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SYNTHESIS & INTEGRATION

Spotted Owls and forest fire: a systematic review and meta-analysis of the evidence

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Citation: Lee, D. E. 2018. Spotted Owls and forest fire: a systematic review and meta-analysis of the evidence. Ecosphere 9(7):e02354. 10.1002/ecs2.2354

Abstract. Forest and Spotted Owl management documents often state that severe wildfire is a cause of recent declines in populations of Spotted Owls and that mixed-severity fires (5–70% of burned area in high-severity patches with >75% mortality of dominant vegetation) pose a primary threat to Spotted Owl population viability. This systematic review and meta-analysis summarize all available scientific literature on the effects of wildfire on Spotted Owl demography and ecology from studies using empirical data to answer the question: How does fire, especially recent mixed-severity fires with representative patches of high-severity burn within their home ranges, affect Spotted Owl foraging habitat selection, demography, and site occupancy parameters? Fifteen papers reported 50 effects from fire that could be differentiated from post-fire logging. Meta-analysis of mean standardized effects (Hedge's *d*) found only one parameter was significantly different from zero, a significant positive foraging habitat selection for low-severity burned forest. Multi-level mixed-effects meta-regressions (hierarchical models) of Hedge's *d* against percent of study area burned at high severity and time since fire found the following: 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; reproduction was positively correlated with 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. Meta-analysis of variation found significantly greater variation in parameters from burned sites relative to unburned, with specifically higher variation in estimates of occupancy, demography, and survival, and lower variation in estimates of selection probability for foraging habitat in low-severity burned forest. Spotted Owls were usually not significantly affected by mixed-severity fire, as 83% of all studies and 60% of all effects found no significant impact of fire on mean owl parameters. Contrary to current perceptions and recovery efforts for the Spotted Owl, mixed-severity fire does not appear to be a serious threat to owl populations; rather, wildfire has arguably more benefits than costs for Spotted Owls.

Key words: adaptive management; evidence-based decision making; meta-analysis; mixed-severity fire; Spotted Owls; *Strix occidentalis;* systematic review; wildfire.

Received 22 April 2018; revised 1 June 2018; accepted 11 June 2018. Corresponding Editor: Joseph A. LaManna.

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Introduction

Wildfires are major natural disturbances in forests of the western United States, and native plants and animals in this region have been coexisting with fire for thousands of years of their evolutionary history (Pierce et al. 2004, Power et al. 2008, Marlon et al. 2012). Western forest fires typically burn as mixed-severity fires with each fire resulting in a mosaic of different vegetation burn severities, including substantial patches (range, 5–70% of burned area; mean, 22%) of high-severity fire (Beaty and Taylor 2001, Hessburg et al. 2007, Whitlock et al. 2008, Williams and Baker 2012, Odion et al. 2014*a*, Baker 2015*a*). High-severity fire (high vegetation burn severity) kills most or all of the dominant vegetation in a stand (>75% mortality; Hanson et al. 2009, Baker 2015*a*, *b*) and creates complex early seral forests, where standing dead trees, fallen logs, shrubs, tree seedlings, and herbaceous plants comprise the structure (Swanson et al. 2011, DellaSala et al. 2014). Post-fire vegetation processes (i.e., succession) then commence according to the pre-fire vegetation, local wildfire processes, propagules from outside the disturbance, and the dynamic biotic and abiotic conditions at the site (Gutsell and Johnson 2006, Johnson and Miyanishi 2006, Mori 2011).

Spotted Owls (*Strix occidentalis*) occur in western U.S. forests and have been intensively studied since the 1970s (Fig. 1). The species is strongly associated with mature and old-growth (i.e., late-successional) conifer and mixed conifer–hardwood forests with thick overhead canopy and many large live and dead trees and fallen logs (Gutiérrez et al. 1995). Its association with older forests has made the Spotted Owl an important umbrella indicator species for public lands management (Noon and Franklin 2002). The scientific literature has established that the optimal habitat for Spotted Owl nesting, roosting, and foraging is provided by conifer and mixed conifer–hardwood forests dominated by medium (30–60 cm) and large (>61 cm) trees with medium (50–70%) to high (>70%) canopy cover (Gutiérrez et al. 1995). The populations of all three subspecies have declined due to widespread historical and ongoing habitat loss, primarily from logging mature and old-growth forests favored by the owls for nesting and roosting (Seamans et al. 2002, Forsman et al. 2011, USFWS 2011, 2012, Conner et al. 2013, Tempel and Gutiérrez 2013, Dugger et al. 2016).

Research on Spotted Owl in fire-affected landscapes did not begin until the early 2000s, and much of what scientists previously understood about habitat associations of Spotted Owl was derived from studies in forests that had generally not experienced recent fire, and where the non-suitable owl habitat was a result of logging (Gutiérrez et al. 1992, Franklin et al. 2000, Seamans et al. 2002, Blakesley et al. 2005, Seamans and Gutiérrez 2007, Forsman et al. 2011, Tempel et al. 2014). Because Spotted Owls are associated with dense, late-successional forests, it has often been assumed that fires that burn at high severity are analogous to clear-cut logging and have a negative effect on population viability. It has become widely believed among wildlife management professionals that severe wildfire is a contributing cause of recent Spotted Owl population declines (USFWS 2011, 2012, 2017), and many land managers believe that forest fires currently pose the greatest risk to owl habitat and are a primary threat to population viability (Davis et al. 2016, Gutiérrez et al. 2017). These beliefs result in fuel-reduction logging projects in Spotted Owl habitat (USDA 2012, 2018) which the USDA Forest Service and US Fish and Wildlife Service state are actions consistent with Spotted Owl recovery (USDA 2012, 2018, Gutiérrez et al. 2017, USFWS 2017). Narrative literature reviews have attempted to summarize the effects of fire on Spotted Owl (Bond 2016, Gutiérrez et al. 2017), but evidence-based conservation decisions should be based upon systematic, transparent reviews of primary literature with quantitative meta-analysis of effects (Sutherland et al. 2004, Pullin and Stewart 2006, Pullin and Knight 2009, Koricheva et al. 2013).

The following systematic review and meta-analysis summarize all available published scientific literature on the effects of wildfire on aspects of Spotted Owl demography (survival, recruitment, and reproduction), site occupancy, and habitat selection, from studies using empirical data to answer the question: How does fire, especially mixed-severity fire with substantial patches of high-severity fire within their home ranges, affect Spotted Owl demography, site occupancy, and habitat selection in the first few post-fire years?

Methods

Literature search

I conducted a systematic review of the primary scientific literature and used meta-analyses and meta-regression to examine the evidence for the direct effects of wildfire on Spotted Owl demography, site occupancy, and habitat selection. My subject was Spotted Owls; the intervention was

