin et al. 1996). We attempted to capture all adult owls detected on territories. We marked captured owls using a locking United States Geological Survey aluminum band on one leg, a uniquely-colored plastic band and tab on the other leg (Franklin et al. 1996), and a backpack radio-transmitter (Holohil Systems Ltd. Model RI-2C, Ontario, Canada) secured with Teflon[®] (Dupont, Wilmington, DE) coated Kevlar[®] (Dupont) ribbon. Total mass of transmitters (including harness) was 14.4–15.4 g, which was <3.0% of the adult body mass of a male spotted owl (Gutiérrez et al. 1995).

Concurrently with telemetry monitoring, we conducted extensive blind tests (known locations of radio transmitters unknown to observers) on observers in several owl territories to estimate bearing error of locations. Absolute bearing error of the naïve observers was 7.2°, which we used to estimate quality of owl telemetry locations. We developed our monitoring procedures a priori to data collection to improve owl (transmitter) location estimates. To triangulate radio signals to estimate an owl's location we first used handheld directional 3-element Yagi antennae and R-1000 handheld receivers (Communication Specialists, Inc., Orange, CA) to receive signals from transmitters. We recorded compass directions on detected signals based on signal strength and quality at ≥ 3 monitoring stations spaced >160 m apart. We triangulated from permanent monitoring stations precisely located using a Trimble Pathfinder Global Positioning System (GPS) capable of ± 3 m accuracy. Second, we

triangulated all locations within 30 min. Third, we immediately plotted compass bearings on 1:15,000-scale topographic maps. Fourth, after we obtained a location we paused for 10 min and then repeated the process. Fifth, we later analyzed the quality of each location using the arithmetic mean estimator in LOAS software (version 4.0b, Ecological Software Solutions, Urnäsch, Switzerland) to calculate the 95% confidence ellipse of all locations for use in habitat selection analyses. Finally, we only used locations for analysis that had confidence ellipses <5 ha.

We partitioned the night into 3 hr segments for monitoring each owl and randomized the night and time each segment's monitoring would begin. Time segments for monitoring started between 30 min before sunset to 30 min after sunrise. The logistics of traveling long distances between owl territories precluded a completely randomized temporal sampling design, so we stratified owls into groups that could be monitored by one person based on the relative proximity of the first randomly selected owl to nearby owls. We randomly assigned each observer 2 owl territories to survey per night, excluding owls that were too remote to allow sufficient travel time to another owl territory during a night, in which case we monitored the owl for 6 hr. We monitored owls for 4 consecutive nights, followed by 3 nights with no monitoring. If we were unable to locate owls because we did not detect a signal or the signal was too faint to determine a direction, we searched adjacent areas using a vehicle mounted RA-5A omni-directional antennae (Telonics, Mesa, AZ). If we were unable to locate an owl for ≥ 2 weeks, we attempted to locate it using aircraft with 2 wing-mounted directional antennae. At the conclusion of the study we recaptured all owls to remove transmitters. Our study was approved by the University of Minnesota (Institutional Animal Care and Use Committee Protocol no. 0512A78787).

Home-Range Size Estimation

We defined a foraging home range as the area used by an owl during its nightly activities between June and October (Burt 1943). Studies of spotted owl breeding-season home range usually end after juveniles fledge (usually late Aug–Sep); however, none of the owls on either our study area or an adjacent demographic study area nested successfully during our study. We calculated the 100% minimum convex polygon (MCP) using Hawth's Analysis Tools (Beyer 2004) for ArcGIS. The MCP estimator has been criticized for many reasons; therefore, several authors have recommended that the MCP never be used (see review in Laver and Kelly 2008). However, we calculated it for comparative purposes because it was the only home-range estimator that had been used in all other California spotted owl home-range studies (Laymon 1988, Call et al. 1992, Zabel et al. 1992, Zimmerman and Gutiérrez 2001). We did not use it to draw inference about home-range size of owls.

To estimate home-range size of owls, we first estimated each owl's home range using 5 home-range estimators (95% isopleths of the adaptive-kernel density, 95% isopleths of the fixed-kernel density, 1-mode bivariate normal, 2-mode

bivariate circle, and 2-mode bivariate normal). We then selected the most parsimonious of the 5 estimators for each owl using an information-theoretic model-selection approach (Horne and Garton 2006a) in Program Animal Space Use 1.2 Beta (Horne and Garton 2007) using the likelihood cross-validation criterion (CVC). We used the CVC because the number of model parameters was not explicit, and, therefore, could be used for non-parametric home-range models (i.e., kernel models). We estimated relative support for each home-range model by the difference in CVC between each model and the model with the lowest CVC value (i.e., ΔCVC). We used only the home-range size estimates from the most parsimonious home-range models for analyses because we assumed these models gave the best estimate of owl home ranges given our data (Horne and Garton 2006a). We used the likelihood-cross-validation (CVh) smoothing parameter in kernel estimates of home ranges calculated in Animal Space Use 1.2 Beta (Horne and Garton 2007) because it produced home-range estimates with better fit and less variability than did other smoothing parameters (e.g., least-squares cross-validation) in simulation studies (Horne and Garton 2006b).

Correlates of Home-Range Size

We developed alternative hypotheses based on spotted owl literature that might explain variation in spotted owl home-range size (Table 1). Our first model was a null (intercept-only) model (model 1). We assumed that small home ranges reflected better habitat conditions or configurations than did large home ranges because the higher the quality of the habitat, the shorter the distance an owl would need to travel to meet its requirements (McNab 1963, Zabel et al. 1995). Therefore, we hypothesized that spotted owls having more mature forest within their home range would have smaller home-range sizes because mature forest has been presumed to be their primary habitat (model 2; Gutiérrez et al. 1995).

We hypothesized that owls having larger core habitat areas would have smaller home ranges because core habitat in close proximity should reduce travel distances of this central-place forager (model 3; McNab 1963, Carey and Peeler 1995, Zabel et al. 1995). We estimated core habitat by summing the area of all vegetation patches, including and contiguous to a traditional (most-used) roost patch, that have been shown to be selected habitats (medium- and mature-sized conifer vegetation with medium and high canopy cover) by California spotted owls (Verner et al. 1992). We hypothesized that owls having higher proportions of selected habitat within their home range would have smaller home ranges than owls having lower proportions of these habitats (model 4; Gutiérrez et al. 1992) because this would also reduce travel time and present owls with more selection options. Model 4 differed from model 3 because model 3 included only habitat adjacent to roost sites and was independent of home range size, whereas model 4 included the proportion of all habitat within the home range. We hypothesized that owls having high habitat heterogeneity (many types of vegetation classes) would have large home ranges because heterogeneity should increase separation of suitable habitat (model 5; Solis 1983, Carey et al. 1992). We hypothesized that males and females may have different home-range sizes, that pair status may affect home-range sizes, and that sex may only affect the home-range size depending on the pair's breeding status because of division of duties between the sexes, sexual dimorphism (females are larger), and greater potential exploratory behavior of single birds within a territory (models 6, 7, and 8, respectively). We hypothesized that topography might influence home-range size (average elevation, SD of elevation, and slope [models 9, 10, 11, respectively]; Irwin et al. 2004) because it influences owl's primary prey base. Northern flying squirrels (*Glaucomys sabrinus*) are the dominant prey base at higher elevations and occur at low density relative to other prey at lower elevations (Gutiérrez et al. 1995, Zabel et al.

Table 1. Model selection results for estimation of home-range size by California spotted owls ($n = 14$) in the central Sierra Nevada, California, June–October 2006 based on likelihood estimation.

Model no.	Model ^a	$-2\log_e(\mathcal{L})^b$	K^c	ΔAIC_c^d	w_i^e	R^2
5	PPA	193.06	3	0	0.615	0.55
3	CORE	195.62	3	2.56	0.171	0.43
12	AVGELEV + EDGE + AVGELEV $\times$ EDGE	188.04	5	4.09	0.08	0.68
8	SEX + PAIR	194.41	4	5.4	0.041	0.52
10	STDEVELEV	199.27	3	6.22	0.027	0.31
11	AVGSLOPE	200.23	3	7.18	0.017	0.26
6	SEX	200.56	3	7.51	0.014	0.24
1	NULL	204.26	2	7.9	0.012	
7	PAIR	201.12	3	8.06	0.011	0.21
2	PROP (MATURE)	202.41	3	9.36	0.006	0.13
4	PROP (SUITABLE)	203.33	3	10.27	0.004	0.05
9	AVGELEV	204.15	3	11.09	0.002	0.01

^a PPA = an index of relative patchiness of each owl's home range; CORE = total amount of area (in ha) of vegetation classes 4, 5, 6, and 7 immediately adjacent to the roost site; AVGELEV = the average elevation of 1,000 random points within each owl's home range; EDGE = an index of the relative amount of edge in each owl's home range; SEX = sex of the owl; PAIR = pair status of the owl; STDEVELEV = SD of the elevation of 1,000 random points within each owl's home range; AVGSLOP = average slope of 1,000 random points within each owl's home range; NULL = no effects (means) model; PROP = proportion of each vegetation classification relative to the home-range size of each owl.

^b $-2 \times \log_e(\text{likelihood})$.

^c No. of parameters in the model.

^d Difference between model Akaike's Information Criterion adjusted for small sample size (AIC_c) and AIC_c value of the best model.

^e AIC_c wt.

1995). Therefore, we hypothesized that owl home ranges would be larger at higher elevations. We hypothesized that owls that prey primarily on woodrats (*Neotoma fuscipes*) used edges whereas owls that prey on flying squirrels used interior forests and, therefore, home-range size would be associated with the amount of edge per area, elevation, and their interaction (model 12; Zabel et al. 1995).

To quantify habitat metrics we created a vegetation classification map because existing United States Forest Service (USFS) vegetation maps of the study area were <60% accurate (M. Bond, University of Minnesota, personal communication). We mapped the vegetation of every owl home range and classified the vegetation polygons encompassing 2,161 random locations throughout the study area to estimate available habitat in the study area (see habitat selection analysis below). We used 8 vegetation classes consistent with the California Wildlife Habitat Relationships system (Mayer and Laudenslayer 1988). These vegetation classes were: 1 = hardwood forest, 2 = areas with low (<40%) canopy cover, 3 = pole-sized (15–28 cm dbh) conifer forest with medium to high ($\geq 40\%$) canopy cover, 4 = medium-sized (28–60 cm dbh) conifer forest with medium (40–70%) canopy cover, 5 = medium-sized conifer forest with high (>70%) canopy cover, 6 = mature (>60 cm dbh) conifer forest with medium canopy cover, 7 = mature conifer forest with high canopy cover, and 8 = water. We used the United States Department of Agriculture, National Agriculture Imagery Program's (2005) County Compressed Mosaics (multi-resolution seamless image database of natural-color, 1 m resolution orthophotographs) and a Geographical Information System (GIS; ArcINFO) to map vegetation classes. We first visually compared the orthophotographs to randomly select sites in the field to train ourselves to correctly identify vegetation classes using the orthophotographs. We continued training until we were confident that we could estimate tree size, canopy cover, and hardwood or conifer forest sufficiently (with minimal error; see below) to define the boundaries of vegetation patches and place patches into vegetation classes using the orthophotographs. We then used the GIS interfaced with the orthophotographs to classify 1) each vegetation patch (polygon) within each owl home range, and 2) each vegetation patch containing 1 of the 2,161 random points. We defined vegetation patches as contiguous areas of the same vegetation class. We assigned 1 of the 8 vegetation classes to each vegetation patch. Minimum mapping unit = 0.5 ha.

We assessed the user and producer map accuracy following Story and Congalton (1986); user accuracy was an estimate of the map's representation of the true vegetation classes, and producer accuracy was an estimate of the efficacy of mapping a specific geographic region. We randomly selected 161 points from the 2,161 random vegetation patches we classified from orthophotographs throughout the study area and measured vegetation at these points. At each of these 161 random locations we estimated the dominant species composition, dominant size class (i.e., dbh), percent canopy cover, and distance to a different vegetation class (if one was visible from our sampling plot), within 0.5 ha plots and

assigned each vegetation patch to a vegetation class based on structure. We then estimated classification accuracy from percent agreement between these 161 sites and the same sites we classified using the orthophotographs.

We created a suite of a priori candidate models based on our alternative hypotheses (Table 1). To examine these models, we calculated the following habitat metrics: proportion of vegetation class (PROP), patches per area (PPA), average elevation (AVGELEV), standard deviation of elevation (STDEVELEV), average slope (AVGSLP), amount of edge per area (EDGE) for each owl home range, and the core area (CORE) for each owl's traditional roost using our vegetation map. Our sampling unit was the individual owl. Our response variable was total home-range size. Our independent variables included the habitat metrics described above. We divided categorical variables as follows: 7 vegetation classes (described above, except we excluded water to avoid trivial comparisons), sex, and pair status (paired or unpaired to account for the potential lack of independence between members of a pair). We then used Akaike's Information Criterion adjusted for small sample size to evaluate model likelihood (AIC_c; Burnham and Anderson 2002). We verified model assumptions by inspecting residual plots using the GRAPHICS package in Program R (R Version 2.9.1, www.r-project.org, accessed 01 Jul 2009). We tested for outliers or other influential data points using the STATS package in Program R.

Habitat Selection

We examined habitat selection by comparing used habitat to available habitat at 2 spatial scales (second- and third-order selection; Johnson [1980]). These scales corresponded to habitat associations within entire home ranges and habitats associated with individual telemetry locations.

We examined home-range (second-order) habitat selection using habitat selection ratios (Manly et al. 2002) combined with Bonferroni simultaneous confidence intervals to assess whether owl home ranges contained a disproportionate amount of certain resources (i.e., vegetation classes) relative to their availability within the study area. We defined used resources as the proportion of each vegetation class in each owl's home range. We estimated available resources by selecting 2,161 random locations within the study area and then mapping all vegetation contiguous to the random location to represent the proportional composition of our entire study area (see Correlates of Home Range Size above). We then compared the proportion of vegetation classes used by each owl (i.e., the proportion of each vegetation class within each owl's home range) to the proportion of available vegetation categories within the study area (design 2 analysis from Thomas and Tayler [1990]; sampling protocol A from Manly et al. [2002]; Table 2). We calculated the resource selection function (RSF), variance of the RSF, and simultaneous confidence intervals using the ADEHABITAT package in Program R.

We examined foraging site (third-order) resource selection by comparing used habitat resources (telemetry locations) to random locations within the home range (available locations)

Table 2. Estimated Manly selection ratios for different vegetation classes used by individual California spotted owls in the central Sierra Nevada, California, June–October 2006. Table modified from Manly et al. 2002:69).

Vegetation class	1	2	3	4	5	6	7	8
Available sample (proportion)	0.08	0.28	0.04	0.10	0.44	0.01	0.03	0.02
Used sample (owl identification, sex, proportion)								
BALDM F	0.00	0.09	0.10	0.13	0.62	0.00	0.06	0.00
CANYC M	0.01	0.20	0.11	0.26	0.37	0.00	0.06	0.00
DIXQM F	0.23	0.40	0.02	0.09	0.18	0.05	0.03	0.00
DOLLY F	0.00	0.03	0.03	0.19	0.22	0.07	0.46	0.00
ED028 F	0.00	0.10	0.16	0.12	0.52	0.02	0.09	0.00
ED028 M	0.00	0.11	0.16	0.23	0.31	0.01	0.18	0.00
ED121 F	0.00	0.10	0.03	0.20	0.58	0.03	0.06	0.00
ED124 F	0.00	0.09	0.11	0.27	0.39	0.01	0.14	0.00
ED124 M	0.00	0.07	0.10	0.33	0.27	0.02	0.22	0.00
ED200 F	0.00	0.03	0.00	0.11	0.74	0.00	0.13	0.00
ROBPK M	0.00	0.15	0.18	0.45	0.19	0.03	0.01	0.00
SUGAR M	0.21	0.02	0.14	0.08	0.17	0.04	0.33	0.00
BALDM M ^a	0.00	0.10	0.10	0.10	0.61	0.00	0.10	0.00
BALDM M ^b	0.05	0.09	0.06	0.30	0.46	0.00	0.03	0.00
Selection ratio								
w_i'	0.44	0.42	1.71	1.98	1.06	2.98	3.68	0.00
SE								
$se(w_i')$	1.51	0.67	8.80	6.10	1.20	40.12	21.28	0.01
Bonferroni confidence limit								
IC lower ^c	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
IC upper	4.21	2.10	23.70	17.21	4.05	103.19	56.82	0.04

^a Data collected prior to 5 Aug 2006 (date of the death of presumed mate).

^b Data collected after 5 Aug 2006.

^c We set negative lower confidence limits to zero.

to assess if owls used certain resources within their home range disproportionately to availability. We estimated available resources by randomly sampling 3 times as many locations within each owl's home range as we had locations used (telemetry) by each owl (sampling protocol A from Manly et al. [2002]). We used the multiplier of 3 because it provided the best estimate of available habitat without introducing a contamination rate (i.e., areas selected as both used and available sites) that would bias parameter estimates

(contamination rate was <25% for all parameters; Johnson et al. 2006). We examined owl use of edges by calculating the distance of used sites to the nearest edge and random sites to nearest edge and then compared their distributions using a Kolmogorov–Smirnov test for each vegetation class.