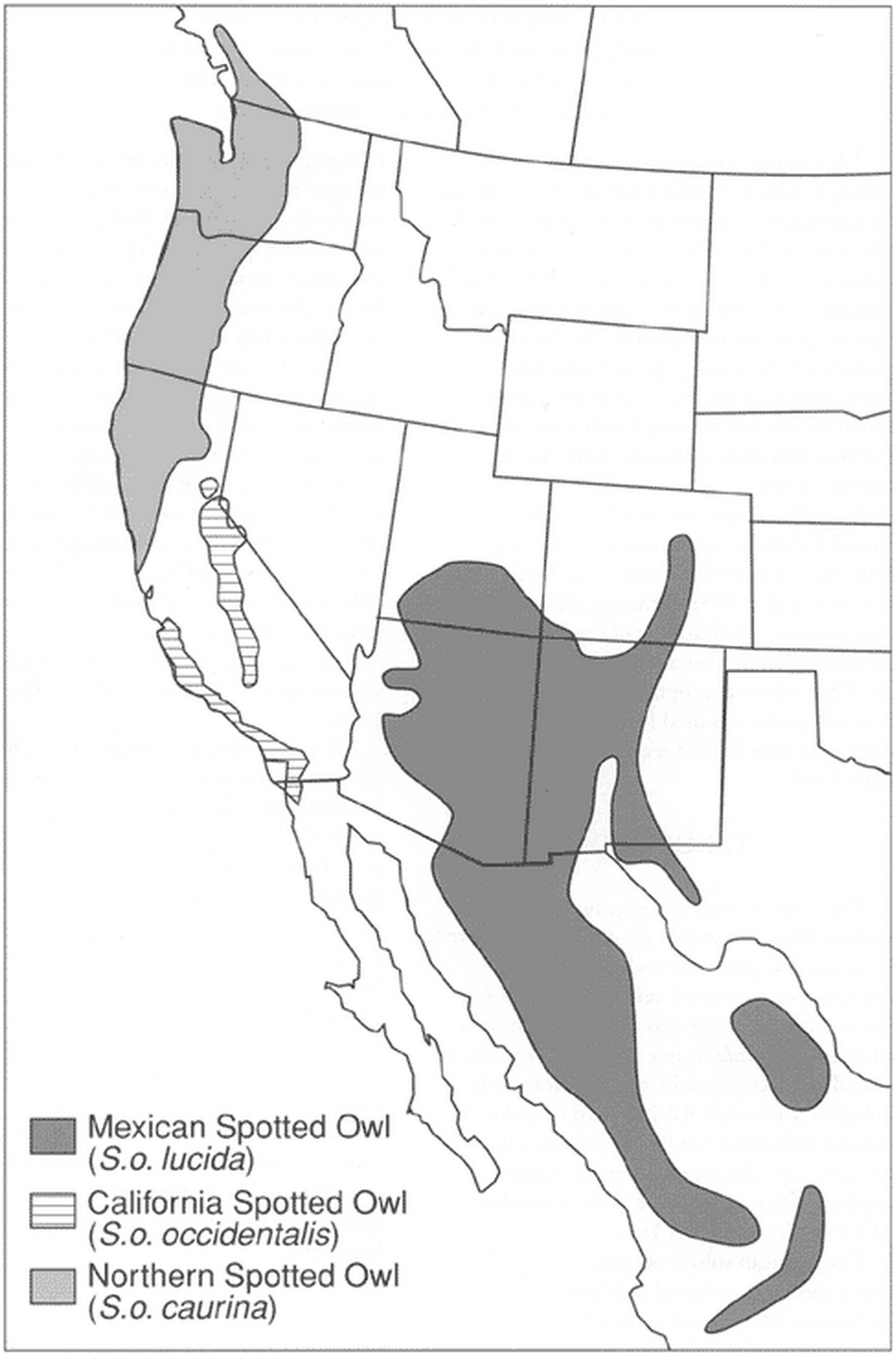

Fig. 1. Range map for the three subspecies of the Spotted Owl (*Strix occidentalis*).

wildfire; the outcomes were change or difference in estimates of demography, site occupancy, and habitat selection probabilities; and the comparator was pre-fire estimates or control estimates from unburned areas (Pullin and Stewart 2006). I searched the following electronic databases on 1 April 2018: Agricola, BIOSIS Previews, ISI Web of Science, and Google Scholar. Search terms were as follows: spotted AND owl AND *fire, Strix AND occidentalis AND *fire. My search included papers published in any year.

I used a threefold filtering process for accepting studies into the final systematic review. Initially, I filtered all articles by title and removed any obviously irrelevant material from the list of articles found in the search. Subsequently, I examined the abstracts of the remaining studies with regard to possible relevance to the systematic review question, using inclusion criteria based on the subject matter and the presentation of empirical data. I accepted articles for viewing at full text if I determined that they may contain information pertinent to the review question or if the abstract was ambiguous and did not allow inferences to be drawn about the content of the article. Finally, I read all remaining studies at full text and either rejected or accepted into the final review based upon subject matter (Pullin and Stewart 2006, Koricheva et al. 2013). Studies that only modeled effects of simulated fires on Spotted Owl habitat and demography were not considered here.

Because post-fire logging often occurred, I also recorded effects of this disturbance where they were reported. I believe all studies in the final review were generally comparable because time since fire and percent of high-severity burn were similar among studies (Tables 1, 2), and the high number of non-significant results reported indicates little to no publication bias exists in this topic (Tables 1, 2; Appendix S1: Fig. S1). I considered the basic sampling unit of all studies to be the central core of the owl breeding-season territory (~400 ha, or a circle with radius 1.1 km centered on the nest or roost stand) because this is the spatial and temporal scale for sampling used in almost all Spotted Owl studies. In contrast, Spotted Owl year-round home ranges vary according to latitude and dominant vegetation, but range from 300 to 11,000 ha, or circles with radius 1.0–5.9 km (Zabel et al. 1992). I considered forest fires to affect the landscape scale (~10,000 ha/decade), but that fires would affect numerous individual owl breeding-season territories (1200 ha) and year-round home ranges (300–19,000 ha) in various ways.

Meta-analyses and meta-regression

I evaluated all final review papers and included all papers where effects of fire were reported and could be differentiated from other disturbances such as post-fire logging. I extracted evidence by reading every paper and tabulating all quantified results from text, tables, and figures (Table 1). I noted the mean ($\bar{x}$) and variation (SD) of burned and unburned groups for all significant and non-significant parameters, the parameters being estimated, sample sizes (n = number of owl breeding sites in burned and unburned groups), amount of high-severity fire in the total fire perimeter and/or within the owl territory core areas examined, time since fire (years), amount of post-fire logging that occurred, subspecies (California = *Strix occidentalis occidentalis*, Mexican = *Strix occidentalis lucida*, or northern = *Strix occidentalis caurina*), and whether the result was statistically significant (as defined in each paper).

I conducted all analyses in R 3.3.1 (www.r-project.org). For meta-analysis, I noted or calculated the mean, variance (SD), and sample size for burned (treatment) and unburned (control) groups. I calculated raw effect sizes as mean differences ($\bar{x}_{\text{burned}} - \bar{x}_{\text{control}}$) and signs (positive or negative) for all reported effects, regardless of their statistical significance. Most papers reported effect sizes as probabilities (occupancy, survival, and foraging habitat selection) so raw effect sizes were scaled between negative and positive one with a mean of zero, making comparison among studies easy. When papers reported multiple effects (e.g., occupancy and reproduction, or survival and recruitment), I recorded each effect individually. Where papers did not report any effect size for a parameter determined to have no significant effects from fire, I included a zero to represent the presence of no significant effect and to avoid a significance bias in the meta-analysis. I stratified data by subspecies (California, Mexican, or northern) and parameter type according to whether the study estimated site occupancy, foraging habitat selection (substratified into selection for low-, moderate-, and high-severity burned forest), and demographic rates (substratified into survival, reproduction, and recruitment). I performed meta-analyses on parameters for which ≥4 estimates existed from ≥4 different fires.

I used three quantitative methods for evaluating the evidence (Koricheva et al. 2013): a random-effects meta-analysis of mean effect sizes as

Table 1. Summary of systematic review of studies examining effects of fire on Spotted Owls.

No.	Ref.	Sample size	HOD	Time since fire	Context	Fire effects (* = statistically significant, NS = non-significant)	Fire	Any effect	Signif. effect	Post-fire logging
1	Bond et al. (2002)	21 owls in 11 burned sites	OD	1 yr post-fire	No effect on survival, site fidelity, mate fidelity, or reproduction. 50% of territories burned 36–88% high severity, 50% burned mostly low–moderate severity, unknown amount of post-fire logging	No significant effects. (3% higher survival NS, 1% lower site fidelity [occupancy] NS, 26% higher repro NS)	0/+/−	+0.032 −0.013 +0.259	na	na
2	Jenness et al. (2004)	33 burned and 31 unburned breeding sites	OD	1-yr study, 1–4 yr post-fire	No effect on occupancy from fire or amount of high-severity fire. No effect on reproduction. 55% of burned territories area burned, 18% at high severity, unknown amount of post-fire logging	No significant effects from fire. (14% lower occupancy NS, 7% lower repro in burn NS)	0/−	−0.14 −0.07	na	na
3	Bond et al. (2009)	Seven radioed owls from four burned sites	H	1-yr study, 4 yr post-fire	Owls preferred burned forest for foraging, especially high-severity burned forest. Owls preferred roost sites burned at low severity and avoided unburned sites and sites burned at moderate and high severity. 69% of foraging area burned, 13% at high severity, <3% post-fire logging	Positive effect from fire on foraging habitat selection (+42%, +42% +33%*), negative and positive effect of fire on roosting nesting habitat selection (+29%, −13%, −28%*)	+/−	+0.33 +0.42 +0.42 +0.29 −0.13 −0.28	+0.33 +0.42 +0.42 +0.29 −0.13 −0.28	na
4	Bond et al. (2010)	Five radioed owls in occupied burned sites	H	1-yr study, 4 yr post-fire	Three of five owls occupied burned forest over winter	No significant effects, perhaps some positive effect	0/+	na	na	na
5	Clark et al. (2011)	11 radioed owls in burned and post-fire logged sites, 12 in unburned sites	D	2-yr study, 3–4 yr post logging	No effects on survival. Reduced survival in salvage-logged areas relative to owls in unburned forest. 14% high severity, 21% post-fire logged	Negative survival effect from combined effects of fire and post-fire logging (−0.07 NS)	?	na	na	−0.07
6	Roberts et al. (2011)	16 burned and 16 unburned survey areas	O	1-yr study, 2–14 yr post-fire	No effect of fire on survey area occupancy. 14% of survey area burned at high severity, little to no post-fire logging	No significant effect from fire. Possible negative effect from basal area and canopy cover model (−26% lower occupancy in burned survey area NS)	0/−	−0.260	na	na

(Table 1. *Continued*)

No.	Ref.	Sample size	HOD	Time since fire	Context	Fire effects (* = statistically significant, NS = non-significant)	Fire	Any effect	Signif. effect	Post-fire logging
7	Lee et al. (2012)	41 burned and 145 unburned breeding sites	O	11-yr study, 1–7 yr post-fire from six large fires	No effect on occupancy probability. 32% high severity. Unknown amount of post-fire logging	No significant effect from fire, perhaps a slightly positive effect (4% higher occupancy in burned sites NS)	0/+	+0.041	na	na
8	Bond et al. (2013)	Seven radioed owls	H	1-yr study, 4 yr post-fire	Owls in burned forest have same size or smaller home ranges than owls in unburned forest. 69% of foraging area burned, 13% at high severity, 3% post-fire logging	No significant effect from fire, possible positive effect (HR size 12% smaller in burned area NS)	0/+	+0.12	na	na
9	Clark et al. (2013)	40 burned and salvage-logged sites and 103 unburned sites	O	13-yr study, 1–4 yr post-fire	Lower site occupancy on salvage-logged sites relative to unburned sites. 11% high severity, 13% post-fire logged	Negative effect on occupancy from combined fire and post-fire logging (−0.39*)	?	na	na	−0.39
10	Lee et al. (2013)	71 burned and 97 unburned breeding sites, post-fire logging on 21 of the burned sites	O	8-yr study, 1–8 yr post-fire	No effects from fire or logging. Burned site occupancy 17% (10% for pairs) lower than unburned sites. Post-fire logged sites occupancy 5% lower than unlogged burned sites. 23% high severity in burned sites, 59% logged in post-fire logged sites	No significant effect from fire, negative effect (17% lower any occupancy, 10% lower pair occupancy in burn NS) Same data as ref. no. 14	0/−	−0.171 −0.107	na	−0.05
11	Ganey et al. (2014)	Four radioed owls	H	1-yr study, 4–6 yr post-fire	Owls moved to burned forest over winter. Burned wintering sites had 2–6 times more prey biomass relative to unburned core areas. 21% high severity, unknown amount of post-fire logged	Positive effect from fire	+	na	na	na
12	Tempel et al. (2014)	12 burned, 62 unburned sites	DO	20-yr study of survival and reproduction, 6-yr study of occupancy.	No effect on survival, reproduction, or site extinction. Reported a negative effect of fire on colonization rate, but colonization parameter was faulty due to low sample size and zero colonization events. Unknown amount of high-severity fire, unknown amount of post-fire logging	No significant effect from fire. Possible negative effect from fire (6% lower occupancy when fire frequency doubled in simulations that assumed zero post-fire colonizations)	0/−	0 0 −0.060	−0.060	na

(Table 1. *Continued*)

No.	Ref.	Sample size	HOD	Time since fire	Context	Fire effects (* = statistically significant, NS = non-significant)	Fire	Any effect	Signif. effect	Post-fire logging
13	Lee and Bond (2015*a*)	45 burned breeding sites	O	Rim Fire, 1-yr study, 1 yr post-fire	Higher burned-site occupancy rates than any published unburned area. 100% high-severity fire in territory surrounding nest and roost sites reduced single owl occupancy probability 5% relative to sites with 0% high severity. Amount of high-severity fire did not affect occupancy by pairs of owls. In fire perimeter: 37% high severity, no post-fire logging	Positive (17% higher occupancy rates*). Small negative effect on site occupancy (3% lower occupancy in burn*). No significant effect on pair occupancy	+/0	+0.175 −0.04 0	+0.175	na
14	Lee and Bond (2015*b*)	71 burned and 97 unburned breeding sites, post-fire logging on 21 of the burned sites	OD	8-yr study, 1–8 yr post-fire	Occupancy of high-quality sites (previously reproductive) that burned was 2% lower than unburned sites. Occupancy of high-quality sites that were post-fire logged was 3% lower. Occupancy of low-quality sites (previously non-reproductive) was 19% lower in burned vs. unburned sites and 26% lower after post-fire logging. Fire did not affect reproduction. 23% high severity in burned sites, 59% logged in post-fire logged sites	Negative effect on site occupancy (2% and 19% lower*), No significant effect on reproduction	−/0	−0.02 −0.19 0	−0.02 −0.19	−0.03 −0.26
15	Bond et al. (2016)	Eight radioed owls in five sites	H	2-yr study, 3–4 yr post-fire	Owls used forests burned at all severities in proportion to their availability, with the exception of significant selection for moderately burned forest farther from core areas. 23% high severity, <5% post-fire logging	No significant effect from fire (3% lower probability of use in high-severity burn NS), some positive effect (15% higher probability of use of low-severity burn NS, 10% higher probability of use in moderate-severity burned forest NS, 3% higher probability of use of moderate severity away from the core*)	0/+	−0.03 +0.15 +0.10	+0.033	na

(Table 1. *Continued*)

No.	Ref.	Sample size	HOD	Time since fire	Context	Fire effects (* = statistically significant, NS = non-significant)	Fire	Any effect	Signif. effect	Post-fire logging
16	Comfort et al. (2016)	23 radioed owls in post-fire logged area	H	2-yr study, 3–4 yr post logging	Scale-dependent effects of logging (+/−). Owls selected a moderate amount of hard edges around logged stands. 14% high severity, 21% post-fire logged	Positive and negative effect from post-fire logging created edges	?	na	na	+/−
17	Jones et al. (2016)	30 burned sites, 15 unburned sites, nine radioed owls in seven sites	OH	23-yr study, 1 yr post-fire	Negative effects from high-severity fire. Positive effect of low- to moderate-severity fire. 64% high-severity burn, 2% post-fire logging	>50% high-severity burned sites had lower occupancy (−0.49*), <50% high-severity burned sites had higher occupancy (+0.07 NS). High-severity burned habitat was avoided (−0.307*), low-tomoderate-severity burn was preferred (+0.04 NS)	+/−	+0.070 −0.490 −0.307 +0.04	−0.490 −0.307 +0.04	na
18	Tempel et al. (2016)	43 burned sites and 232 unburned sites in four study areas	O	19-yr study, examined 3-yr post-fire effects	No effects of fire. One study area had positive effect of fire. Lower site extinction probability correlated with proportion of site where wildfire reduced canopy >10%. 1% of all territories burned, unknown amount of post-fire logging	No significant effect from fire, some positive effect (1% lower extinction rate in burned sites NS)	0/+	+0.003 0 0 0	na	na
19	Eyes et al. (2017)	13 radioed owls in eight sites (14 owl-year data sets)	H	3-yr study, 1–14 yr post-fire	No effect of fire on foraging habitat selection, owls foraged in all burn severities in proportion to their availability. 6% high severity, little to no post-fire logging	No significant effect from fire. Possibly negative effect (6% lower probability of use for highest burn severity NS; 3% lower use of moderate severity NS)	0/−	−0.06 −0.03	na	na
20	Rockweit et al. (2017)	193 burned and 386 unburned encounter histories from 28 burned (8, 2, 4, 14) and 70 unburned sites	D	26-yr study, 4–26 yr post-fire	Four fires had different effects. Generally, fires reduced survival and increased recruitment. 10%, 12%, 16%, and 48% high severity, no post-fire logging reported	Two fires had no significant effects on survival or recruitment. Two fires had reduced survival (−0.17 and −0.30*), one had increased recruitment (+0.22*)	0/+/−	−0.03 −0.10 −0.17 −0.30 +0.01 +0.02 +0.04 +0.22	−0.17 −0.30 +0.22	na