We examined the correlation between habitat metrics and owl foraging sites using model selection based on models developed a priori to the analysis (Table 3). We included a null (intercept-only) model (model 1). We hypothesized that

Table 3. Model selection results for models predicting foraging locations (third-order selection) of California spotted owls in the central Sierra Nevada, California, June–October 2006, based on likelihood estimation.

Model no.	Model ^a	$-2\log_e(\mathcal{L})^b$	K^c	ΔAIC^d	w_i^e
15	VEGTYPE + PATCHSIZE + VEGTYPE × PATCHSIZE	177.32	14	0	1
11	ELEV + PATCHSIZE + ELEV × PATCHSIZE	196.16	4	18.84	0
13	VEGTYPE + PATCHSIZE + DISTROAD + DISTWATER + ELEV + SLOPE + ASPECT	203.46	13	22.13	0
12	VEGTYPE + PATCHSIZE + DISTROAD + DISTWATER + ELEV	231.24	11	43.92	0
14	VEGTYPE + PATCHSIZE	272.56	8	79.23	0
6	PATCHSIZE	281.19	2	83.87	0
8	DISTWATER + ELEV + DISTWATER × ELEV	296.37	4	105.05	0
7	DISTWATER	328.4	2	135.08	0
2	VEGTYPE	321.09	7	143.77	0
4	TREESIZE	337.52	3	144.2	0
5	CANOPY	338.05	3	148.72	0
1	NULL	349.31	1	151.98	0
3	POTENTIAL	350.01	2	152.68	0
9	DISTROAD	353.59	2	156.27	0
10	DISTROAD + ELEV + DISTROAD × ELEV	356.51	4	157.18	0

^a AREA = vegetation patch area; PERIM = vegetation patch perimeter; VEGCLASS = vegetation class of the vegetation patch; ELEV, SLOPE, and ASPECT = elevation, slope, and aspect, respectively, at the sample point within the vegetation patch; DISTWATER = distance from the sample point to the nearest permanent water body; DISTROAD = distance from the sample point to the nearest road.

^b $-2 \times \log_e(\text{likelihood})$.

^c No. of parameters in the model.

^d Difference between model Akaike's Information Criterion (AIC) and AIC value of the best model.

^e AIC wt.

certain vegetation classes would be selected as foraging sites over others (model 2) because different vegetation classes may provide different foraging opportunities (e.g., prey availability, forest structure). Of the different vegetation classes, we hypothesized that owls would select medium- and mature-sized coniferous forest with medium to high canopy cover more frequently than other classes because these vegetation classes have been shown to be selected by California spotted owls (model 3; Gutiérrez et al. 1992). Because spotted owls are associated with old growth and mature-sized tree classes (Gutiérrez et al. 1995), we hypothesized that owls would select vegetation classes having larger trees more often than vegetation classes having smaller trees (model 4). Owls in our area selected sites with higher canopy cover, so we included a model representing this hypothesis (model 5; Call et al. 1992). We hypothesized that owls would select sites in large vegetation patches because larger vegetation patches result in less fragmented or heterogeneous landscapes, which may enhance foraging efficiency (model 6). We hypothesized owls would select sites at higher elevations and shorter distances to water because both water and high elevation are associated with cooler microclimates, which we hypothesized were beneficial to owls between June and October (models 7 and 8, respectively; Gutiérrez et al. 1995). In model 8 we included an interaction because the effect of selecting cooler microclimates associated with water may be dependent on elevation (i.e., owls may not select areas near water at higher elevation because of cooler microclimates at higher elevations). Wasser et al. (1997) suggested traffic may stress owls near roads. Therefore, we hypothesized owls would select areas farther from roads (model 9). It was also plausible that roads at higher elevations would have less traffic and, thus, would have less effect on owls than roads at lower elevations so we included an interaction between roads and elevation (model 10). As with correlates of home-range size (see model 12, Table 1), we also hypothesized that at this scale owls that prey primarily on woodrats used edge habitats whereas owls that prey on flying squirrels used interior forests. Therefore, owls at lower elevations would select smaller patches than would owls at higher elevations because of the change in prey base (model 11). We hypothesized that vegetation class, patch size, distance to roads and water, and elevation may all be associated with habitat selection by owls (model 12). Further, we considered all of the variables of model 12 plus 2 additional topographical variables, aspect and slope, because they may be correlated with habitat selection (model 13). Models 12 and 13 were compositions of several models above, and we included them because we thought each of the variables included in the models might contribute to habitat selection by owls. We hypothesized owls would select large areas of certain vegetation classes (model 14; Verner et al. 1992) or that the selection of certain vegetation classes depended on the size of that vegetation class, thus, we included an interaction between vegetation class and patch size (model 15).

We created statistical hypotheses (Table 3) from our alternative models and analyzed the data using logistic regression. We ranked each of the logistic regression models

using AIC and evaluated each model's likelihood using Akaike weights (w_i ; Burnham and Anderson 2002; Table 3). We estimated RSF model parameters $\beta_0, \beta_1, \dots, \beta_{n-1}$ from the weighted mean of coefficient estimates from the generalized linear logistic regression model applied to each owl with weight = 1/variance of each parameter estimate (Murtaugh 2007). We assessed the goodness-of-fit of the top model by calculating the area under the receiver operating characteristic (ROC) curve with the pROC package in Program R. We assessed goodness-of-fit for 2 sets of parameter estimates. First, we used the weighted mean of the coefficient estimates from the 14 samples to assess the goodness-of-fit for our final model to our sample. Second, we fit the top model to each owl, estimated model coefficients for each owl, and used those estimates to assess the area under the ROC curve for individual owls.

RESULTS

Sample Selection and Telemetry Monitoring Results

We radio-marked 14 adult California spotted owls during 2006 (4 pairs, 4 single F, and 2 single M). These owls were distributed across a 271,320-ha area. Tracking periods among owls averaged 99.9 days (SE = 8.7 days) but varied greatly (45–136 days, median = 77 days). We removed 1 female from the analysis because she disappeared from her territory shortly after her capture. We found her remains on 11 July 2007 on private property approximately 18 km from her capture site. Another female was killed in her territory by a vehicle around 5 August 2006, but we had obtained 52 telemetry locations prior to her death, which was sufficient to estimate a home-range size, so we included data from this bird in our analyses. Shortly after this female's death, her mate dispersed and established a new home range 4.5 km from his previous activity center. Therefore, we treated this owl as 2 separate samples (pre- and post-5 Aug) because the 2 home ranges were in completely different areas, the 2 areas had different management regimes (the first on public land and the second on private land), his pair status changed, and he represented a breeding dispersal (Blakesley et al. 2006). A male we captured on 1 June 2006 disappeared sometime after 10 August 2006. We were unable to relocate him despite conducting extensive ground and air searches. However, we obtained 41 telemetry locations over 71 days so we included him in our analysis. Therefore, our sample size for analysis was 14 data sets from 13 owls. We collected 1,337 usable (i.e., error ellipse <5 ha) telemetry locations from 8 June to 27 October 2006, ranging from 41 to 209 ($\bar{x}$ = 95.5, SE = 13.4) locations per owl. We also obtained daytime roost locations for owls because we visually monitored their reaction to radios.

Home Range

Mean home-range sizes varied from 508 ha to 946 ha, depending on the home-range estimator we used. Generally, the MCP produced the largest estimates and the fixed-kernel density estimator produced the smallest. However, the adaptive-kernel or the fixed-kernel were always the most parsimonious estimators of owl home range

(adaptive $n = 5$, fixed $n = 9$). Mean home-range size of the most parsimonious home-range models was 554.9 ha (SE = 99.9 ha). All home-range models appeared to meet model assumptions (linear relationship between predictors and response, constant variance, and normally distributed), with the exception that paired owls may not have been independent, which is why we included pair status as a model covariate (model 7, Table 1). Patch heterogeneity (PPA) was most correlated with differences in home range sizes of owls (model 5). The relative likelihood of this model ($w = 0.615$) was 3.60 times more likely than the second-ranked model ($w = 0.171$) and 51.25 times more likely than the no-effect (null) model ($w = 0.012$; Table 1). The parameter estimate for heterogeneity ($\beta = 55.17$, SE = 14.38; 95% CI = 23.86–87.40; Fig. 1) indicated that home-range size increased as heterogeneity increased.

Male and female mean home-range sizes averaged 378.7 ha and 722.0 ha, respectively, suggesting that females had larger home ranges. However, the model that included only sex (model 6) had little support from the data ($w = 0.014$; Table 1), and the confidence interval for the parameter estimate overlapped zero ($\beta = -352.3$, SE = 181.5; 95% CI = -747.68, 43.08). The parameter estimate was heavily influenced by one female (ED200) who made large erratic movements (perhaps a floater, *sensu* Franklin 1992). We estimated the influence of this owl on model parameters by calculating the DFBETAS value for each parameter using the STATS package in Program R. The DFBETAS value for the slope of the variable sex was 0.72, which exceeded the sample-size corrected cut-off value ($2/\sqrt{n} = 0.53$) that indicates influential observations (Belsley et al. 1980). After excluding this owl from the analysis, male and female

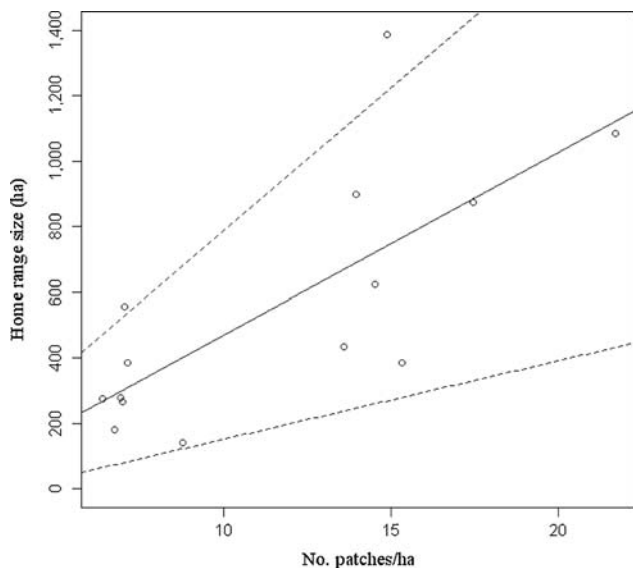


Figure 1. California spotted owl home-range sizes as a function of the relative patchiness within owl home ranges (TOT_HR = $55.17 \times \text{PPA}$ [an index of relative patchiness of each owl's home range] - 86.12) in the central Sierra Nevada, California, June–October 2006. We estimated patchiness by dividing the number of different vegetation patches by the home-range size for each owl. The 95% confidence intervals for the slope did not overlap zero (CI = 29.64, 81.62).

mean home-range sizes were 378.7 ha and 622.0 ha, respectively ($\beta = -243.3$, SE = 157.7; 95% CI = -552.68, 65.79). Therefore, these data were not sufficiently precise to detect a difference in male and female home-range sizes, if a difference was present.

Habitat Selection

Of 2,161 random vegetation patches classified throughout the study area, the percent cover of available vegetation categories were: hardwood forest = 8%, areas with low canopy cover = 28%, pole-sized conifer forest (medium to high canopy cover) = 4%, medium-sized conifer forest with medium canopy cover = 10%, medium-sized conifer forest with high canopy cover = 44%, mature conifer forest with medium canopy cover = 1%, mature conifer forest with high canopy cover = 3%, and water = 2%. Vegetation-patch size ranged from 0.5 ha to 5,049.1 ha ($\bar{x} = 70.0$ ha). User and producer mapping accuracy of all vegetation classes were >80%, except producer accuracy of mature conifer forest with medium canopy cover (50%) and user and producer accuracy of mature conifer forest with high canopy cover (71% and 67%, respectively). The proportions of vegetation classes within home ranges (used home-range habitat) varied widely among owls (Table 2), but on average consisted of: hardwood forest = 3.5%, areas with low canopy cover = 11.8%, pole-sized conifer forest (medium to high canopy cover) = 6.3%, medium-sized conifer forest with medium canopy cover = 19.0%, medium-sized conifer forest with high canopy cover = 47.1%, mature conifer forest with medium canopy cover = 1.6%, mature conifer forest with high canopy cover = 10.7%, and water = 0.0%. Mature forests with medium canopy cover and mature forest with high canopy cover were selected most often relative to their availability (i.e., had the highest selection ratios; selection ratios = 2.98 and 3.68, respectively; Table 2). However, due to variability among owls all vegetation classes had a selection ratio with a 90% Bonferroni confidence interval that overlapped one.

Foraging habitat selection within the home range was most correlated with vegetation class, patch size, and their interaction (model 15, Table 3, $n = 14$). There were no competing models ($\Delta\text{AIC} < 2$; Burnham and Anderson 2002). Therefore, we used this top model to make inferences about owl foraging-habitat selection. The effect of increasing patch size varied among vegetation classes (Fig. 2). In general, the relative probability that hardwood forests and pole-sized conifer forests were used increased as patch size increased, whereas probability of use of areas with low canopy cover, medium-sized conifer forests with either medium or high canopy cover, and mature forests with either medium or high canopy cover decreased as patch size increased (Fig. 2). In relation to patch size, relative probability of using mature forests with medium canopy cover and pole-sized conifer forests decreased and increased the most dramatically, respectively (Fig. 2). The substantial decrease in relative probability of using mature forests with medium canopy cover may be due to the scarcity of that vegetation class in patch sizes >38.13 ha ($\bar{x} = 8.48$ ha). For all patch sizes

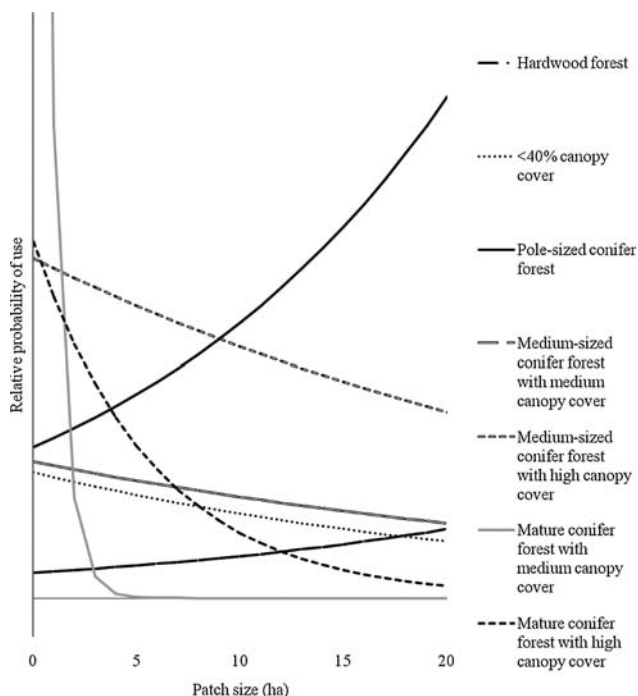


Figure 2. Relative probability of use by California spotted owls of 7 vegetation types in relation to vegetation patch size in the central Sierra Nevada, California from June to October 2006. We estimated relative probability of use using exponentiation of the parameter estimates of the most parsimonious model for our data [resource selection function = $w_i = \exp(\beta_1 \text{vegetation type}_i + \beta_2 \text{vegetation type}_i \times \text{patch size})$]. Vegetation size classes were: pole (15–28 cm dbh), medium (28–68 cm dbh), and mature (>60 cm dbh). Canopy cover classes were: medium (40–70%) and high (>70%).

>10 ha, pole-sized coniferous forests had the highest relative probability of use; for all patch sizes <1 ha mature forests with medium canopy cover had the highest relative probability of use (Fig. 2). The goodness-of-fit tests (area under the ROC curve) indicated that our final model (in which we calculated the parameter estimates using the weighted mean of the parameter estimates from all owls in our sample) only fit the data moderately well (area under the ROC = 0.66). However, mean area under the ROC curve when we fit the model to individual owls was 0.88 (range = 0.69–0.98). Kolmogorov–Smirnov tests on the distance-to-edge distributions of used sites versus random sites were statistically significant ($P < 0.05$) for hardwood forests, medium-sized conifer forests with medium canopy cover, medium-sized conifer forests with high canopy cover, and mature forest with high canopy cover. However, differences in mean values of distance-to-edge between used and random locations were <10 m and unlikely to be biologically significant, except for mature forests with high canopy cover. Owls using this type of forest on average used areas 30.5 m closer to edges than random areas ($P < 0.001$).

DISCUSSION

Home-Range Estimation

The fixed- and adaptive-kernel density estimators were always the most parsimonious of home-range estimators

of California spotted owls, likely due to the flexibility of nonparametric estimation in modeling complex patterns (Worton 1989). Previous studies of California spotted owl home ranges used the MCP as their primary estimator. Although this estimator is biased, we estimated it for comparative purposes. Our MCP estimate ($\bar{x} = 946$ ha) was similar to the mean MCP estimate from 3 previous home-range studies of the California spotted owl in the central Sierra Nevada (combined weighted [by sample size] $\bar{x} = 862$ ha; Laymon 1988, $\bar{x} = 856$ ha, $n = 12$; Call et al. 1992, $\bar{x} = 1,520$ ha, $n = 5$; Zabel et al. 1992, $\bar{x} = 728$ ha, $n = 24$). However, our median estimate (547.1 ha) was smaller than previous studies (Laymon 1988, median = 1,005 ha; Call et al. 1992, median = 1,439 ha; Zabel et al. 1992, median not reported).

We did not find support for our hypothesis that owls having the highest proportion of mature vegetation within their home range would have the smallest home range despite many studies linking spotted owls to old growth or mature forests (Forsman et al. 1984, Carey et al. 1990, Gutiérrez et al. 1995). Home-range size variation was most correlated with the number of patches within home ranges (i.e., habitat heterogeneity). There were alternative explanations for this result: owls may have been occupying patchy landscapes that enhanced their foraging opportunities or fitness (Franklin et al. 2000); the patterns may simply have reflected the nature of habitat distribution in the central Sierra Nevada because most areas we studied did not contain large contiguous areas of old forest; or it may have meant that owls in heterogeneous areas have to travel longer distances to forage, which would have been reflected as a larger home-range size.

Habitat Selection

None of the selection ratios for any particular vegetation class was different from 1 given the 90% Bonferroni confidence intervals. Thus, we could not distinguish whether owls selected vegetation classes in proportion to their availability, or alternatively, that estimates of selection ratios were not sufficiently precise to detect selection or avoidance for any particular vegetation class. However, mature forests with medium and high canopy cover had the highest selection ratios, whereas water, hardwoods, and areas with low canopy cover had the lowest selection ratios, which was consistent with other studies of home-range habitat selection by spotted owls (Gutiérrez et al. 1995).

The goodness-of-fit tests for our final model suggested that vegetation type, patch size, and their interaction were good predictors of owl habitat use within a home range (area under ROC for this model fit to each owl = 0.69–0.98, $\bar{x} = 0.88$). However, because foraging habitat selection varied among owls, the model with coefficients estimated from all of the owls in our sample did not predict data as well as covariates we estimated from individual owls. This variation in habitat selection suggests that vegetation type, patch size, and their interaction were correlated with spotted owl habitat selection but that there was considerable variation in selection among owls. In general, foraging sites having mature forests with

medium (40–70%) canopy cover (vegetation class 6) had a high relative probability of selection for patches <1 ha. However, due to limited availability of patches of this vegetation class >30 ha, and its low mapping accuracy (50% and 83% for user and producer accuracy, respectively), this probability of selection result was inconclusive. Mature forests with high (>70%) canopy cover did not have a high relative probability of selection at this scale. Owls using this class foraged more closely to edges than random points, which was consistent with the findings by Franklin et al. (2000), who reported that annual survival and reproductive output were positively correlated with the amount of edge between mature and old-growth forests and other vegetation classes. There was also the possibility that the size of very small patches were incorrectly identified to foraging location because the size of acceptable confidence ellipses was larger than these small patches. Pole-sized conifer forests had the highest probability of selection in all patches >10 ha. Although owls showed selection for this vegetation class for habitat within home-ranges (second-order selection; Table 2), the selection ratio was not as high as it was for medium- to large-sized conifer forests. Selection probability of hardwood forests was also high in large patch sizes. Laymon (1988) reported similar results for spotted owls in the central Sierra Nevada.

Our results were also consistent with Franklin et al. (2000) who suggested that a mosaic of older forest interspersed with other vegetation types was correlated with high fitness in northern spotted owls (*S. o. caurina*). California spotted owls in the central Sierra Nevada 1) had home-range sizes that correlated with landscape habitat heterogeneity, 2) had home ranges with high proportions of mature forests, and 3) selected large areas of pole-sized coniferous forests. Although pole-sized coniferous forests had a higher selection probability than mature forests for foraging areas, mature forests were also related to home-range selection; thus, both forest types were related to owl home-range selection. Folliard et al. (2000) also reported that owls did not use landscapes dominated by young forests for nesting if they lacked patches of older forest. It was possible that small patches of mature forests were embedded within the larger patches of pole-sized stands that owls were using for foraging, but our mapping techniques were not sufficiently precise to detect these areas. In addition, some habitats we classified as pole stands might actually have been stands of younger forest that had residual trees. Residual trees were uncommon outside of mature or old growth stands but their presence within stands seems to facilitate owl use (e.g., Moen and Gutiérrez 1997). These residual trees were less likely to be detected by our habitat delineation techniques than if we had used an advanced mapping technology such as light detection and ranging (LIDAR).

We conducted our study during a year when owls failed to reproduce and, thus, our study may not be indicative of the habitat required by spotted owls when raising offspring because foraging areas may change when owls have dependent young. Further, the subset of habitat metrics we examined probably did not incorporate all habitat

components important to owls selecting foraging habitat (e.g., differences in vegetation structure between stands used and not used for foraging) and probably did not reflect habitat required to meet other needs (e.g., nest sites). However, we believe our results represented an unbiased estimate of general foraging habitat use of central Sierra Nevada spotted owls during a year of poor reproduction. Studies of selection patterns over time would be more likely to reveal the influence of patterns on owl fitness or population growth.

MANAGEMENT IMPLICATIONS

Management of California spotted owls in the central Sierra Nevada has relied on protecting 121 ha of the best habitat (i.e., vegetation classes 4, 5, 6, and 7) around owl nest or roost sites (Protected Activity Centers [PACs]; U. S. Forest Service 2004). There are numerous studies that suggest owls in our study area center their territories in areas that have greater amounts of these vegetation classes than are available to them (Verner et al. 1992, Chatfield 2005). Although forests dominated by medium-sized trees with >40% canopy cover (vegetation classes 4 and 5) are common in our study area, the distribution of large stands of mature forests (vegetation classes 6 and 7) outside of PACs is sparse. Because our results suggest that owls select home ranges with high proportions of mature forest, of which little remains in the central Sierra Nevada, we recommend that mature forest continue to receive protection.

We found that home-range size was positively correlated with heterogeneous landscapes. This finding was somewhat confounded by the different landscape compositions among owl home ranges. Moreover, our results were observational and because of this, we did not infer either cause and effect relationships or that heterogeneous landscapes were better or worse for owls. However, our study did provide a framework for thinking about forest or fire management strategies in the future. If landscape heterogeneity (i.e., disjunct patches of foraging habitat) requires owls to expend greater energy to move between hunting patches, then the landscape habitat heterogeneity we observed associated with home-range selection would be disadvantageous to foraging owls. It would imply that what we observed were landscapes owls used because they had no other alternatives, which was also supported by the sparseness of mature forest in our study area. Alternatively, if owl fitness in the central Sierra Nevada was associated with landscape heterogeneity (e.g., older forests interspersed with other vegetation types as in Franklin et al.'s [2000] study), then it suggests owls might be selecting heterogeneous landscapes and management of some level of heterogeneity may be desirable.

Although our results suggest owls were selecting pole-sized conifer forests for foraging locations, we do not recommend simply managing for this type of forest without further examining the relationship between these forests, owl foraging, and owl fitness. We recommend that management for pole-sized conifer forest proceed with caution and under an adaptive management framework to monitor owl population response to management. Nevertheless, our study supports

the hypothesis that owls will use a much broader array of forests for foraging than they will for nesting.

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Original Article

Use of Private Lands for Foraging by California Spotted Owls in the Central Sierra Nevada

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ABSTRACT The use of private land by owls has long been of interest to wildlife managers in the Sierra Nevada, California, USA, because private lands could contribute to owl conservation if it is used extensively. Therefore, we studied the use of private lands for foraging by 14 California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada, California during 2006. We modeled foraging locations as a function of 2 land-ownership categories within an owl's territory: public and private land. The log probability of an owl using a public-land location was 15% greater than for a private-land location. Private-land distribution was relatively consistent with respect to the geometric center of owl home ranges, suggesting that our result was not influenced by a peripheral distribution of private land in owl home ranges. Based on our findings, national forest lands within our study area currently have more foraging habitat for California spotted owls than do private lands. We recommend that managers consider owl use of private land within the context of our results when developing conservation strategies for California spotted owls in the central Sierra Nevada. © 2014 The Wildlife Society.

KEY WORDS California spotted owl, managed forests, public land, radiotelemetry, resource selection function, *Strix occidentalis occidentalis*.

California spotted owls (*Strix occidentalis occidentalis*) occur primarily on public lands in the Sierra Nevada. Therefore, management of California spotted owls has relied on protecting the owl's primary habitats within national forests (Verner et al. 1992, U.S. Forest Service 2004). Management plans for California spotted owls have ignored potential habitat contributions from private land because of the variability in land practices, uncertainty in long-term distribution and suitability of these habitats, and the legal status of the owl (i.e., it is not currently listed under the Endangered Species Act; Verner et al. 1992, U.S. Forest Service 2004). This decision has been controversial because 30–40% of forested land in the Sierra Nevada is on private land (Verner et al. 1992, Davis and Stoms 1996). Owls use forests on private land when they are adjacent to owl territories on public land (Williams et al. 2011), and, in some areas, private land is the primary land used by owls (Irwin et al. 2007). In general, California spotted owls use a broader

array of forest types and edge habitats for foraging than they do for nesting and roosting. If California spotted owls were listed as threatened under the Endangered Species Act, the potential contribution of private lands, for foraging, nesting, and roosting, to recovery would be assessed across the Sierra Nevada. Thus, it is important to understand the extent to which owls use private land for foraging to allow comprehensive planning for owls in the Sierra Nevada. The U.S. Forest Service (2003) reported that >15% of known California spotted owl locations had >15% of their potential home range on private lands, and there were 135 known owl territories on private land. In addition, in one area of the Sierra Nevada more owl roost and nest locations were located on public land than on private land (Gutiérrez 1994), which has raised additional uncertainty about the value of private land to owls in this region (i.e., is it used primarily for foraging if not for nesting and roosting?).

Therefore, we modeled habitat selection by California spotted owls as a function of land ownership to evaluate the potential contribution of private land to owl conservation in the Sierra Nevada. Specifically, we examined whether owls selected public land with a higher probability than private land.

STUDY AREA

Our study area was 3,188 km² in the approximate center of the Sierra Nevada, California. The topography was

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mountainous and bisected by steep river drainages. Elevations ranged from 233 m to 3,041 m. The study area had a Mediterranean climate with hot, dry summers and cold, wet winters. Vegetation at lower elevations was dominated by ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), Douglas-fir (*Pseudotsuga menziesii*), sugar pine (*Pinus lambertiana*), incense cedar (*Calocedrus decurrens*), and California black oak (*Quercus kelloggii*), and at higher elevations by California red fir (*A. magnifica*; Küchler 1977). Vegetation was influenced by land ownership, aspect, climate, fire, logging, livestock grazing, edaphic conditions, and elevation (Laymon 1988, Bias and Gutiérrez 1992, Verner et al. 1992, Skinner and Chang 1996). These influences resulted in a diverse pattern of forest types. National forests (public land) comprised 2,363 km² (74%) of the study area and were managed according to the Sierra Nevada Framework (U.S. Forest Service 2004). Private land comprised 825 km² of our study area. Industrial private timber companies were the largest private-land owners (88%), and were required to manage their land in accordance with the California Forest Practices Act (California Forest Practices Rules 2010 Title 14, California Code of Regulations Ch. 4, 4.5, and 10) but not specifically for California spotted owls. The spatial arrangement of private lands within the study area varied, but was often arranged in a checkerboard distribution (Bias and Gutiérrez 1992).

METHODS

Owl Population Description and Sample Selection

We selected our sample of owls randomly from among a subset of all known owl territories in the study area. Our subset included the owl territories that met the following 4 criteria. First, owl territories could not have had tree harvest within their hypothetical home range within the past 5 years or during our study. Second, territories had to be located in areas with a high ratio of public to private land (i.e., <50% private land). Third, owl territories had to have sufficient suitable habitat to allow for a harvest treatment of up to 121 ha and still retain enough (121 ha) suitable habitat for owl management (242 ha total). Fourth, owls could not be captured and radiomarked if they were part of demographic studies in the region. We developed these 4 constraints because this sample of owls was also used to examine the effects of fuel reduction treatments on owls in a separate study. The first and second criteria allowed us to avoid recent or concurrent timber harvest in the territory of owls, which could confound the results. The third criterion ensured that we only included territories that contained enough suitable habitat for owls after the planned harvest occurred. Finally, the fourth criterion ensured that we did not interfere with other research studies in the area by radiomarking owls (i.e., potential to confound estimates of vital rates; Paton et al. 1991).

The fact that we avoided territories with a high ratio of private to public land meant we had the potential to bias our inference because we were interested in comparing relative use between these 2 ownership categories. For example,

theoretically, when eliminating those territories that had a high proportion of private land, we could have inadvertently been selecting owl home ranges whose center was public but whose periphery was private because the closest 300 acres (121 ha) surrounding an owl's nest or roost site were designated as a protected habitat area by the U.S. Forest Service. Thus, with all home ranges centered on public land, one might predict that private land would be on the periphery of home ranges. If private lands were on the periphery of home ranges, owls would show disproportionate use of public land because they are central place foragers (Carey and Peeler 1995, Rosenberg and McKelvey 1999). To address this issue we did the following: first, we only made inference to the territories in our study site that met these criteria; second, within each territory we examined the ratio of public to private land to determine whether this ratio changed from the center of the owl's territory to the periphery of their territory. We did this because we wanted to know what proportion of private land was available to owls, and if the availability changed as a function of the distance from the center of an owl territory to its periphery. We examined how this ratio changed as a function of distance by first identifying the geographic center of each owl's recorded telemetry locations. We then created a circle for each owl with the center of the circle at the geometric center of telemetry locations, and radius extending from the center to the owl's furthest telemetry location. We then generated a grid of systematic points spaced every 50 m within each circle and identified the land ownership at each point. Using these land-ownership identifications, we calculated the proportion of points that were public. Finally, we examined how this proportion changed as a function of increasing distance from the center of the circles.

From our population of territories that met our sampling criteria, we randomly selected 12 owl territories representing 24 owls (12 pairs). At each of the 12 territories, we surveyed for owls following the methods described by Forsman (1983). We determined their sex by vocal characteristics (Forsman et al. 1984), their age by plumage characteristics (Forsman 1981), and their pair status by behavioral associations (Franklin et al. 1996). We attempted to capture all owls and outfit them with a backpack very high frequency radiotransmitter (Model RI-2C; Holohil Systems Ltd., Carp, ON, Canada) attached with a Teflon[®]-coated harness, a U.S. Geological Survey locking aluminum band, and a uniquely colored plastic band and tab (Franklin et al. 1996). To locate radiomarked owls we triangulated on radio signals and recorded the compass direction to the strongest radio signal detected at ≥ 3 monitoring stations spaced >160 m apart within 30 min. We only used locations that had confidence ellipses <5 ha for analysis. We used telemetry locations collected one-half hour before sunset to one-half hour after sunrise (Williams et al. 2011).

Modeling Resource Use by Owls

We examined habitat use using the exponential form of the resource selection function (RSF): $w_j = \exp\{\beta_1 x_{1j} + \dots + \beta_k x_{kj}\}$, where w_j was the relative probability of selection at

location j and $x_{1j}, \dots, x_{kj}$ were covariates we measured at each telemetry location for models with $\beta_0, \dots, \beta_k$ estimated parameters. For the RSF, we excluded the estimated parameter β_0 (Manly et al. 2002). We estimated our parameter values and selected our model for our RSF using generalized linear mixed-effects regression models (GLMM). In our GLMM we assumed a binomial distribution of the response variable and a logit link. Our response variable was whether the location was a nighttime telemetry location (i.e., used) or a randomly selected location (i.e., available). We selected our random locations from within the minimum bounding circle (i.e., the smallest circle that enclosed every point) around all of each owl's radiotelemetry locations (for the purposes of this study, we termed this an owl's home range). The mean minimum bounding circle was 3,775 ha (SD = 4,725 ha). We used a systematic grid of samples, with 1 location every 50 m within each owl's home range. The number of available locations depended on the size of the territory and ranged from 1,043 to 64,977 locations. We examined the effect the number of available points we used had on our parameter estimates by inspecting trace plots of the parameter value against available sample size to ensure each parameter converged.

Because our main objective was to examine the relative land-ownership use by owls we considered a covariate that identified land ownership at each location as public or private. We used land-ownership data from the Placer and Eldorado County Assessor offices, interfaced with owl location data using a Geographical Information System (ArcMAP Version 10.1), to estimate whether a location was on public or private land. In addition to land ownership, we also considered distance from a location to the center of the owl's observed activity. We did this because we thought the probability an owl would use a location would decline for locations further from the center of their observed activity. Rosenberg and McKelvey (1999) showed that nesting spotted owls exhibited this behavior. Specifically, in their study, owls selected forage locations near their nest tree with higher probability than more distant locations. Because owls in our study did not nest, and because they used multiple roosts, we selected the geometric center of the nighttime telemetry locations as the center from which to measure distance to locations. We considered distance functions up to a third-order polynomial in our model suite. Lastly, we

considered owls a random effect, and thus, the intercept of our model was able to change for each owl. Thus, our most general GLMM was

$$Y_{ij} \sim \text{Binomial}(1, p_{ij})$$

$$\text{logit}(p_{ij}) = \beta_0 + \beta_1(\text{owner}_{ij}) + \beta_2(\text{dist}_{ij}) + \beta_3(\text{dist}_{ij}^2) + \beta_4(\text{dist}_{ij}^3) + a_i$$

$$a_i \sim N(0, \sigma_a^2)$$

where p_{ij} was the probability that the i th owl would use the j th location; owner = 0 for private land and owner = 1 for public land; dist_{ij} was the distance between each location and the i th home-range center; a_i was a random effect for each owl that had a normal distribution with mean 0, and variance σ_a^2 .