(Table 1. *Continued*)

No.	Ref.	Sample size	HOD	Time since fire	Context	Fire effects (* = statistically significant, NS = non-significant)	Fire	Any effect	Signif. effect	Post-fire logging
21	Hanson et al. (2018)	54 burned sites in eight fires that were occupied immediately before fire, before–after comparison	O	14-yr study, 1 yr post-fire	Eight large fires (4 included in Tempel et al. 2016). Four groups: 20–49% and 50–80% high-severity fire; and <5% and ≥5% post-fire logging within 1500 m of site center. Mean 63% high severity in core areas, mean 17% logged if ≥5% of core was post-fire logged Compared burned site occupancy with unburned occupancy from Tempel et al. (2016)	No significant effect from fire, significant negative effect of post-fire logging (3% reduction in occupancy if 50–80% of core burned high-severity fire NS, 52% reduction in occupancy from ≥5% post-fire logging*)	0/-	−0.017 −0.013	na	−0.52

Notes: HOD indicates habitat selection (H), occupancy (O), or demographic (D) parameters were estimated. A question mark (?) indicates confounded fire and post-fire logging effects, so fire effects could not be estimated.

the standardized difference in means (Hedge's *d*; Hedges and Olkin 1985); multi-level linear mixed-effects models (hierarchical models) meta-regression of time since fire and percent of high-severity fire in the study area as covariates to explain heterogeneity in mean effect sizes (Hedges and Vevea 1998, Nakagawa and Santos 2012); and a random-effects meta-analysis of variation to examine differences in parameter variances due to fire with effect sizes as the natural logarithm of the ratio between the coefficients of variation (lnCVR; Nakagawa et al. 2015). For analyses, I used the metafor package of R (Viechtbauer 2010) and used function metacont for random-effects meta-analyses, function rma.mv for multi-level linear mixed-effects model meta-regression, and function rma for random-effects meta-analysis of variation (Viechtbauer 2010). Study within geographic area was included 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 (because several studies used data from there).

I used all three methods at three levels: on all parameters, on three main groups of parameters (occupancy, foraging habitat selection, and demography), and on subgroups of habitat selection (for low-, moderate-, and high-severity burned forest) and demography (survival, reproduction, and recruitment). In meta-analyses, I used z tests to determine if effects were significantly different from zero (95% confidence interval excluded zero). In meta-regression, z tests determined whether intercepts or slope coefficients were significantly different from zero. I quantified heterogeneity among effects as Cochran's Q (Hedges and Olkin 1985) and I^2 (Higgins and Thompson 2002). I used a funnel plot and the rank correlation test (Kendall's τ) to assess publication bias (Begg and Mazumdar 1994).

Results

Literature search

I found 21 papers reporting empirical evidence relevant to direct fire effects on owls (Table 1). Three papers presented data from a study area which was extensively logged post-fire and results did not discriminate between effects of fire and post-fire logging (Clark et al. 2011, 2013, Comfort et al. 2016), so these three papers were not included in meta-analyses with the meta-analysis set of papers that were not confounded

Table 2. Summary statistics for published effects of mixed-severity fire on Spotted Owls (*Strix occidentalis*) 1987–2018 used in meta-analysis.

Ref no.	Study	Subspecies	Region	Parameter	*n* burned	*n* unburned	Raw effect size (mean difference)	Significant (in study)	Time since fire (yr)	Percentage of high-severity fire in burned territories
1	Bond (2002)	CNM	NotCal	Occupancy	18	100	−0.013	na	1	30
1	Bond (2002)	CNM	NotCal	Reproduction	7	100	0.259	na	1	30
1	Bond (2002)	CNM	NotCal	Survival	21	100	0.032	na	1	30
2	Jenness (2004)	M	NotCal	Occupancy	33	31	−0.14	na	2.5	16
2	Jenness (2004)	M	NotCal	Reproduction	33	31	−0.07	na	2.5	16
3	Bond (2009)	C	SN	Foraging High	7	7†	0.42	0.42	4	13
3	Bond (2009)	C	SN	Foraging Low	7	7†	0.33	0.33	4	13
3	Bond (2009)	C	SN	Foraging Mod	7	7†	0.42	0.42	4	13
6	Roberts (2011)	C	NP	Occupancy	16	16	−0.26	na	8	12
7	Lee (2012)	C	SN	Occupancy	41	145	0.041	na	4	32
10	Lee (2013)	C	SoCal	Occupancy	71	97	−0.171	na	4.5	23
10	Lee (2013)	C	SoCal	Occupancy	71	97	−0.107	na	4.5	23
12	Tempel (2014)	C	Eldorado	Occupancy	12	62	−0.06	−0.06	3	23‡
12	Tempel (2014)	C	Eldorado	Reproduction	12	62	0	na	3	23‡
12	Tempel (2014)	C	Eldorado	Survival	12	62	0	na	3	23‡
13	Lee (2015*a*)	C	SN	Occupancy	45	45	−0.04	na	1	37
13	Lee (2015*a*)	C	SN	Occupancy	45	45	0	na	1	37
13	Lee (2015*a*)	C	SN	Occupancy	45	145	0.175	0.175	1	37
14	Lee (2015*b*)	C	SoCal	Occupancy	71	97	−0.19	−0.19	4.5	23
14	Lee (2015*b*)	C	SoCal	Occupancy	71	97	−0.02	−0.02	4.5	23
14	Lee (2015*b*)	C	SoCal	Reproduction	71	97	0	na	4.5	23
15	Bond (2016)	C	SoCal	Foraging High	8	8†	−0.093	na	3.5	15
15	Bond (2016)	C	SoCal	Foraging High	8	8†	−0.035	na	3.5	16
15	Bond (2016)	C	SoCal	Foraging High	8	8†	0.092	na	3.5	9
15	Bond (2016)	C	SoCal	Foraging Low	8	8†	0.115	na	3.5	15
15	Bond (2016)	C	SoCal	Foraging Low	8	8†	0.167	na	3.5	9
15	Bond (2016)	C	SoCal	Foraging Low	8	8†	0.169	na	3.5	16
15	Bond (2016)	C	SoCal	Foraging Mod	8	8†	−0.042	na	3.5	15
15	Bond (2016)	C	SoCal	Foraging Mod	8	8†	0.033	0.033	3.5	16
15	Bond (2016)	C	SoCal	Foraging Mod	8	8†	0.102	na	3.5	9
17	Jones (2016)	C	Eldorado	Foraging High	9	9†	−0.307	−0.307	1	19

(Table 2. *Continued*)

Ref no.	Study	Subspecies	Region	Parameter	*n* burned	*n* unburned	Raw effect size (mean difference)	Significant (in study)	Time since fire (yr)	Percentage of high-severity fire in burned territories
17	Jones (2016)	C	Eldorado	Foraging Mod	9	9†	0.04	+0.04	1	19
17	Jones (2016)	C	Eldorado	Occupancy	14	15	−0.490	−0.490	1	64
17	Jones (2016)	C	Eldorado	Occupancy	16	15	0.07	na	1	19
18	Tempel (2016)	C	SN	Occupancy	12	78	0	na	4	23‡
18	Tempel (2016)	C	Eldorado	Occupancy	14	60	0	na	4	23‡
18	Tempel (2016)	C	SN	Occupancy	3	63	0	na	4	23‡
18	Tempel (2016)	C	NP	Occupancy	14	31	0.003	0.003	4	23‡
19	Eyes (2017)	C	SN	Foraging High	13	13†	−0.06	−0.06	7	6
19	Eyes (2017)	C	SN	Foraging Mod	13	13†	−0.03	−0.03	7	6
20	Rockweit (2017)	N	NotCal	Recruitment	8	8	0.01	na	12.5	10
20	Rockweit (2017)	N	NotCal	Recruitment	2	2	0.02	na	6.5	16
20	Rockweit (2017)	N	NotCal	Recruitment	4	4	0.04	na	4	48
20	Rockweit (2017)	N	NotCal	Recruitment	14	14	0.22	0.22	2	12
20	Rockweit (2017)	N	NotCal	Survival	4	4	−0.30	−0.3	4	48
20	Rockweit (2017)	N	NotCal	Survival	14	14	−0.17	−0.17	2	12
20	Rockweit (2017)	N	NotCal	Survival	2	2	−0.10	na	6.5	16
20	Rockweit (2017)	N	NotCal	Survival	8	8	−0.03	na	12.5	10
21	Hanson (2018)	C	SN	Occupancy	13	201	−0.017	−0.017	1	63
21	Hanson (2018)	C	SN	Occupancy	15	201	0.013	0.013	1	35