To examine the hypothesis that the ownership was correlated with location selection by owls, we created 8 models. Four of the 8 models included the ownership variable, and the other 4 models did not (Table 1). Each set of 4 models consisted of a model with no distance function, a linear distance function, a quadratic distance function, and a third-order polynomial for the distance function (Table 1). We estimated the parameters and model fit using the lme4 package in Program R (function:glmer). We compared our models using the approximated Akaike's Information Criterion (AIC). We selected the model with the lowest AIC value to use in our RSF.

RESULTS

We collected 1,339 nighttime telemetry locations (range = 41–209 locations/owl) distributed among 14 data sets obtained from 13 radiomarked owls (1 owl was considered as 2 separate samples because it dispersed to a new (non-overlapping) territory after its mate died and, therefore had access to a different landscape comprising a different proportion of private land). Thus, our sample of owls for home-range analysis consisted of 4 pairs, 4 single female owls, and 2 single male owls. We recorded 156,297 systematic, available locations within the bounded home ranges of owls. Of foraging locations and random locations, 19% ($n = 256$) and 26% ($n = 41,152$), respectively, were on private land. The maximum difference in the ratio of public:

Table 1. Generalized linear mixed models developed to examine the functional relationship between California spotted owl resource selection and land ownership in the Sierra Nevada, California, USA, during 2006, and the model selection results. We used generalized linear mixed models to obtain our parameter estimates for our resource selection function and for Akaike's Information Criterion (AIC) estimates. The model was: $\text{logit}(p_{ij}) = \mathbf{x}_{ij}^T \boldsymbol{\beta} + a_i$, where p_{ij} was the relative probability of use for the i th owl and j th location, and $\mathbf{x}_{ij}^T \boldsymbol{\beta}$ were the 8 models below, and a_i was a random effect for each owl.

Model ($\mathbf{x}_{ij}^T \boldsymbol{\beta}$)	No. fixed effects parameters	ΔAIC
$\beta_0 + \beta_1(\text{dist}) + \beta_2(\text{dist}^2) + \beta_3(\text{dist}^3) + \beta_4(\text{public})$	5	0.00
$\beta_0 + \beta_1(\text{dist}) + \beta_2(\text{dist}^2) + \beta_3(\text{dist}^3)$	4	1.67
$\beta_0 + \beta_1(\text{dist}) + \beta_2(\text{public})$	3	15.60
$\beta_0 + \beta_1(\text{dist})$	2	17.38
$\beta_0 + \beta_1(\text{dist}) + \beta_2(\text{dist}^2) + \beta_3(\text{public})$	4	17.50
$\beta_0 + \beta_1(\text{dist}) + \beta_2(\text{dist}^2)$	3	19.36
$\beta_0 + \beta_1(\text{public})$	2	179.30
β_0	1	183.57

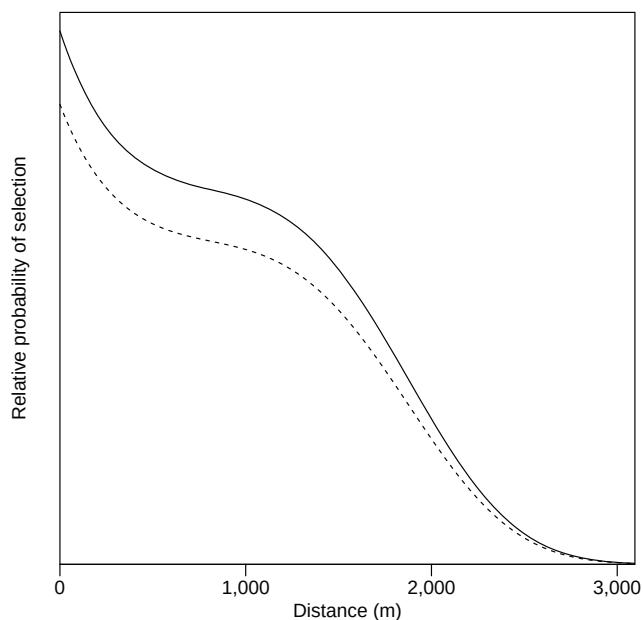


Figure 1. Estimated resource selection function for a population of California spotted owls in the central Sierra Nevada, California, USA, during the summer of 2006. The solid line is the estimated function for public land, and the dashed line is for private land. Distance from center is the distance from the geometric center of owl use locations.

private land from between 0 m and 1,000 m of the geometric center (approx. 315 ha; 79% public) and 0–5,000 m of the geometric center (approx. 7,850 ha; 74% public) was 5%.

Our model with the lowest approximated AIC included the owner variable, and all 3 distance variables (Table 1). This model indicated that our sample of owls were more likely to select public land than private land (Table 1). The RSF with the estimated parameters from our top model was:

$$w_j = \exp \{0.15 (\text{owner}_j) - 2.06 (\text{dist}_j) + 4.35 (\text{dist}_j^2) - 3.46 (\text{dist}_j^3)\}$$

where 0.15 was the increase in the log relative probability of use for public land, and -2.06 , 4.35 , and -3.46 described the change in log relative probability of use for one standard deviation change in distance from the center of the territory (1 SD = approx. 2,000 m; Fig. 1). None of the confidence intervals for the parameter estimates overlapped 0 (Table 2). The distance function included in the model indicated that owls selected locations near the center of their home range with higher probability than more distant locations (Fig. 1).

Table 2. Parameter estimates and their associated 95% confidence intervals for our top model estimating resource selection by California spotted owls in the central Sierra Nevada, California, USA, during summer 2006.

Fixed effects	Estimate	Lower 95% CI	Upper 95% CI
public	0.15	0.10	0.20
dist	-2.06	-2.69	-1.42
dist ²	4.35	2.30	6.39
dist ³	-3.46	-5.08	-1.83

These values were estimated using a generalized linear mixed model, and were used for the parameter estimates in the resource selection function.

The estimate of the variance of the population of owls for the random intercept (i.e., σ_a^2) was 0.57.

DISCUSSION

As is the case with all studies using model-based inference, our inference is to the population whose observable characteristics of habitat use are similar to our observed sample. We selected our sample over a large geographical area (3,188 km²) randomly from a subset of owls based on the specific inclusion criteria listed in the methods. Thus, our sampling procedure increased the probability that our sample was representative of the owls in our study area that fit these criteria.

We examined the functional relationship between owl foraging use and land ownership. Both public and private land in the central Sierra Nevada have experienced a complex history of logging, which has resulted in a highly heterogeneous landscape on both public and private land (Bias and Gutiérrez 1992). This history has created uncertainty about habitat relationships of spotted owls in the Sierra Nevada (Verner et al. 1992). One of these uncertainties was the use of private lands by spotted owls. We found that, although owl home ranges overlapped a large amount of private land, they used private land disproportionately less than they did public land. Thus, our findings supported previous observations that owls will forage on private land, but, at least in the central Sierra Nevada, it was used less than public land.

Although, land ownership alone did not influence habitat selection by owls, there were several potential explanations for our results of differential use of public and private land. First, the distribution of public and private land within the home ranges of owls we studied could have influenced owl use patterns. If private lands were found primarily on the periphery of home ranges, we would expect owls to use it less because owls are central place foragers and more likely to use areas near their nest for foraging (Carey and Peeler 1995, Rosenberg and McKelvey 1999). This was not the case because the proportion of private land only varied by about 5% from the geometric center of an owl's home range to its periphery. Second, it was possible that either vegetation composition or structure or both could have been different between public and private land. Many studies have shown that spotted owls are habitat specialists that use late-successional forest stands with complex structure and composition disproportionately to its availability (Gutiérrez et al. 1995). A greater amount of these forest types was likely found on public land because of conservation requirements and other constraints on land management placed on national forest managers (Collins et al. 2010). Laymon (1988) and Bias and Gutiérrez (1992) reported that private lands within our study area were more heavily logged than public lands, with both large trees and dead or dying trees removed during logging operations. Bias and Gutiérrez (1992) further noted that the number of possible nest trees, basal area of old-growth trees, mean height of old-growth trees, number of possible nests in old-growth trees, and basal area of snags were different between public and private land.

Therefore, differences in land use by California spotted owls might have reflected differences in vegetation and/or structure available to these radiomarked owls. When one considers that habitat heterogeneity is positively correlated with owl home-range size in the central Sierra Nevada (Williams et al. 2011), it is not surprising that owl home ranges in the central Sierra Nevada contain a mix of public and private lands because of the intermixed distribution of these ownerships. Yet, the owl's disproportionate use of private lands suggests that private land is not of as high value to the owls as public land.

MANAGEMENT IMPLICATIONS

Our results suggest privately owned land is not equivalent to publicly owned land as a contributor to spotted owl conservation in the central Sierra Nevada. Hence, conservation strategies should rely primarily on public land management. Moreover, timber harvest and management actions that reduce the amount of suitable owl habitat in potential home ranges that have a high proportion of private land should be minimized. We also suggest that managers of private land consider timber harvest strategies that, at minimum, maintain foraging habitat because owls will use a broader array of habitats and structure for foraging than they do for nesting and roosting.

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From the Field

Illuminating the Nocturnal Habits of Owls with Emerging Tagging Technologies

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ABSTRACT Owls play important cultural, ecological, and indicator roles throughout the world. Yet owls' cryptic behavior has led to uncertainties about their basic ecology, including foraging, communication, and functional roles within the community, and potentially hindered the implementation of effective conservation measures. Here we demonstrate the potential for next-generation GPS tags capable of recording high-precision, minute-by-minute locations paired with other technologies to resolve some of these uncertainties. We combined high-precision GPS tagging data with infrared (IR) video recorded by arboreally-mounted cameras at 5 spotted owl (*Strix occidentalis*) nest sites in the Sierra Nevada, USA to provide a uniquely detailed examination of owl foraging patterns. Our approach allowed us to identify the precise time and location of 54 predation events and prey identity. We also used high-precision GPS tags with on-board audio recorders to map the vocal activity of 8 individuals by matching the time of vocalizations in the audio data to GPS locations recorded at one-minute intervals. The combined spatial and acoustic data revealed that nonbreeding males had the most widespread territorial vocal activity (i.e., producing 4-note territorial calls), while females provisioning fledglings displayed extensive nonterritorial vocal activity (i.e., producing many contact calls). Thus, the GPS-tag technologies we employed can provide opportunities to better understand owl foraging, communication, territoriality, and population dynamics. The methods we describe are time- and resource-intensive but can be paired with techniques that are more applicable at landscape scales, such as stable isotope analyses, LiDAR-based habitat analyses, and passive acoustic monitoring to link local processes to broad-scale ecological patterns. Therefore, our approach could be applied to many species whose behavior inhibits direct observation. © 2021 The Wildlife Society.

KEY WORDS behavioral ecology, bioacoustics, communication, foraging ecology, GPS tag, infrared camera, passive acoustic monitoring, single-rope technique, *Strix occidentalis*.

Owls are a dominant nocturnal predator in many forests and can exert cascading ecosystem effects, are sensitive indicators of ecological change, and are important culturally

(Marcot and Johnson 2003, Whelan et al. 2008, McClure et al. 2018). Traits such as the regurgitation of undigested prey remains in pellets (Heisler et al. 2016) and the use of nest boxes by some species (Zárybnická et al. 2016) have facilitated studies of foraging habits and functional and numerical responses to changing prey populations (Korpimäki and Norrdahl 1991). Similarly, the relative ease of capturing and marking some species has facilitated extensive studies of habitat selection and demographics

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(Noon and Franklin 2002). Nevertheless, nocturnality generally precludes direct observations of owl behaviors such as hunting, mating, territory defense, and competitive interactions. This limitation has led to considerable uncertainties about owl behavioral ecology, factors regulating owl populations, and the magnitude of their ecosystem-level effects. Such knowledge gaps can have important consequences for conservation because, for example, foraging ecology can influence landscape-scale population dynamics (Hobart et al. 2019). Additionally, spatiotemporal variation in acoustic communication can affect prey populations (Eilam et al. 1999) and have implications for passive acoustic monitoring (PAM) programs designed to detect population changes (Wood et al. 2019b). Therefore, methods that can fill knowledge gaps would be valuable for research and conservation.

Recent advances in GPS technology and battery capacity and size provide new opportunities to study owl ecology because GPS tags can now provide minute-by-minute locational information with greater precision than previous generations of tags of comparable size (Marsh et al. 2014a, Blakey et al. 2019, San-Jose et al. 2019). The new generation of high temporal resolution (HTR) tags allow behaviors such as hunting and resting to be inferred by classifying locations based on the speed of movements, distance traveled, and turning angles (Marsh et al. 2014a, San-Jose et al. 2019), which was not practical with previous tags. However, inferring behavior from movement paths alone depends on the assumption that specific behaviors (e.g., hunting) are characterized by diagnostic flight speeds and directions. Alternatively, behaviors with similar movement paths can be aggregated into broad categories, but doing so requires grouping ecologically-distinct activities, for example, placing territorial vocalizations and resting into a single perching category (San-Jose et al. 2019). Thus, the full potential of new GPS-tag technologies may not be realized without applying complementary methods.

Here, we report how combining HTR GPS tags with other technologies can substantially improve our understanding of owl ecology. First, we demonstrate how arboreal video monitoring of the nests of HTR GPS-tagged owls enhances determination of the location of prey capture sites by identifying species brought to nests. Second, we show how the addition of on-board audio recorders to HTR GPS tags can be used to characterize the spatiotemporal vocalization patterns of individual owls, including the location where different calls are made. The methods we describe here have the potential to provide mechanistic explanations for critical aspects of owl ecology.

FORAGING ECOLOGY

Improving our understanding of owl foraging ecology is important because owls are apex avian predators that may exert wide-reaching ecological effects (Whelan et al. 2008), and because doing so can improve conservation outcomes (Hobart et al. 2019). High temporal resolution GPS tags used simultaneously with video surveillance of nest sites can

allow researchers to identify with high precision both prey identity and locations of capture. Prey captures can be inferred from HTR GPS data when a tight cluster of sequential location points is followed by rapid but widely-spaced location points that lead directly to the nest, and can be confirmed as successful by video footage of a prey delivery to the nest site (Marsh et al. 2014a, San-Jose et al. 2019). To illustrate the feasibility of identifying prey and capture location in arboreally-nesting owls, we deployed HTR GPS tags (Alle-300, Ecotone Telemetry, Gdynia, Poland), programmed to record locations at two-minute intervals, for 4–12 days on five male California spotted owls (*Strix occidentalis occidentalis*) in the central Sierra Nevada during May to June 2019. We captured owls by hand and with snare poles and we used tags weighing 11 g (~2% of the average body weight of a spotted owl), which we mounted on the two central retrices. Our settings yielded an effective battery life of 7–10 days. Birds were recaptured after 10–14 days and the tags removed so the data could be recovered. Birds jettison tail-mounted tags when they molt, ensuring that they are not subject to carrying the tag forever if they are not recaptured.

While the tags were deployed we monitored prey deliveries to females and dependent young at nests with infrared (IR) video cameras (Q1786-LE Network Camera, Axis Communications, Emdalavägen, Sweden) installed in adjacent trees. Male spotted owls regularly exhibited characteristic, straight-line flights from tight clusters of points, which we assumed to be indicative of foraging sites, back to nests where we recorded them delivering prey upon arrival (Fig. 1A). By using both HTR GPS data and nest video monitoring, we identified 54 locations associated with successful prey captures and identified prey in 36 cases (Fig. 1B). The number and species consumed included 21 woodrats (*Neotoma* spp.), 10 Humboldt's flying squirrels (*Glaucomys oregonensis*), 2 voles (*Microtus* spp.), 2 mice (*Peromyscus* spp.), and 1 pocket gopher (*Thomomys* spp.).

High temporal resolution GPS tags have been used in similar settings—notably in conjunction with in-nest video monitoring of burrowing owls (*Athene cunicularia*) (Marsh et al. 2014a, b) and nest-box video monitoring of barn owls (*Tyto alba*) (San-Jose et al. 2019). However, similar technology has not been used in conjunction with unobtrusive video monitoring of natural, arboreal nest sites typically selected by owls. We used the single-rope technique (SRT) (Perry and Williams 1981, Picart et al. 2014) to mount high-resolution IR video cameras 10–40 m above ground and 10–50 m from nest sites, thus mitigating observer effects induced by direct observation (e.g., in-nest cameras). The SRT method entails anchoring a static rope at the base of a tree and launching the line across a branch above the desired camera location and leaving one end of the rope hanging freely. We used an arborist harness, ascenders, a flip line (or some form of a backup system), and personal protective equipment (e.g., a helmet, gloves, and protective glasses) to reach the desired height. Once the camera was mounted, we used a belay device to lower the researcher

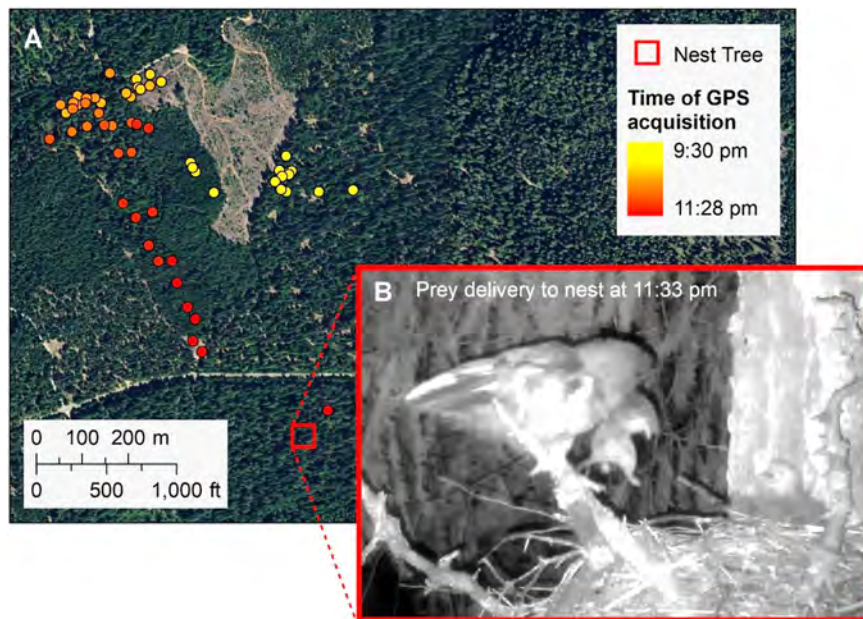


Figure 1. Map showing A) the sequence of owl HTR GPS locations for the two hours preceding a prey delivery, and B) an image of the subsequent prey delivery at the nest. The prey delivery image is a single frame from an infrared camera mounted 25 m above ground in a tree 40 m from the nest tree and shows the delivery of a woodrat to the nest and the waiting owlet in May 2019 in the central Sierra Nevada, USA. The approximate location of the capture could be inferred from the cluster of GPS locations before the owl's nearly direct flight back to the nest.

safely to the ground. The entire process took 4–5 hours depending on the height of camera placement, size of tree, and complexity of limb structure.

Deploying cameras in tall trees using the SRT method requires substantial training by a certified arborist. Nevertheless, using cameras has the potential to substantively improve our understanding of the foraging ecology of arboreally-nesting owls and of other large-bodied avian predators. The inferences drawn from resource selection functions (RSFs) without prey capture locations can differ substantially from those drawn from RSFs made with capture data yielded by HTR GPS tags and video cameras because prey-capture success may vary among habitat types in which owls forage (Marsh et al. 2014a). Because most studies do not consider known prey capture locations in RSFs, it raises the question of how well we actually understand owl foraging behavior. However, if enough prey deliveries are observed, researchers could develop individual RSFs for different species or categories of prey. Combining HTR GPS tags and video cameras to identify the habitat features that promote successful prey capture by owls and other raptors would provide opportunities to address many questions in ecology about how habitat influences predator-prey interactions.

Identifying patterns in prey capture locations may also contribute to improved raptor management by providing better estimates of microhabitat features that promote successful foraging. Foraging studies could be further enhanced by the incorporation of aerial LiDAR data, which can provide data at the resolution of individual trees and can characterize vegetation features at and below the canopy at the landscape scale. Thus, with HTR GPS tags capable of

generating data with comparable spatial precision, we believe that the synergistic use of these two technologies could improve the conservation of owls.

ACOUSTIC ECOLOGY

Owls employ vocalizations for territorial defense, pair bonding, and other biological processes, and researchers commonly use such vocalizations to locate owls and monitor population status. Improving our understanding of the spatiotemporal patterns of vocal behavior can therefore benefit both basic and applied owl research. However, the use of conventional research methods such as VHF tags and handheld microphones cannot duplicate the spatial and temporal coverage, precision, and context of vocalizations that combining technologies enables (Finck 1990, Zuberogoitia et al. 2019). Consequently, we deployed novel HTR GPS tags equipped with onboard acoustic recording devices (Vesper 3.2, Alexander Schwartz Developments, Haifa, Israel) that were encapsulated in epoxy (Lotek Wireless, Wareham, UK) to collect locations at 1–2 minute intervals for 3–5 days on 8 spotted owls (4 males and 4 females) in the central Sierra Nevada. As before, owls were captured by hand and with snare poles and tags were mounted on the two central retrices. The tags weighed 11.6 g (~2% of the average body weight of a spotted owl) and our recording settings yielded an effective battery life of 3–4.5 days. Birds were recaptured after 7–8 days and the tags removed so the data could be recovered.

We then matched the recorded vocalizations to minute-by-minute GPS locations, allowing us to study owl vocal behavior at an unprecedented level of detail. We observed differences in the call rate, type, and timing, and in

the location of calls based on sex and breeding status. Non-nesting owls, especially males, produced more territorial vocalizations ($\bar{x}_{\text{non-nesting male}} = 646$; $\bar{x}_{\text{nesting female}} = 3$) and were more likely to give calls throughout their range (Fig. 2A). In contrast, nesting spotted owls primarily produced nonterritorial calls indicative of communication between mates and between parents and offspring <300 m from their activity center; however, females provisioning fledglings were particularly vocal within that range ($\bar{x} = 801$ calls; Fig. 2B). Our findings suggest that further work has the potential to provide considerable insight to the sociobiological context of vocalizing spotted owls.

Deployment of HTR GPS tags with onboard audio recording capacity can create new opportunities to study acoustic communication in owls. For example, evidence suggests that owls face trade-offs when vocalizing during foraging. Spotted owls appear to reduce vocal activity in the preferred habitat of flying squirrels, a key prey species, possibly to mitigate prey vigilance (Wood et al. 2019c). In contrast, our data revealed that mated pairs of spotted owls employed and responded to vocal signals while foraging.

Another trade-off with acoustic underpinnings is conducting territorial defense while avoiding conflict or predation. Spotted owls increase their territorial vocal activity (i.e., produce more four-note calls) in response to barred owls (*S. varia*), an invasive competitor, when barred owls are scarce (Wood et al. 2020). However, their vocal activity is reduced in response to barred owl calls when the latter species is common (Crozier et al. 2006). Thus, variation in time and space of territorial vocalizations may provide additional information about how species are affected by competition.

High temporal resolution GPS+audio tags allow estimation of the acoustic home range, or the area in which a species is vocally active (Fig. 2). Understanding spatio-temporal variation in the acoustic home range would be particularly valuable in the development of passive acoustic monitoring (PAM) programs, which typically use territorial vocalizations as indicators of site occupancy and can be implemented for multiple species simultaneously (Wood et al. 2019a, b). Therefore, HTR GPS tags also have the potential to provide a realistic estimate of an avian

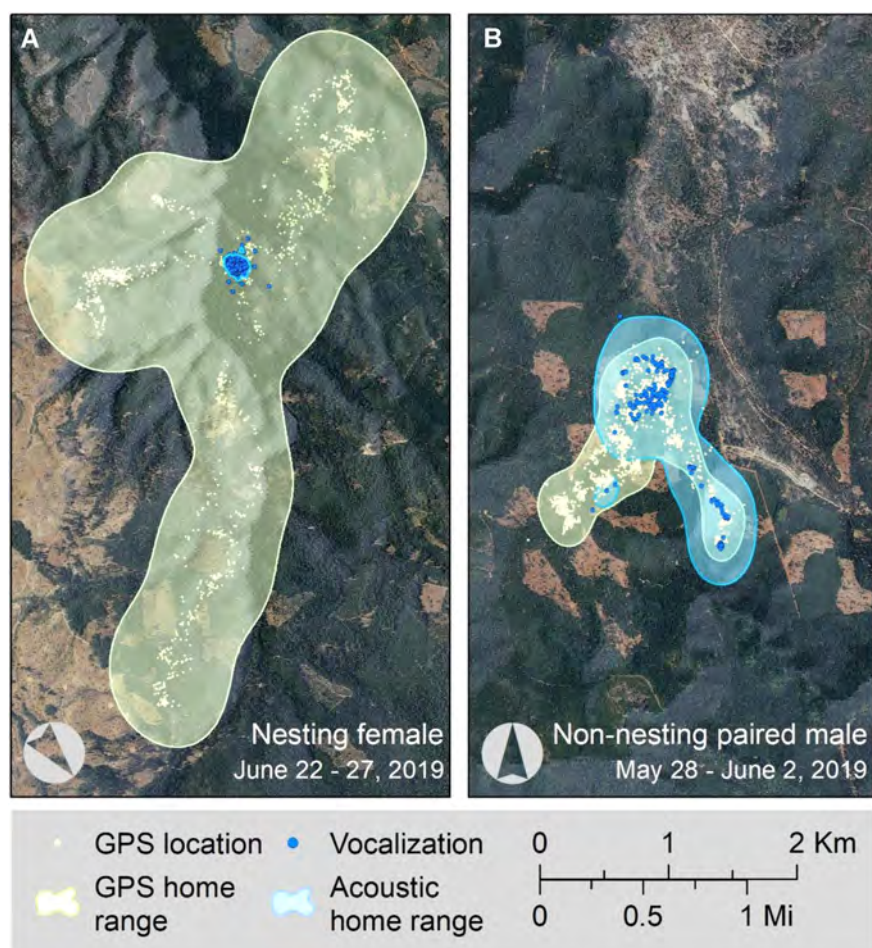


Figure 2. High temporal resolution GPS locations of spotted owls in the central Sierra Nevada, USA, and the locations of vocalizations, as well as traditional and acoustic home ranges, for A) a nesting female in late June, shortly after two young fledged, and B) a non-nesting male in late May. Differences in sex, nesting status, resource availability, and time of year of data collection all may have impacted the absolute and relative size and overlap of the acoustic and traditional home range. The home ranges were estimated using a 95% kernel density estimate of HTR GPS locations for physical location and location of vocalization.

predator's territory. Recent studies suggest that spotted owls regularly make forays into nearby, often unoccupied, territories (i.e., sites that had a history of occupation but were not occupied at the time of the forays) (Berigan et al. 2019, Blakey et al. 2019). However, if individuals are vocally active during extra-territorial movements, they could be recorded at multiple PAM survey sites that are assumed to be occupied by separate single or paired owls. Consequently, occupancy estimates would be biased high and important habitat associations could be obscured (Berigan et al. 2019). The spatiotemporal vocalization patterns revealed by estimating acoustic home ranges of relevant territorial vocalizations could inform the development of criteria to eliminate such false positive detections. Additionally, if vocalizations are found to be infrequent or spatially constrained in one or both sexes or during important reproductive stages, PAM could be ineffective if implemented at inappropriate scales, either because individuals simply would not be detected or because detection probabilities would be low and thus reduce statistical power to detect population change (Wood et al. 2019b). Therefore, HTR GPS+audio tag studies can be an important phase in the development of PAM programs for owls and other vocally active species.

CONCLUSIONS AND EMERGING FRONTIERS

We show that using HTR GPS tags in combination with other technologies has considerable potential to provide previously unattainable insights into the behavior of owls, as well as other raptors. Thus, many aspects of raptor ecology that have remained unstudied are now potentially open for scientific inquiry. Pairing HTR GPS tags with arboreally-mounted IR cameras can provide capture locations and identities of specific prey items of the many owl species that do not nest on the ground. High temporal resolution GPS tags with on-board audio recording devices can reveal variation in owl vocal behavior between sexes and breeding status, and across habitat and temporal gradients. This information could then be used to refine PAM projects designed to measure population change over time and in response to disturbance.

We encourage researchers to employ parallel methods that are less invasive and can be applied across broader areas. In this way, mechanistic understandings provided by tag data can be linked to broad-scale ecological patterns. For example, if spatial patterns in prey capture and delivery studies can be connected with stable isotope values, and if stable isotope analyses are conducted across a larger population, the results could be extended to entire landscapes (Hobart et al. 2019). Acoustic tag results could be used to inform studies that draw on landscape-scale passive acoustic survey data to study animal behavior (Wood et al. 2019c) and interspecific interactions (Wood et al. 2019a). The combinations of emerging technologies and methods that we have described here have the potential to resolve long-standing mysteries in owl ecology.

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RESEARCH ARTICLE

Large trees and forest heterogeneity facilitate prey capture by California Spotted Owls

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ABSTRACT

Predators are among the most threatened animal groups globally, with prey declines contributing to their endangerment. However, assessments of the habitat conditions that influence the successful capture of different prey species are rare, especially for small, cryptic predators. Accordingly, most predator conservation plans are based on the relative importance of habitats inferred from coarse-scale studies that do not consider habitat features contributing to hunting success, which can vary among prey species. To address this limitation, we integrated high-resolution global positioning system tracking and nest video monitoring to characterize habitat features at prey capture locations during the nestling provisioning stage for the Spotted Owl (*Strix occidentalis*) a small, cryptic predator that has been at the center of a decades-long forest management conflict in western North America. When all prey species were considered collectively, males provisioning nests tended to capture prey: (1) in areas with more large-tree forest, (2) in areas with more medium trees/medium canopy forest, and (3) at edges between conifer and hardwood forests. However, when we considered the owl's two key prey species separately, males captured woodrats (*Neotoma fuscipes*) and Humboldt flying squirrels (*Glaucomys oregonensis*) in areas with markedly different habitat features. Our study provides clarity for forest management in mixed-ownership landscapes because different prey species achieve high densities in different habitat types. Specifically, our results suggest that promoting large trees, increasing forest heterogeneity, and creating canopy gaps in forests with medium trees/high canopy cover could benefit Spotted Owls and their prey, which has the ancillary benefit of enhancing forest resilience. Combining high-resolution global positioning system tagging with video-based information on prey deliveries to breeding sites can strengthen conservation planning for small predators by more rigorously defining those habitat features that are associated with successful prey acquisition.

Keywords: forest heterogeneity, large trees, predator–prey interactions, prey availability, Sierra Nevada, Spotted Owl, young forest

LAY SUMMARY

- Predators capture their prey where prey are both present and available for capture. Therefore, mapping and analyzing habitat at capture locations can aid management of quality habitat for predator conservation.
- It is difficult to find the exact places where predators capture their prey. This is especially challenging for smaller, cryptic predators that do not leave behind obvious kill sites.
- We attached global positioning system (GPS) tags to Spotted Owls and placed video cameras at their nests. We assessed the GPS movements to identify places they captured prey, which we then classified into species based on the video data.
- Spotted Owls captured prey in places with big trees, with medium trees and medium canopy cover, and with a greater mixture of forest types (heterogeneity) and forest edge.
- Forest management that promotes big trees, increases forest heterogeneity, and creates canopy gaps in forests will likely result in greater foraging success by owls, as well as increase forest resilience.

Los grandes árboles y la heterogeneidad del bosque facilitan la captura de presas por parte de *Strix occidentalis* de California

RESUMEN

Los depredadores se encuentran entre los grupos de animales más amenazados a nivel mundial, y la disminución de presas contribuye a su peligro. Sin embargo, las evaluaciones de las condiciones del hábitat que influyen en la captura exitosa de diferentes especies de presas son raras, especialmente para depredadores pequeños y crípticos. En consecuencia, la mayoría de los planes de conservación de depredadores se basan en la importancia relativa de los hábitats inferidos a partir de estudios de escala gruesa que no consideran las características del hábitat que contribuyen al éxito de la caza, las cuales pueden variar entre las especies de presa. Para abordar esta limitación, integramos el seguimiento por GPS de alta resolución y el monitoreo mediante grabaciones de video de los nidos, para caracterizar las características del hábitat en las ubicaciones de captura de presas durante la etapa de aprovisionamiento de polluelos de *Strix occidentalis*, un depredador pequeño y críptico que ha estado en el centro de un conflicto de manejo forestal que lleva décadas en el oeste de América del Norte. Cuando todas las especies de presas fueron consideradas colectivamente, los machos que aprovisionaban los nidos tendieron a capturar presas: (1) en áreas de bosques con árboles grandes, (2) en áreas con más árboles medianos/bosques de dosel mediano, y (3) en los bordes entre coníferas y bosques de maderas duras. Sin embargo, cuando consideramos las dos especies de presa clave de *S. occidentalis* por separado, los machos capturaron ratas (*Neotoma fuscipes*) y ardillas (*Glaucomys oregonensis*) en áreas con características de hábitat marcadamente diferentes. Nuestro estudio proporciona claridad para el manejo forestal en sitios de propiedad mixta porque diferentes especies de presas alcanzan altas densidades en diferentes tipos de hábitat. Específicamente, nuestros resultados sugieren que la promoción de árboles grandes, el aumento de la heterogeneidad del bosque y la creación de huecos en el dosel en bosques con árboles medianos/cobertura de dosel alta podría beneficiar a *S. occidentalis* y sus presas, lo que tiene el beneficio adicional de mejorar la resiliencia del bosque. La combinación del seguimiento por GPS de alta resolución con información basada en grabaciones de video de la entrega de presas a los sitios de reproducción puede fortalecer la planificación de la conservación para los pequeños depredadores, al definir de manera más rigurosa aquellas características del hábitat que están asociadas con la adquisición exitosa de presas.