Notes: Study indicates first author and year. Subspecies are C, California (*Strix occidentalis occidentalis*); N, northern (*Strix occidentalis caurina*); M, Mexican (*Strix occidentalis lucida*); CNM, study included all subspecies. Regions are SN, Sierra Nevada, California (except El Dorado study area and national parks); SoCal, southern California; Eldorado, El Dorado study area in Sierra Nevada, California; NotCal, not California Spotted Owl subspecies; NP, national parks. Parameters: habitat selection (foraging or roosting) in low-, moderate-, (mod) or high-severity burned forest; occupancy, recruitment, reproduction, and survival. Sample sizes (*n*) are number of breeding site territories burned and unburned. Raw mean effect size is $\bar{x}_{\text{burned}} - \bar{x}_{\text{control}}$, significant repeats effects that the individual study determined was statistically significant. Time since fire is the median number of years between the fire and the parameter estimate(s). Percent high-severity fire in burned study territories is the mean relevant to the estimate, or the grand mean if percentage of high severity was not reported (see ‡).

† Habitat selection occurred within territories that contained a mosaic of burn severities and unburned forest.

‡ Percent high-severity fire was not reported for burned territories only for all territories burned and unburned, so the grand mean of reported percentages was used.

by extensive post-fire logging (Table 2). All 21 papers are summarized in Appendix S1.

Fifteen of the 18 papers in the meta-analysis set reported evidence explicitly pertaining to mixed-severity wildfires that burned during the past few decades and which included proportions of high-severity burn characteristic of this fire regime, while three reported evidence from an undifferentiated mix of wildfire and prescribed fires. The studies reported varying amounts of high-severity fire, a defining feature of mixed-severity fires, and the burn severity type that is most responsible for vegetation changes in wildfires, with an overall mean percent of high-severity fire of 26% (standard error [SE] = 3.6, range 6–64) within the study area. Because almost all the studies in this review reported on effects from recent wildfires (all fires burned in the past 30 yr, mean time since fire = 4 yr, SE = 1.1, range 1–26), the reported effects are representative of natural mixed-severity fires as they burned through currently existing forest structure, fire regime, and climate conditions. Papers reported effects of fire on site occupancy (11), foraging habitat selection (4), reproduction (4), apparent survival (3), overwinter roosting habitat selection (2), site fidelity (1), mate fidelity (1), breeding-season nesting and roosting habitat selection (1), home-range size (1), and recruitment (1). Sample sizes measured as number of burned sites were variable among studies (demography CV = 122%, site occupancy CV = 56%, and habitat selection CV = 24%).

Meta-analyses

Meta-analysis of 50 reported effects on occupancy, foraging habitat selection, and demographic rates found effect sizes and signs were variable (Table 2 and Fig. 2), with high heterogeneity among effects ($Q = 1091$, df = 51, $P < 0.0001$; $I^2 = 95.3\%$). Funnel plot (Appendix S1: Fig. S1) and rank correlation test (Kendall's $\tau = 0.108$, $P = 0.27$) showed no publication bias or unusual heterogeneity. Sample sizes (n = number of reported effects) were variable among parameter types (Fig. 3). The number of reported effects were occupancy = 20; demography = 14; and foraging habitat selection = 16. The number of reported effects by demography subtype were survival = 6; reproduction = 4; and recruitment = 4. The number of reported effects by habitat selection subtype were low-severity burned forest = 4; moderate-severity burned forest = 6; and high-severity burned forest = 6.

The mixed-effects model meta-analysis of fire effects on Spotted Owl parameters grouped by type (occupancy, demography, and foraging habitat selection), and subtypes of demography (survival, reproduction, and recruitment) or foraging habitat selection (selection for low-, moderate-, and high-severity burned forest), found mixed-severity fire has generally no significant effect on Spotted Owls (Fig. 3a). Mean overall raw effect size was positive (+0.001), but weighted mean Hedge's d from the random-effects model was not significantly different from zero (Fig. 3a, 95% confidence interval included zero). Mean raw effect sizes were negative for occupancy (−0.060), demography (−0.006), and survival (−0.095), but no Hedge's d value for these three negative effects was significantly different from zero (Fig. 3a). Mean raw effect sizes were positive for reproduction (+0.047), recruitment (+0.073), foraging habitat selection (+0.083), selection of high-severity (+0.004), moderate-severity (+0.087), and low-severity burned forest (+0.195), but Hedge's d values were not significantly different from zero for any of these positive effects, except for significant selection of low-severity burned forest (Fig. 3a).

Variation was generally higher among parameter estimates from burned areas compared to estimates from unburned areas (mean $CV_{burned} - CV_{unburned} = 23\%$; range 4–57%). The mixed-effects meta-analysis of variation in fire effects on Spotted Owl parameters (lnCVR) found mixed-severity fire resulted in significantly higher variation in parameter estimates in all parameters and in occupancy, demography, and survival (Fig. 3b). There was significantly lower variation in estimates of foraging habitat selection probability for low-severity burned forest (Fig. 3b).

Meta-regression

Meta-regression of all standardized mean effects found significant effect of time since fire (Table 3), and a nearly significant effect of percent high-severity burn in territory cores (Table 3), so those effects were included in parameter-specific meta-regressions. Subspecies was not a significant factor (Table 3), so effects from different subspecies were pooled in subsequent parameter-specific analyses.

Meta-regression of occupancy probability found no significant immediate effect of fire on occupancy (intercept not significantly different from zero; Table 4). There was a significant negative effect of time since fire (Fig. 4, Table 4), but no effect of percent high-severity fire in study territories (Table 4). The negative effect of time since fire was sensitive to one study (Roberts et al. 2011), and when that study was omitted, the effect disappeared.

Meta-regression of demographic parameters found a significant positive effect on recruitment immediately after the fire (intercept significantly different from zero), but the effect diminished