Palabras clave: árboles grandes, bosque joven, disponibilidad de presas, heterogeneidad forestal, interacciones depredador-presa, Sierra Nevada, *Strix occidentalis*

INTRODUCTION

Predators are among the most endangered animal groups (Estes et al. 2011). Many anthropogenic factors threaten predators, but prey depletion resulting from habitat degradation is an important source of endangerment (Manlick and Pauli 2020). Recent work suggests that habitat conditions can mediate trophic interactions between predators and their prey through a variety of processes (Smith et al. 2019). This recognition, coupled with the fundamental importance of prey to predators (Mitchell and Powell 2004), suggests bolstering prey populations through habitat management could contribute to the recovery of imperiled predators.

Management that seeks to enhance prey populations will benefit from understanding how habitat influences predator-prey relationships. First, prey vary in both quality (e.g., nutritional content) and habitat needs, with different species reaching different densities in different habitats. Thus, in heterogeneous landscapes, promoting high-quality habitat for populations of more energetically valuable prey might benefit predator populations (Hobart et al. 2019a). Alternatively, when populations of prey species fluctuate asynchronously, ensuring habitat for multiple or alternative prey could buffer predators from declines in any one species (Sinclair et al. 2013). Second, prey can achieve high densities in habitats that do not constitute high-quality hunting habitat for the predator because of

a lack of suitable foraging structures (Dubey et al. 2019). Mismatches between predator-foraging habitats and high-density prey habitats can reduce predator access to prey but can also create prey refuges that indirectly benefit predators by producing source populations that disperse into predator-foraging habitat (Klecka and Boukal 2014). Thus, while the mechanisms by which habitat mediates predator-prey interactions are complex, understanding these processes can facilitate the development of more effective habitat-based conservation plans for endangered predators.

Studies of the interplay between habitat and predator-prey relationships have focused primarily on large mammalian predators because prey capture locations can be characterized based on the remains of kills made by global positioning system (GPS) or very high frequency (VHF) tagged individuals (Anderson and Lindzey 2003). However, identifying prey capture sites is much more difficult for smaller-bodied, more cryptic predators because discernable remains at kill sites are typically either absent or difficult to locate. For these reasons, studies of habitat selection by small or cryptic species typically “assume” foraging behavior using locations of tagged individuals during periods when foraging activities normally occur (e.g., during nocturnal hours), when in reality few of those locations are likely to represent actual prey capture locations (Marsh et al. 2014). Thus, logistical and technological limitations associated with studying foraging ecology

of small or cryptic predators have challenged a mechanistic understanding of prey habitat and conservation of predator–prey relationships.

Recent advances in GPS tagging technology such as the design of lightweight tags that record fine-scale movements with very high spatial and temporal resolution have facilitated identification of prey capture locations of small-bodied predators (Studd et al. 2021, Wood et al. 2021). For example, Marsh et al. (2014) integrated GPS dataloggers and digital video recorders to study the nocturnal foraging ecology of Burrowing Owls (*Athene cunicularia*) and identified successful captures based on (1) clusters of GPS locations followed by a straight-line movement back to a nest or den; and (2) video observation of prey delivery to the nest or den simultaneous with the arrival determined via GPS. This integrative approach can thus provide otherwise impossible insights into the successful hunting locations (and habitats) of adult individuals provisioning dependent offspring during this critical life history phase. However, to our knowledge, no previous study has characterized differences in habitat associated with the successful acquisition of different prey species in small-bodied predators.

We leveraged these new technologies to gain a more mechanistic understanding of how forest conditions influenced foraging strategies and the successful capture of prey species during the nestling-provisioning phase for the Spotted Owl (*Strix occidentalis*), a mature forest nesting species of conservation concern that is experiencing population declines across many parts of its range (e.g., Franklin et al. 2021). Concern about the Spotted Owl and its habitat has placed this species at the center of forest management planning in many forests of western North America, with substantial implications for both timber harvesting on private lands and forest management efforts intended to curb the spread of unprecedented large severe fires on public lands (Peery et al. 2017). Additionally, Spotted Owls are known to be nest site specialists, but GPS-tagging and VHF telemetry studies suggest that nocturnal activities (and therefore, inferred foraging activities) by Spotted Owls may occur in a broader range of forest types than nesting (e.g., Call et al. 1992, Atuo et al. 2019, Kramer et al. 2021). However, these nocturnal locations likely represent a range of activities besides foraging such as territory defense, pair bonding, and resting, and thus do not necessarily provide insights into the forest conditions that promote successful prey acquisition and associated fitness benefits. Given the profound effects prey availability has on Spotted Owl population dynamics (e.g., Franklin et al. 2000, Hobart et al. 2019a), an improved understanding of how forest conditions relate to the acquisition of primary prey and how habitat conditions differ among prey could substantially enhance forest management intended to benefit this species and meet other management and conservation objectives.

Two of the primary prey of Spotted Owls in California's Sierra Nevada—Humboldt flying squirrels (*Glaucomys oregonensis*) and woodrats (*Neotoma* spp.) (Gutiérrez et al. 2020)—tend to occur in different forest types. Woodrats, which are typically large in body size (mean woodrat consumed by owls = 187 g; C. Zulla personal communication) and more energetically profitable (1,205 kJ; Weathers et al. 2001), can be particularly abundant in some younger forests and brushy areas and are positively related to the presence of large oaks (Sakai and Noon 1993). Conversely, flying squirrels, which are typically smaller in body size (mean flying squirrel consumed by owls = 98 g; C. Zulla personal communication) and less energetically profitable (592 kJ; Weathers et al. 2001), tend to be more abundant in mature coniferous forests that have more arboreal lichens and tree cavities (Meyer et al. 2005). Thus, flying squirrels are more common in forest types considered to be Spotted Owl nesting habitat, while woodrats occur at high densities in areas that may be less suitable for Spotted Owl nesting (North et al. 1999). When brushy areas or some younger forest types having high woodrat density occur adjacent to mature coniferous forests, the resulting edge may provide foraging opportunities for Spotted Owls (Sakai and Noon 1993, 1997), although this hypothesis has not been tested. The consumption of woodrats, facilitated by the juxtaposition of older forest with other vegetation types (i.e. heterogeneous forest) may, in some ecological contexts, promote high territory occupancy rates, fitness, and landscape-scale density in Spotted Owls (Franklin et al. 2000, Hobart et al. 2019a).

We tested the hypothesis that forest type and structure (including edges) are related to acquisition of prey by Spotted Owls. Under this hypothesis, we predicted that Spotted Owls would tend to capture prey in mature forests overall, but that forest structure would differ between successful woodrat and flying squirrel capture sites. Specifically, we predicted that owls would capture woodrats at the edge between mature forests and areas dominated by younger forest, hardwoods, or shrubs—as well as in areas with a high diversity of vegetation types—compared to what is available within owl home ranges. Conversely, we predicted that Spotted Owls would tend to capture flying squirrels in mature forests without selecting for edges or a diversity of vegetation types. Gathering data to assess this long-standing hypothesis could substantially enhance opportunities to promote habitat for prey species that support stable owl populations.

MATERIALS AND METHODS

Study Area

Our study took place in the central and northern Sierra Nevada in 2019 and 2020 on or immediately adjacent to two long-term California Spotted Owl monitoring areas,

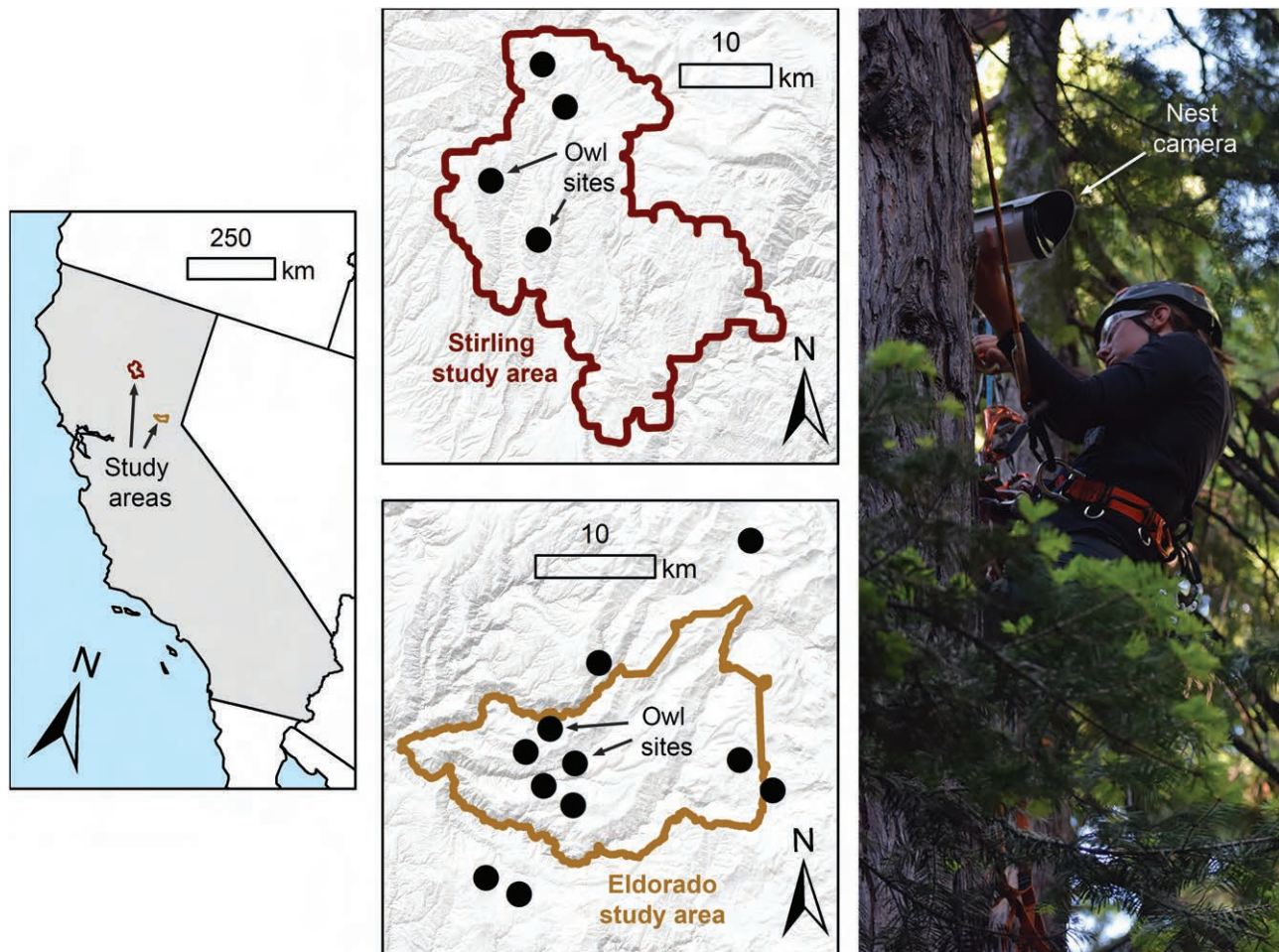


FIGURE 1. Map depicting the 15 locations where Spotted Owls were GPS tagged and video cameras were deployed in the Sierra Nevada, California, USA. Image on the right illustrates a camera installation adjacent to a California Spotted Owl nest.

the Eldorado Demography Study Area (EDSA) and Sierra Pacific Industries' Stirling Study Area (SSA) (Roberts et al. 2017, Hobart et al. 2019b; Figure 1). Elevation in the EDSA ranged from 366 to 2,257 m across 355 km² and elevations in the SSA ranged from 424 to 2,080 m across this 648 km² study area in mountainous terrain. The EDSA area was composed of ~60% public land managed by the U.S. Forest Service (USFS) and ~40% private land managed largely for commercial timber production, whereas the SSA was predominantly privately owned (81%). Forests on USFS-managed lands were typically a mix of mature forests and homogenous/dense forests dominated by small to medium-sized trees, sometimes containing residual large trees, owing to a history of fire-suppression and selective logging of large trees. Conversely, privately owned forests were a mixture of recent clear-felled areas (open and shrubby areas), tree plantations (densely stocked conifer stands), and forests similar to those on public lands. The vegetation on both study areas was typical of Sierran mixed-conifer forest dominated by the following

tree species: 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*). Tanoak (*Lithocarpus densiflorus*) formed a dense understory in some areas.

GPS Tagging

We located territorial breeding Spotted Owls as part of our routine monitoring surveys conducted annually on the EDSA and SSA (e.g., Roberts et al. 2017, Hobart et al. 2019b). Briefly, owls were located during call-based surveys at night and found during dawn/dusk surveys the following day to ascertain their reproductive status and locate nests (Franklin et al. 1996). Owls were fed live mice during follow-up surveys, which breeding owls then typically delivered to nest sites (Franklin et al. 1996).

We captured 15 nesting males (5 in 2019 and 10 in 2020) for GPS tagging using noose poles and "hand capture" (Wood et al. 2021). Females were not tagged

because they spend most of their time incubating eggs and brooding nestlings while nesting and relatively little time foraging (Forsman et al. 1984). Males were selected opportunistically for tagging based on the accessibility of the nest for video-monitoring (see below) throughout the nesting months (May to July) and the likelihood of recapture to remove transmitters. We affixed GPS tags (Alle-300, Ecotone, Poland) weighing 10 g and with remote downloading capability as tail mounts following methods described in Kramer et al. (2021) (Figure 1). We programmed tags to collect locations at 2-min intervals to characterize Spotted Owl nocturnal movements and ultimately identify prey capture locations (described below). We recaptured 5 individuals for a second deployment to increase the number of observations of prey captures. Following the final deployment, we attempted to recapture all owls to remove GPS tags; 2 individuals that were not recaptured were expected to molt during that season or the following season, thus shedding the GPS tag.

Nest Video Monitoring

We monitored prey deliveries using infrared (IR) video cameras placed at the nest sites of the 15 GPS-tagged males concurrent with the collection of GPS locations. To do so, we climbed a nearby adjacent tree (10–50 m from the nest tree) using a single rope technique and secured a video camera across from the nest tree (Figure 1). We monitored nests using AXIS Q1786–LE 4 megapixel outdoor IR video cameras that continuously recorded high-quality video throughout the nocturnal foraging period that coincided with GPS tag data collection (2000 to 0630 Pacific Daylight Time). We reviewed each video to detect and identify the different prey species delivered to each nest.

Identifying Prey Capture Locations

We located successful foraging sites (hereafter “prey capture locations”) by visually identifying tight clusters of GPS points followed immediately by a straight flight path back to the nest tree (Marsh et al. 2014, Wood et al. 2021). We defined a prey capture location as a cluster of up to 10 GPS points (within the 20 min prior to movement back to the nest), all within 250 m of one another based on that likely being the maximum hunting radius of a perched owl (S. A. Whitmore personal observation). If the two farthest points were >250 m apart, we removed the oldest point (the first point that defined the prey capture location) and continued to remove the points until they were all within 250 m of one another. Each cluster of points was transformed into a minimum convex polygon (mean: 0.38 ha, range: 0.002–2.713 ha) surrounding the cluster and assumed to represent the prey capture location. Although this approach, including the criterion of <250 m among pairs

of points, was somewhat subjective in that it was based on field observations, it was repeatable and typically yielded tight, defined clusters of points (compared to the distribution of owl GPS points overall) followed by distinct straight-line movements back to the nest site (Figure 2). We then matched the time stamp of the video with the time stamp of the GPS return to the nest to link the species of prey to its putative capture location (Figure 2). The area contained by the minimum convex polygon of these GPS points that matched with a prey delivery caught on video was defined as a prey capture location. Three prey capture locations were excluded from the analysis because they likely represented the retrieval of prey from a cache site. We suspected these deliveries to be from a cache location because of their close proximity to the nest site (within 50 m) and the early timing of the delivery (all 3 instances were the first delivery of the night and occurred before sunset), which both indicated a cache delivery (S. A. Whitmore, personal observation).

Vegetation Classification

We visually interpreted aerial imagery from the National Agriculture Imagery Program (NAIP) collected in 2018 and 2020 to characterize vegetation conditions within prey capture locations (as well as random locations, see below) following methods developed and described by Tempel et al. (2014) that typically results in >80% classification accuracy. Specifically, we considered 10 possible vegetation classes based on species composition, canopy cover, and the size of the dominant trees that was largely based on the California Wildlife Habitat Relationships system (Mayer and Laudenslayer 1988) (Table 1). Areas classified as hardwood typically represented patches of black oaks, with tanoaks in the understory typically being obscured by overstory conifer trees and thus not measured. We digitized polygons around relatively homogenous areas of vegetation with a minimum mapping unit of 20 m² and then classified the area within the polygon as 1 of the 10 vegetation classes.

Prey Capture Analysis

We used mixed-effects resource-selection functions (RSFs) to test for the selection of forest structural characteristics (Table 1) and several derived covariates, described below. First, we fit a model that included data from all prey (species pooled together) to examine habitat characteristics of prey capture locations and whether and how these locations differed in forest structure compared to random locations within the home range. Second, we fit models that included only data from either of the owl's 2 primary prey items—flying squirrels and woodrats (see below)—to characterize

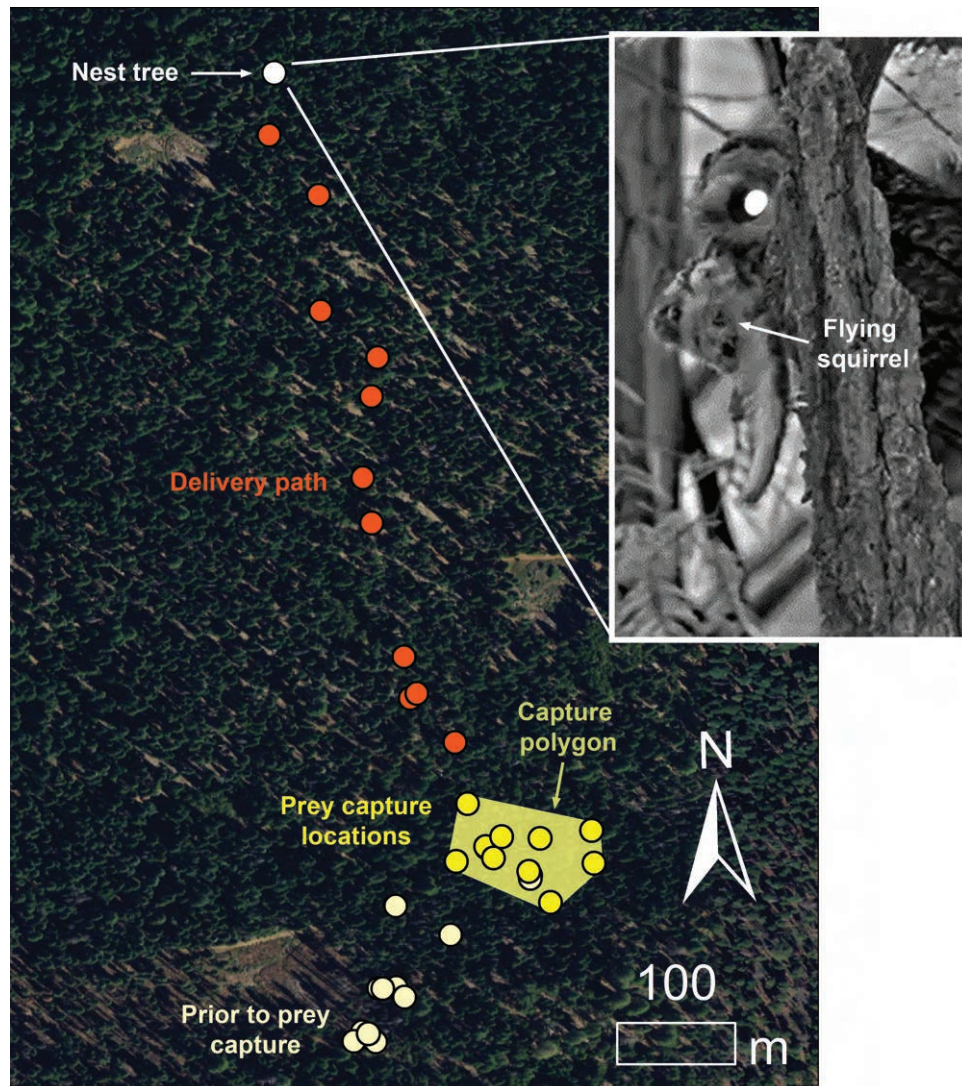


FIGURE 2. Map showing a sequence of Spotted Owl GPS locations preceding a prey delivery, and an image of the subsequent prey delivery at the nest. The prey delivery image is a single frame from an infrared camera mounted in a tree 10 m from the nest tree and shows the delivery of a flying squirrel to the nest. The approximate location of the capture can be inferred from the cluster of GPS locations before the owl's nearly direct flight back to the nest.

the forests where owls caught these 2 important prey species.

The RSFs relied on a use-availability framework to compare habitat characteristics at used locations to randomly generated available locations within a Spotted Owl's home range (Manly et al. 2002). Intercepts within the model varied by individual to account for correlation and unequal sample sizes (Muff et al. 2020). Models with random slopes (Muff et al. 2020) failed to converge; therefore, our models included only fixed covariate effects. For this analysis, a used location refers to the area within a prey capture location (explained above). We generated 5 corresponding available areas for each used area, where the size and shape of the available polygon were identical to that of the used

polygon. Spotted Owl home ranges were estimated using 95% fixed-kernel density estimators (KDE; Seaman and Powell 1996). Each available polygon was centered on a random location within the given owl's home range and rotated to a random orientation. To account for GPS error and potential neighborhood effects of surrounding habitat, we buffered all used and available polygons by 50 m. Available polygons were assigned a high weight ($W = 1000$) to facilitate approximate convergence to the inhomogeneous Poisson process likelihood (following Muff et al. 2020). We fitted RSFs using the R package "glmmTMB," version 3.6.3 (Brooks et al. 2017).

Our model covariates (fixed effects) included the proportion of each polygon containing various vegetation

TABLE 1. Vegetation classes used to characterize forest conditions used by Spotted Owls in the Sierra Nevada, California, USA.

Vegetation class	Description	Diameter at breast height (cm)	Canopy cover (%)
1	Hardwoods	N/A	>50 hardwood
2	Shrubs	<15.2	N/A
3	Young forest	15.2–30.4	N/A
4	Medium trees/medium canopy cover	30.5–60.9	30–69
5	Medium trees/high canopy cover	30.5–60.9	≥70
6	Large trees/medium canopy cover	≥61.0	30–69
7	Large trees/high canopy cover	≥61.0	≥70
8	Water or barren rock ^a	N/A	N/A
9	Medium or large trees/low canopy cover ^a	≥30.5	<30
10	Road ^a	N/A	N/A

^aNot included in resource selection models.

characteristics derived from NAIP imagery (Table 1) and the Shannon diversity index of the proportional contribution of those vegetation characteristics (i.e. heterogeneity). We excluded 3 vegetation classes (water or barren rock, medium/large trees with very sparse canopy cover, and road) given their rarity. We also included the total length of edges between hardwood, young forest, and shrubs with the other adjacent forest cover classes used in the analysis (Table 1) because these ecotones may provide owls with access to their most energetically profitable prey, the dusky-footed woodrat (*Neotoma fuscipes*), which are often most common in these 3 habitat types (Sakai and Noon 1993, 1997). Distributions of covariate values for both used and available prey capture locations are presented in Supplementary Material Figures S1 and S2. The size of buffered prey capture locations varied from 0.93 to 6.77 ha, so we also included a covariate for polygon area to control for potential area effects. We included an interaction term between percent public land and large trees/high canopy cover within owl home ranges to examine whether selection of this key forest type differed as a function of ownership given the different forest management approaches on public and private land.

We tested for collinearity among model covariates using the Pearson's correlation coefficient with a threshold of $r = 0.6$. If 2 variables were correlated where $r > 0.6$, we retained the variable that we assumed was more biologically informative. We z -standardized all continuous covariates. When making inferences about statistical relationships, we evaluated the direction of the effect (positive or negative), the effect size (biological magnitude), and uncertainty (95% confidence intervals [CIs]). However, we did not interpret the “statistical significance” of effects because the use of arbitrary thresholds based on P -values is problematic (Amrhein et al. 2019). Therefore, we sometimes made inferences about statistical relationships with P -values greater than 0.05 (but not greater than 0.1) to avoid accepting a false null hypothesis and therefore ignoring variables that were potentially biologically meaningful (Fidler et al. 2006).

We used odds ratios to aid our interpretation of the effects of vegetation classes on Spotted Owl prey capture location selection. For vegetation classes (i.e. non-edge categories), we scaled the odds ratio to represent a change in odds of selection for a 10% increase in that vegetation class. For edge categories, we scaled odds ratios to represent the change in odds of selection for an increase of 10 m ha⁻¹ of edge. For example, we interpreted an odds ratio of 1.2 for “medium trees/medium canopy cover” as follows: each 10% increase in medium tree/medium canopy cover forest was associated with a gain in the odds of prey capture by a factor of 1.2 (or a 20% increase in the odds).

RESULTS

We acquired 33,056 usable nocturnal GPS locations from the 15 tagged males after culling locations taken below 3.7 voltage that typically have greater positional error (S. A. Whitmore personal communication). We identified 127 prey capture locations, of which we were able to identify specific prey species using video monitoring for 91 (72%). Spotted Owls captured 43 dusky-footed woodrats, 29 Humboldt flying squirrels, 11 white-footed mice (*Peromyscus* spp.), 3 voles (*Microtus* spp.), 2 moles (*Scapanus* spp.), 2 Botta's pocket gophers (*Thomomys bottae*), and 1 bird (Order: Passeriformes). These patterns reinforced the importance of woodrats and flying squirrels as primary Spotted Owl prey and supported only conducting species-specific resource selection analyses for these 2 prey species.

All Prey Capture Analysis

All vegetation classes were present in prey capture locations, but Spotted Owls tended to capture more prey in areas with forests characterized by more medium trees/medium canopy cover forest ($\beta = 0.41$, 95% CI: 0.10 to 0.71, $P = 0.009$), more large trees/medium canopy cover forest ($\beta = 0.41$, 95% CI: 0.18 to 0.64, $P = 0.0004$), more large trees/high canopy cover forest ($\beta = 0.61$, 95% CI: 0.07 to 1.14, $P = 0.02$) and along hardwood edges

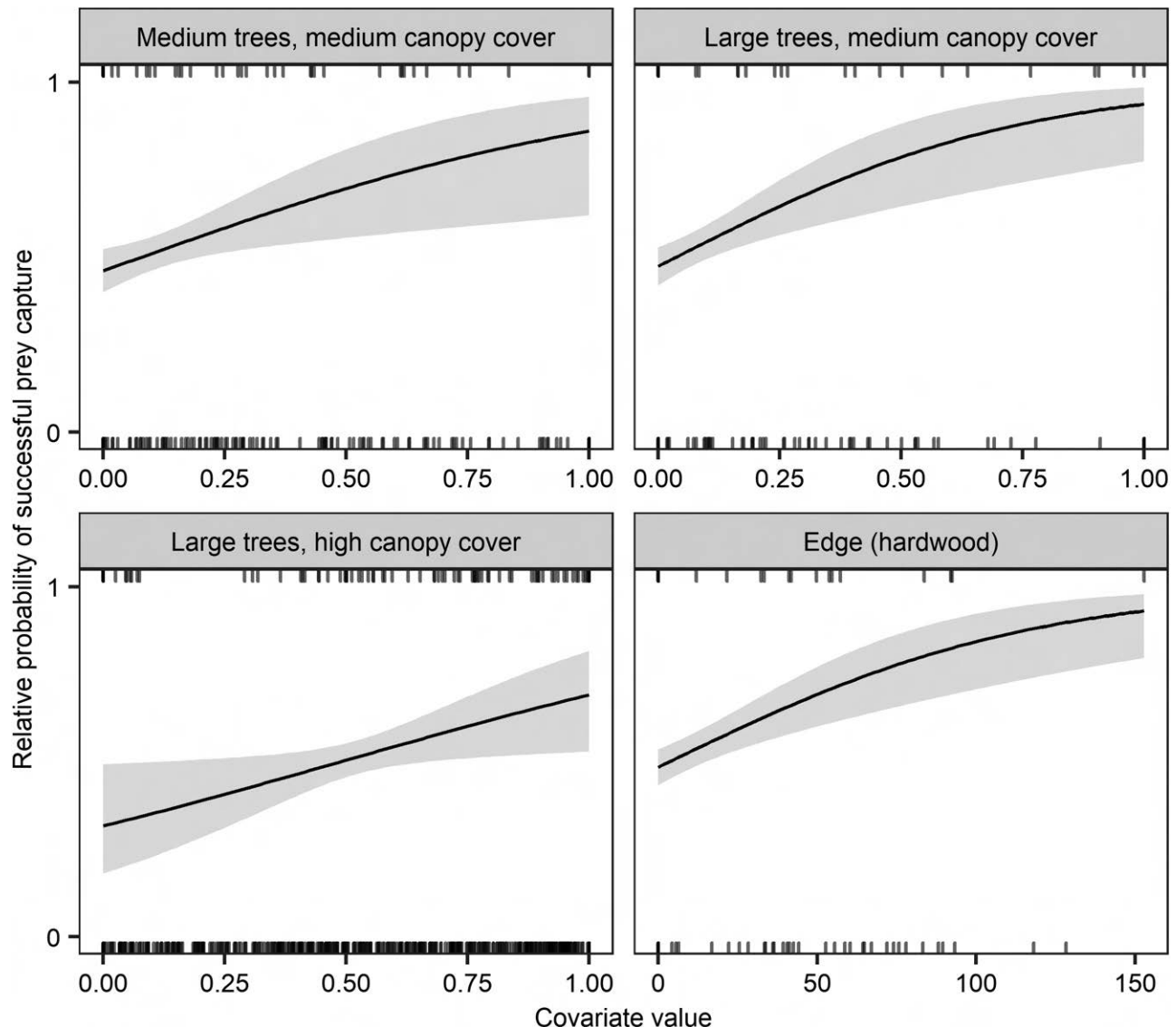


FIGURE 3. Relative probability of prey captures (with shaded areas representing 95% confidence intervals) as a function of habitat conditions for foraging Spotted Owls. Covariate values for prey capture and random polygons are visualized as rug plots at the top and bottom of each panel, respectively.

($\beta = 0.27$, 95% CI: 0.13 to 0.40; $P < 0.0001$) (Figure 3). Odds ratios indicated that with each 10% increase in medium trees/medium canopy cover forest, the odds of prey capture increased by a factor of 1.20 (i.e. a 20% increase in odds). The odds of prey capture increased by a factor of 1.30 and 1.16 with each 10% increase in large trees/medium canopy cover forest and large trees/high canopy cover forest, respectively. Lastly, odds of prey capture increased by a factor of 1.12 with every additional 10 m ha⁻¹ of hardwood edge.

Woodrat Capture Analysis

Spotted Owls tended to capture woodrats in areas with more young forest ($\beta = 0.55$, 95% CI: -0.01 to 1.12,

$P = 0.056$), more medium trees/medium canopy cover forest ($\beta = 0.62$, 95% CI: -0.02 to 1.27, $P = 0.06$), more large trees/medium canopy cover forest ($\beta = 0.71$, 95% CI: 0.24 to 1.19, $P = 0.003$), more large trees/high canopy cover forest ($\beta = 1.96$, 95% CI: 0.83 to 3.09, $P = 0.0007$), in areas with a higher density of hardwood edges ($\beta = 1.29$, 95% CI: 0.53 to 2.04, $p = 0.0008$), and areas with higher forest heterogeneity ($\beta = 0.48$, 95% CI: -0.02 to 1.00, $P = 0.06$; Figure 4). Odds ratios indicated that the odds of prey capture increased by a factor of 1.39 with every 10% increase in young forest and by a factor of 1.33 with every 10% increase in medium trees/medium canopy cover forest. The odds of prey capture increased by a factor of 1.60 with every 10% increase in large trees/medium canopy cover forest and 1.61 with

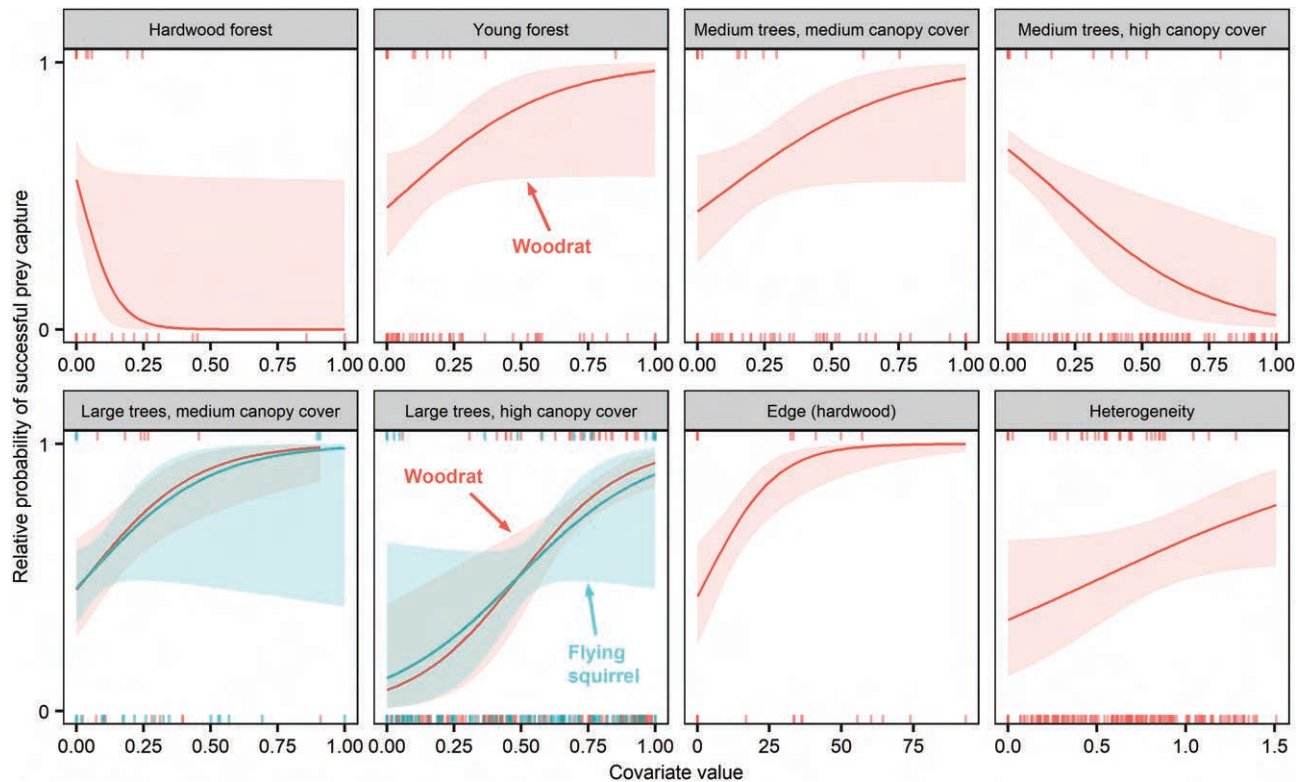


FIGURE 4. Relative probability of woodrat and flying squirrel captures (with shared areas representing 95% confidence intervals) as a function of habitat conditions for foraging Spotted Owls. Covariate values for prey capture and random polygons are visualized as rug plots at the top and bottom of each panel, respectively.

every 10% increase in large trees/high canopy cover forest. Each 10 m ha⁻¹ increase in hardwood edge increased the odds of prey capture by a factor of 1.73, and each 10% increase in cover type heterogeneity increased the odds of prey capture by a factor of 1.22.