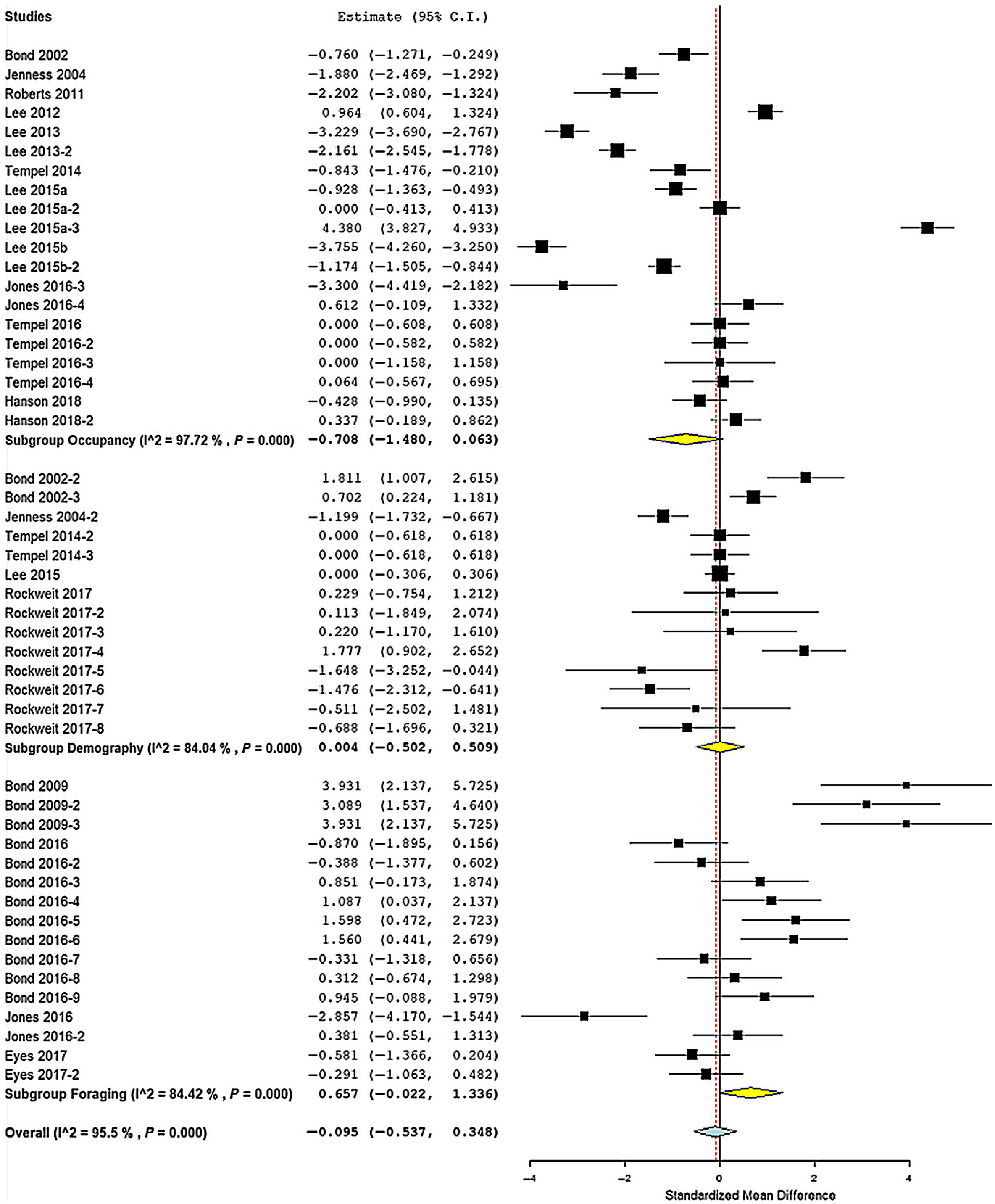

Fig. 2. Forest plot of effect sizes for 50 Spotted Owl (*Strix occidentalis*) parameters (grouped into occupancy, demography, and foraging habitat selection) affected by mixed-severity wildfire as standardized mean difference (Hedge's *d*) between burned and unburned samples. Studies and parameters are listed in Table 2.

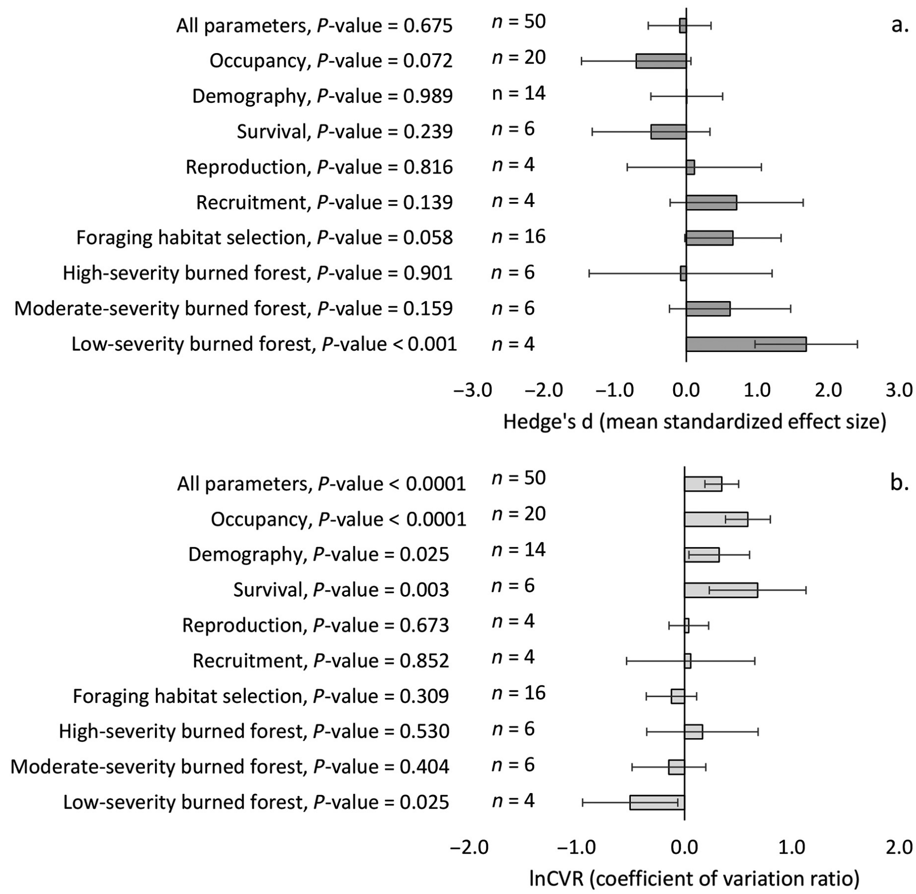

Fig. 3. Results of mixed-effects meta-analyses of mixed-severity fire effects (n = 50 effects from 21 studies) on Spotted Owl (*Strix occidentalis*) parameters grouped by type (occupancy, demography, and foraging habitat selection) and subtype of demography (survival, reproduction, and recruitment), or habitat selection (selection for low-, moderate-, and high-severity burned forest). (a) Hedge's d is standardized mean effect size, and error bars are 95% confidence intervals. The only significant effect (95% confidence intervals excluded zero) was a positive effect of habitat selection for low-severity burned forest. (b) lnCVR is the natural logarithm of the ratio between the coefficients of variation, a measure of differences in variation of parameter estimates between burned and unburned areas. Mixed-severity fire resulted in significantly higher variation in parameter estimates in all parameters, occupancy, demography, and survival, and significantly lower variation in habitat selection for low-severity burned forest.

with time since fire (Fig. 5, Table 4). Reproduction intercept was not significantly different from recruitment (Table 4), and not significantly different from zero ($z = -0.218$, $P = 0.86$), but reproduction was significantly positively correlated with the percent of high-severity fire in owl territories (Fig. 5, Table 4). Survival was significantly lower than recruitment (Table 4), but survival intercept was not significantly different from zero ($z = -0.052$, $P = 0.97$). There were no significant survival effects of time since fire or percent of high-severity fire (Table 4).

Meta-regression of foraging habitat selection parameters found a significant positive selection for low- and moderate-severity burned forest, with high-severity burned forest used in proportion to its availability, but not avoided (Fig. 5, Table 4). Time since fire did not affect foraging habitat selection during the period covered by the studies I examined (up to 7 yr), and the

Table 3. Results from multivariate mixed-effects meta-regression model of mixed-severity fire effects (n = 50 effects from 21 studies) on Spotted Owl (*Strix occidentalis*) parameters related to occupancy, demography, and foraging habitat selection.

Covariates	β	SE	z	P
Intercept (California subspecies)	1.601	1.070	1.497	0.134
Time since fire	−0.199	0.099	−2.017	**0.044**
Percentage of area high-severity fire in study territories	−0.044	0.023	−1.866	0.062
Mix of California, northern, Mexican subspecies	0.467	1.592	0.294	0.769
Mexican subspecies	−1.947	1.608	−1.211	0.226
Northern subspecies	0.360	1.571	0.229	0.819

Notes: SE, standard error. Time since fire was significant, and percent high-severity burn in territory cores was nearly significant, so those effects were included in parameter-specific meta-regressions. Subspecies was not a significant factor, so effects from different subspecies were pooled in subsequent parameter-specific analyses. Bold values are significant at alpha = 0.05.

amount of high-severity fire did not affect habitat selection overall (Table 4).

Post-fire logging had negative effects on Spotted Owls in 100% of the papers that examined this disturbance and where effects from fire and post-fire logging could be differentiated, with large effect sizes (−0.18 occupancy, −0.07 survival).

Discussion

This systematic review and summary of effects from the primary literature indicated Spotted Owls are usually not significantly affected by mixed-severity fire as 83% of all studies and 60% of all effects found no significant impact of fire on owl parameters. Meta-analysis of mean effects found no significant effects of fire on owls, except a positive effect on foraging habitat selection for low-severity burned forest. Meta-regression indicated significant positive effects in recruitment, reproduction, and foraging habitat selection for low- and moderate-severity burned forest. Meta-regression found a significant negative effect of time since fire on occupancy probability. Meta-analysis of variation found mixed-severity fire resulted in greater parameter variation overall, and specifically in occupancy, demography, and survival, and significantly less variation in foraging habitat selection for low-severity burned forest.