Spotted Owls were less likely to capture woodrats in areas with more hardwoods ($\beta = -1.27$, 95% CI: -2.47 to -0.06 , $P = 0.049$; Figure 4). The odds of prey capture decreased by a factor of 0.24 (or a 4.2-fold decrease) with each 10% increase in hardwood forest. Spotted Owls also tended to avoid areas characterized by medium trees/high canopy cover forest when capturing woodrats ($\beta = -1.13$, 95% CI: -1.85 to -0.41 , $P = 0.002$; Figure 4). The odds of prey capture decreased by a factor of 0.71 (or a 1.4-fold decrease) with each 10% increase in medium trees/high canopy cover forest.

Flying Squirrel Habitat Selection Analysis

Spotted Owls tended to capture flying squirrels in areas with more, large tree/medium canopy cover forest ($\beta = 0.63$, 95% CI: -0.09 to 1.36 , $P = 0.09$) and more large tree/high canopy cover forest ($\beta = 1.56$, 95% CI: -0.23 to 3.36 , $P = 0.09$; Figure 4). The odds of prey capture increased by a factor of 1.51 with every 10% increase in large trees/medium canopy cover forest and increased by a factor of

1.65 times for each 10% increase in larger trees/high canopy cover forest. Unlike the “all prey” and “woodrat” analyses, we found evidence of a negative interaction between ownership and large trees/high canopy cover forest for flying squirrels ($\beta = -0.42$, 95% CI: -0.91 to 0.06 , $P = 0.09$). The odds of flying squirrel prey capture increased by a factor of 1.65 with each 10% increase in large trees/high canopy cover forest when no public land was present, but weakened by a factor of 1.25 when all land in an owl’s home range was public. Example capture locations illustrating areas with high values for selected covariates are provided in Figure 5.

DISCUSSION

We leveraged recently developed GPS tagging technologies to identify capture sites of different prey species for Spotted Owls, which led to novel inferences and implications for species conservation and forest management. Importantly, several of the habitats that promoted the capture of one prey species (woodrats), such as forest heterogeneity and young forests, were not identified as informative covariates in RSFs when all prey species were considered jointly. Thus, our work builds on the findings of Marsh et al. (2014) who found that RSFs for predators including all GPS points do

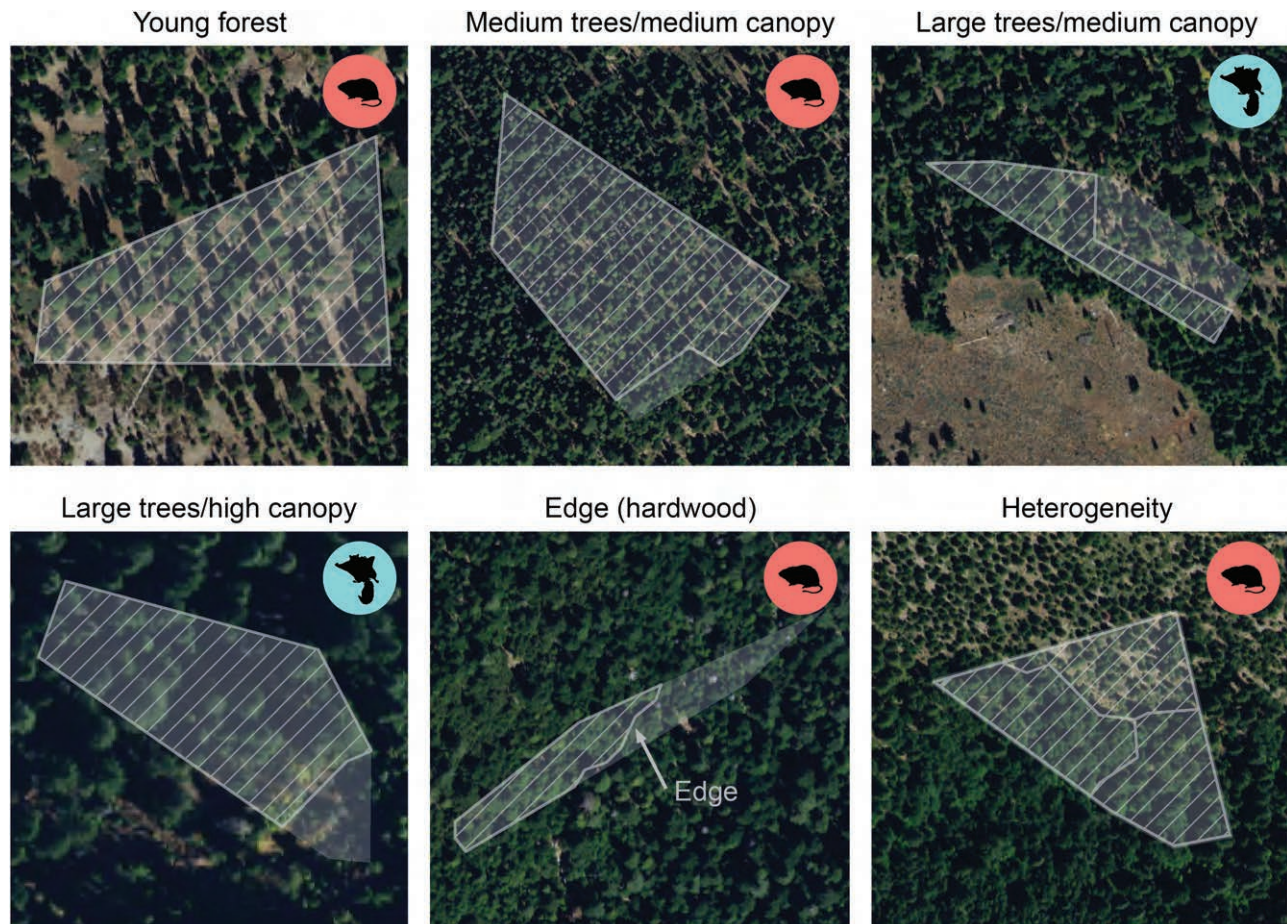


FIGURE 5. Example polygons where Spotted Owls captured either a woodrat or flying squirrel. The capture polygon is the entire shaded area, while the areas in each capture polygon containing the focal covariate (noted above each panel) are illustrated with cross-hatching. The relevant covariate value for the “edge (hardwood)” panel is the length of the internal line between the cross-hatched area (representing hardwood forest) and the shaded area (other cover types). The “heterogeneity” panel shows a mixture of three cover types (separated by thick lines) within a single capture polygon.

not necessarily reveal habitat types that confer successful prey capture. Had we not ascertained the species identity of individual prey items using nest video monitoring, we would not have identified young forests as an important habitat type, nor forest heterogeneity as important for the capture of woodrats by Spotted Owls. Such a limitation could lead to sub-optimal habitat management, given that the consumption of woodrats—a large and energetically profitable prey species—has been closely and positively linked to population-level density, reproductive rates, and territory occupancy rates of Spotted Owls (Smith et al. 1999, Hobart et al. 2019a). Indeed, the fact that previous GPS and VHF telemetry studies of Spotted Owls have been conducted without specifically accounting for prey capture locations, or linking the capture locations to the species of those prey, could account for the fact that these features are often not found to be selected by owls (Call et al. 1992). Accordingly, when practical, we encourage future studies of predator habitat selection to not only distinguish

successful prey capture from other locations (e.g., resting, commuting, territorial defense) but also to discriminate among the capture of different prey species so key ecological relationships are not obscured. Studies of prey delivery rates and/or biomass of different prey types are critical to building a more complete picture of the foraging needs and tradeoffs of nesting Spotted Owls.

Whereas we have known for many decades that Spotted Owls preferentially use mature forest for nesting, roosting, and foraging (Gutiérrez et al. 2020), more recent work has indicated the importance of other habitat types (e.g., Call et al. 1992, Atuo et al. 2019, Kramer et al. 2021). These different habitat preferences can perhaps be explained by our results, which demonstrate that successful hunting—particularly for woodrats—tends to occur in a broad range of conditions, including in areas with more young forest and higher heterogeneity. Thus, our results may partially explain observations of high owl densities on some private lands (which include young forest and higher

heterogeneity; Roberts et al. 2017), as well as the potential for life-history tradeoffs hypothesized to occur owing to forest heterogeneity (Franklin et al. 2000). In addition, the finding that Spotted Owls tended to not capture woodrats in areas with medium trees and high canopy cover supports previous stable isotope analyses demonstrating that owls with relatively high proportions of this forest type in their territories consume fewer woodrats, which can lead to lower territory occupancy rates and landscape-scale density (Hobart et al. 2019a). Similarly, the higher likelihood of woodrat capture in areas of high heterogeneity and young forests supports stable isotope analyses suggesting that these conditions promote woodrats that are then more available to owls (Hobart et al. 2019a)—and that young forests with a hardwood component can increase Spotted Owl reproductive success presumably because they promote populations of this energetically valuable prey species (Hobart et al. 2019b). Thus, our resource selection analysis appears to provide a mechanistic explanation for previously observed population-level phenomena in Spotted Owls.

Habitats that conferred successful prey captures by Spotted Owls likely did so by promoting hunting efficiency, high prey densities, access to areas with high prey densities, or some combination of these processes. Spotted Owls, as ambush predators, may have increased hunting efficiency due to a prevalence of suitable perching structures characteristic of mature forests with substantial vertical heterogeneity in tree height that conferred relatively high hunting success for multiple prey species (North et al. 1999). Further, forests with larger trees, and thus taller canopies, can harbor higher densities of flying squirrels due to accessibility to denning options and suitable microclimate conditions for lichen and hypogeous fungi—key food resources of flying squirrels (Waters and Zabel 1995). Spotted Owls may have rarely captured woodrats in medium tree forests with high canopy cover because of sparse shrub cover (due to reduced sunlight reaching the understory), which represents a key feature of woodrat habitat; conversely, owls may have selected for medium tree forests with medium canopy cover because of a more robust shrub component and denser woodrat populations. Furthermore, higher landscape heterogeneity in cover types may increase flying squirrel densities in remnant mature forests (Sollmann et al. 2016) and therefore might increase hunting success by owls in those areas. This could partly explain our result (Figure 6) of a stronger selection of large tree forests with high canopy cover in areas with more private lands, where mature forests occur in more discrete units and are surrounded by a greater variety of cover types. High woodrat capture success in young forests was likely the result of what can be very high woodrat densities in this forest type (Sakai and Noon 1993, Hamm and Diller 2009). While we originally predicted that edges between young forests and

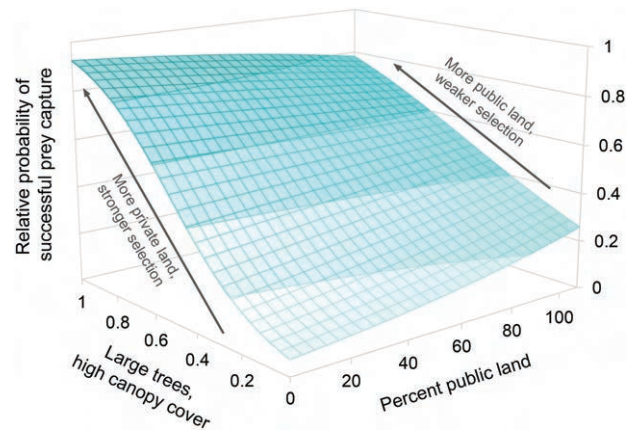


FIGURE 6. Relative probability of flying squirrel capture as a function of an interaction between large trees/high canopy cover forest and percentage of public land in a home range. The interaction term shows that positive selection for large tree forests with high canopy cover tends to weaken (though remains positive) for owls that have more public land in their 95% kernel density estimated (KDE) home range.

forests with medium and large trees would confer higher woodrat capture success by providing owls access to high-density woodrat areas (Sakai and Noon 1993), some young forests perhaps contained sufficient perching structures in the form of residual old trees or other structures (Atuo et al. 2019). Conversely, woodrats were captured less frequently in hardwood forests, which can also contain high densities of woodrats (Sakai and Noon 1993), whereas edges between hardwood and coniferous-dominated forests promoted woodrat captures by owls—consistent with our predictions. This finding suggests that hardwood forests may not provide suitable foraging structures but do appear to provide a source of woodrats for Spotted Owls foraging along the edge of hardwood and conifer forests as was hypothesized several decades ago (Sakai and Noon 1993). In this study, areas of forest classified as hardwood were generally patches of black oaks, with tanoaks in the understory typically being obscured by overstory conifer trees and thus not measured—yet are also likely potential sources of woodrats for Spotted Owls (Sakai and Noon 1993).

Our study demonstrates the opportunity to promote the conservation of Spotted Owls through habitat management. By understanding the specific habitat types and configurations that confer hunting success during a critical life-history period (the provisioning of young in nests and dens), management actions can promote higher prey densities in areas where capture is likely. Numerous predators have become endangered because of direct exploitation (Carter et al. 2017), yet declines in prey resources that reduce reproduction (Becker and Beissinger 2006), as well as indirect effects associated with anthropogenic habitat change (Hanski 2011),

can also cause species declines. Hence, enhancing the habitat of key prey species, especially large-bodied or nutritionally important ones that promote individual fitness components and population density, hold promise for recovering endangered predators. Recent advances in very small GPS packages with high accuracy, combined with video-based breeding site monitoring, now make fine-scale studies practical for a broader suite of predators, including small-bodied and cryptic ones (Studd et al. 2021, Wood et al. 2021). Such investigations will certainly be fruitful in forested systems such as the one studied here, but similar opportunities also exist in other terrestrial and aquatic ecosystems.

Several findings in this study point to co-benefits between Spotted Owl conservation and forest management activities intended to reduce forest fuels, two objectives often seen as diametrically opposed in a region experiencing megafires without modern precedent that can lead to Spotted Owl population losses (Jones et al. 2016, 2021). First, the selection of forests with large trees for the capture of both key prey species underscores that these structures are both “ecological backbones” of dry forests and a key component of foraging habitat for mature forest species such as Spotted Owls (Hessburg et al. 2015). Second, Spotted Owls tended not to capture woodrats in forests characterized by medium trees and high canopy cover, a forest type that is often synonymous with the historical legacy of fire exclusion and selective large tree removal in the dry forest ecosystems in western North America, which are now at great risk of large severe fires (Peery et al. 2017). Thus, promoting large tree recruitment and creating canopy openings in such forests as part of management activities could enhance the ability of Spotted Owls to capture and consume woodrats and lead to population-level benefits. Such forests could benefit Spotted Owls even prior to large tree recruitment given that medium tree forests with medium canopy cover tended to promote successful woodrat hunting. Further, promoting heterogeneous forests characterized by a mosaic of mature and younger forests, as well as a mixture of conifer and hardwood species, could both reduce severe fire risk and benefit Spotted Owls and other taxa.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement: Data collectors were trained in the responsible handling of birds following our IACUC (Institutional Animal Care and Use Committee) protocol # A005367-R02 and were authorized from California Department of Fish and Wildlife’s scientific collection permit (S-193180001-19324-001) and under USGS Bird Banding Lab permit # 23685 before undertaking the work. We also adhered to the University of Wisconsin–Madison Responsible Conduct of Research policy in carrying out this work.

Conflict of interest statement: The authors declare no conflict of interest.

Author contributions: J.J.K., K.N.R., B.P.D., S.C.S., and M.Z.P. conceived the idea, design, experiment (supervised research, formulated question or hypothesis). C.J.Z. performed the experiments (collected data, conducted the research). C.J.Z., H.A.K., G.M.J., and M.Z.P. developed or designed statistical methods. C.J.Z., H.A.K., G.M.J., A.K.W., and M.Z.P. analyzed the data. All authors contributed to writing the or substantially editing the paper.

Data availability: Analyses reported in this article can be reproduced using the data provided by Zulla et al. (2022).

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