Table 4. Table of model coefficients from multi-level linear mixed-effects model meta-regression for effects of mixed-severity fire on Spotted Owls 1987–2018.

Coefficient	β	SE	z	P
Occupancy				
Intercept	1.854	1.115	1.662	0.096
Time since fire	−0.512	0.216	−2.375	**0.018**
Percentage of area high-severity fire in study territories	−0.036	0.022	−1.645	0.100
Demography				
Intercept (Recruitment)	2.328	1.152	2.021	**0.043**
Time since fire (Recruitment)	−0.153	0.065	−2.347	**0.019**
Percentage of area high-severity fire in study territories	−0.032	0.022	−1.466	0.143
Reproduction	−6.479	3.337	−1.942	0.052
Survival	−2.558	1.206	−2.121	**0.034**
Time since fire (reproduction)	0.034	0.422	0.081	0.936
Time since fire (survival)	0.101	0.112	0.900	0.368
Percentage of area high-severity fire (reproduction)	0.234	0.109	2.142	**0.032**
Percentage of area high-severity fire (survival)	0.031	0.033	0.924	0.356
Foraging habitat selection				
Intercept (High severity)	1.167	2.926	0.399	0.690
Time since fire	−0.061	0.529	−0.115	0.908
Percentage of area high-severity fire in study territories	−0.084	0.068	−1.236	0.216
Low severity	1.936	0.732	2.644	**0.008**
Moderate severity	0.777	0.321	2.416	**0.016**

Note: SE, standard error. Bold values are significant at alpha = 0.05.

These results represent Spotted Owl responses to mixed-severity wildfires that burned within the past 30 yr with representative proportions of high-severity fire in a landscape mosaic. Additionally, because most of the studies in this review reported on effects from wildfire, rather than prescribed fire, the fires and their effects are representative of wildfires as they burned through currently existing forest structure, fire regime, and climate conditions. Several studies have reported that fires during the past few decades have been larger and more severe than the historical mean (Miller and Safford 2012, 2017, Mallek et al. 2013, Steel et al. 2015), but others have disputed this

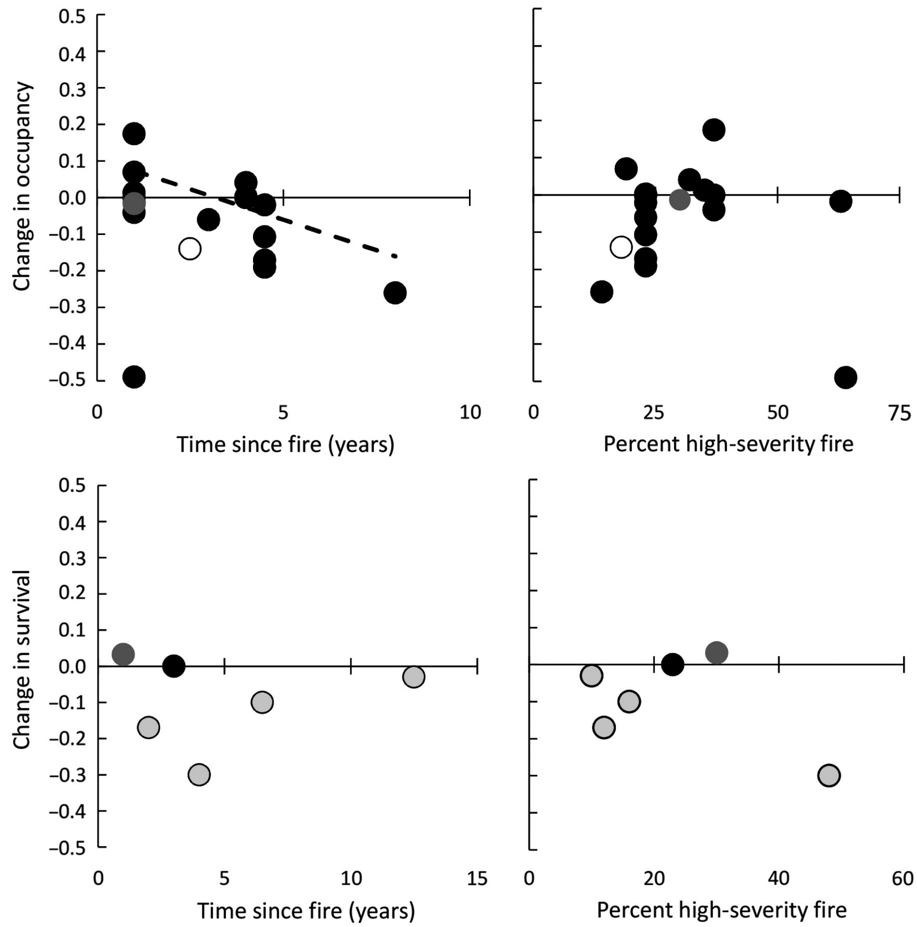

Fig. 4. Results of multi-level linear mixed-effects models (hierarchical models) meta-regression of time since fire and percent of high-severity fire in the study area as covariates to explain heterogeneity in effect sizes from mixed-severity fire on Spotted Owl (*Strix occidentalis*) parameters of breeding site occupancy and survival. The only significant effect was a reduction in occupancy with increasing time since fire, but the effect was sensitive to one study. Symbols indicate subspecies: filled black circles, California; white circles with black outline, Mexican; light gray circles with black outline, northern; and dark gray circles, all three subspecies.

point (Odion and Hanson 2006, Hanson et al. 2009, Odion et al. 2014*a*, Baker 2015*a*). Regardless of what is correct about trends in fire severity, Spotted Owls appear fairly resistant and/or resilient to effects from recent hot, large fires, wherever these fires fall in the long-term range of variability for size and amount of high-severity burn. This is corroborated by the meta-regressions that explicitly quantified the relationship between amount of high-severity fire and Spotted Owl parameters and found only a positive significant correlation (reproduction). My finding of no significant negative relationships between amount of high-severity fire and Spotted Owl parameters demonstrates that large high-severity fire patches, including territories that burn 100% at high severity as was seen in sites within several of the studies in this review, do not have unequivocally negative outcomes for Spotted Owls.

Contrary to current perceptions, recovery efforts, and forest management projects for the Spotted Owl (USFWS 2011, 2012, 2017, USDA 2012, 2018, Gutiérrez et al. 2017) mixed-severity fire as it has been burning in recent decades does not appear to be an immediate, dire threat to owl populations that require landscape-level fuel-reduction

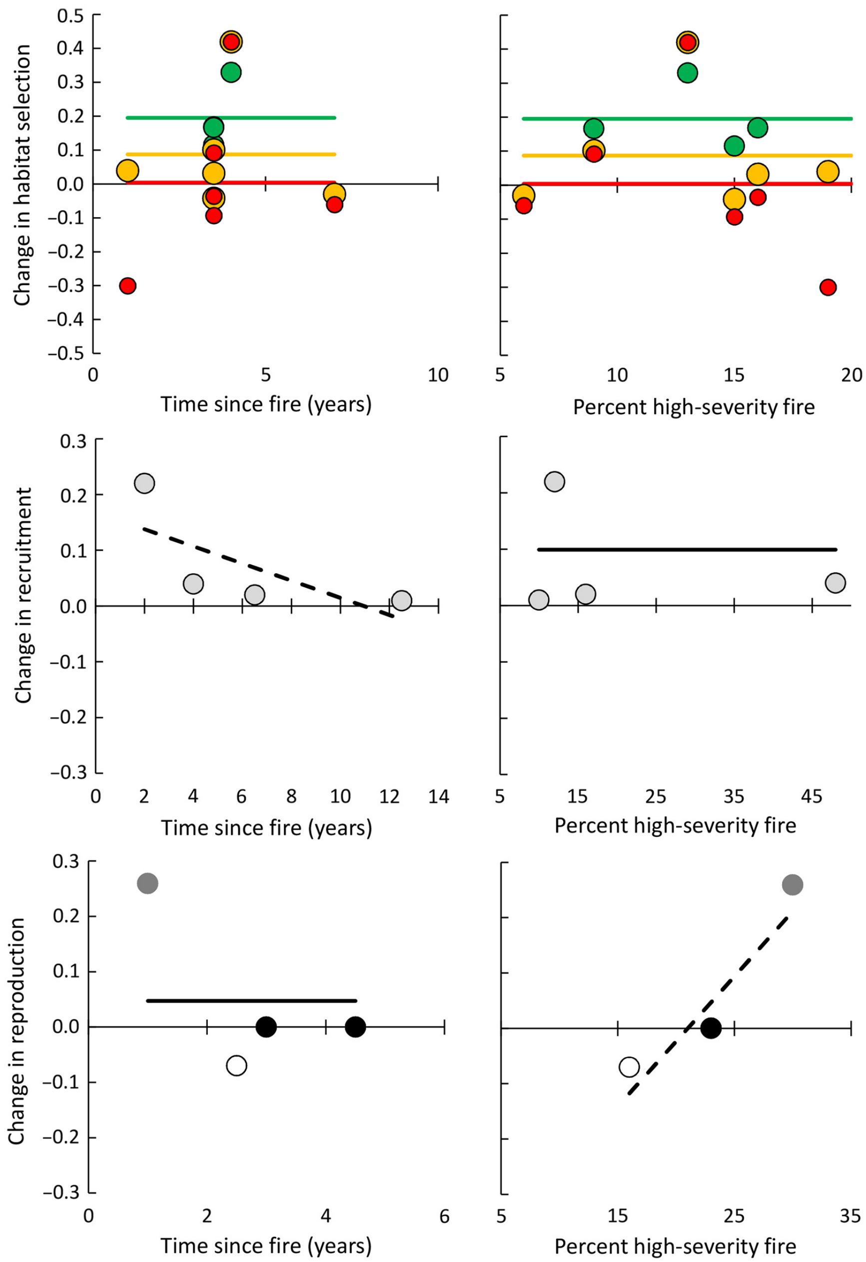

Fig. 5. Results of multi-level linear mixed-effects models (hierarchical models) meta-regression of time since fire and percent of high-severity fire in the study area as covariates to explain heterogeneity in effect sizes from mixed-severity fire on Spotted Owl (*Strix occidentalis*) parameters of foraging habitat selection, recruitment, and reproduction. Significant effects included positive selection for low- and moderate-severity burned forest for foraging, increased recruitment immediately post-fire that diminished with increasing time since fire, and increased reproduction with a positive correlation with amount of high-severity fire. In top two panels, all studies were California subspecies, and colors indicate forest in different burn severity categories: green, low severity; orange, moderate severity; red, high severity. In bottom four panels, symbols indicate subspecies: filled black circles, California; white circles with black outline, Mexican; light gray circles with black outline, northern; and dark gray circles, all three subspecies.

treatments to mitigate fire severity. Empirical studies reviewed here demonstrated that wildfires can generally have no significant effect, but effects can include improved foraging habitat, reduced site occupancy, and improved demographic rates. Most territories occupied by reproductive Spotted Owl pairs that burn remain occupied and reproductive at the same rates as sites that did not experience recent fire, regardless of the amount of high-severity fire in core nesting and roosting areas.

To place my results into perspective, mixed-severity fire typically affects (≥50% vegetation basal area mortality) a very small portion (0.02–0.50%) of Spotted Owl nesting and roosting habitat per year (Odion et al. 2014*b*, Baker 2015*b*, Stephens et al. 2016). Breeding sites that experienced a typical mixed-severity burn mosaic can be expected to have occupancy probability reduced by −0.06 on average. A 0.06 decline in occupancy is less than typical annual declines in occupancy rates observed in the Sierra Nevada in the absence of large fires (Jones et al. 2016: Fig. 3f). In comparison, post-fire logging caused a mean occupancy probability reduction of −0.18.

Post-fire logging is likely to be partially responsible for some of the negative effects attributed to high-severity fire in the studies reviewed here (Tempel et al. 2014, Jones et al. 2016, Rockweit et al. 2017, Hanson et al. 2018). Because Spotted Owl studies typically characterize territory vegetation only in the breeding core area within 1.1 km of the nest, these studies ignore habitat changes and alterations in the year-round home-range area that can extend up to 5.9 km from the nest (Zabel et al. 1992). Spotted Owl habitat protections have generally not included areas beyond 1 km from the nest, a management policy that has not contributed to population recovery.

Complex early seral forests created by fire differ from post-fire salvage-logged forests in that dead trees remain on-site, providing perching sites for hunting owls as well as food sources and shelter for numerous wildlife species (Hutto 2006, Swanson et al. 2011, DellaSala et al. 2014). Longitudinal studies also indicated that burned breeding sites where owls were not detected immediately after fire were often recolonized later (Lee et al. 2012, 2013, Tempel et al. 2016), and this review shows burned forest habitat is used for foraging, demonstrating the mistake of concluding severely burned sites or habitats are lost to Spotted Owls or require restoration (Davis et al. 2016). A recent global meta-analysis found post-fire logging is generally not consistent with ecological management objectives (Thorn et al. 2018).

This review on fire and Spotted Owls forms one portion of the evidence base for data-driven forest management. A recent systematic review of thinning and fire found 56 studies addressing fuel treatment effectiveness in real (not simulated) wildfires from eight states in the western United States (Kalies and Kent 2016). There was general agreement that thin + burn treatments (thinning immediately followed by burning) had some positive effects in terms of reducing fire severity, while treatments by burning or thinning alone were less effective or ineffective (Kalies and Kent 2016). There is also evidence that doing nothing can achieve many forest restoration goals related to age structure and fuels' density (Zachmann et al. 2018). Additional systematic reviews are needed to examine (1) the quantifiable risk of fire to Spotted Owl habitat, as there are disparate lines of evidence regarding whether fire is impeding the recovery of late-seral-stage forests; and (2) the impacts of fuel treatments on Spotted Owl demography and site occupancy. Thinning immediately followed by burning to reduce wildfire risk may or may not have adverse effects on Spotted Owls (Franklin et al. 2000, Dugger et al. 2005, Tempel et al. 2014, 2016, Odion et al. 2014*b*), but the evidence presented here indicates fire itself has arguably more benefits than costs to the species and thus suggests thinning is not necessary.

The results presented here should serve to guide management decisions, but also should be understood as limited by the available data. The sample sizes of number of estimated effects from mixed-severity fire on survival and recruitment were small and limited mainly to the northern subspecies. There were also very few studies from the Mexican subspecies. A few studies presented effect sizes that were influential on results, especially meta-regression results (Roberts et al. 2011), so studies examining longer times since fire are needed. We encourage future studies to increase sample sizes of each parameter and to provide a more balanced sample of studies from all subspecies, and over longer time frames.

Management Implications

The preponderance of evidence presented here shows mixed-severity forest fires, as they have burned through Spotted Owl habitat in recent decades under current forest structural, fire regime, and climate conditions, have no significant negative effects on Spotted Owl foraging habitat selection, or demography, and have significant positive effects on foraging habitat selection, recruitment, and reproduction. Forest fire does not appear to be a serious threat to owl populations and likely imparts more benefits than costs for Spotted Owls; therefore, fuel-reduction treatments intended to mitigate fire severity in Spotted Owl habitat are unnecessary. These findings should inform revisions to planning documents to consider burned forest, including large patches of high-severity burned forest, as useful habitat that imparts significant benefits to Spotted Owls. Forest and wildlife planning documents promote a diverse mosaic of heterogeneous tree densities and ages (USFWS 2017, USDA 2018), the very conditions created by mixed-severity wildfire, and it follows that heterogeneous post-fire structure would lead to greater variation in some Spotted Owl parameters, as was observed in the meta-analysis of variation. Planning documents (USFWS 2011, 2012, 2017, Gutiérrez et al. 2017, USDA 2018) claiming that forest fires currently pose the greatest risk to owl habitat and are a primary threat to population viability appear outdated in light of this review.

Acknowledgments

I thank the many Spotted Owl researchers and field technicians who are responsible for the collection and analyses of the data reviewed here. I also thank Monica Bond and Justin Augustine for thoughtful comments on the manuscript. I have no conflict of interest.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2354/full

Ecosphere

Spotted Owls and forest fire: A systematic review and meta-analysis of the evidence

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Appendix S1

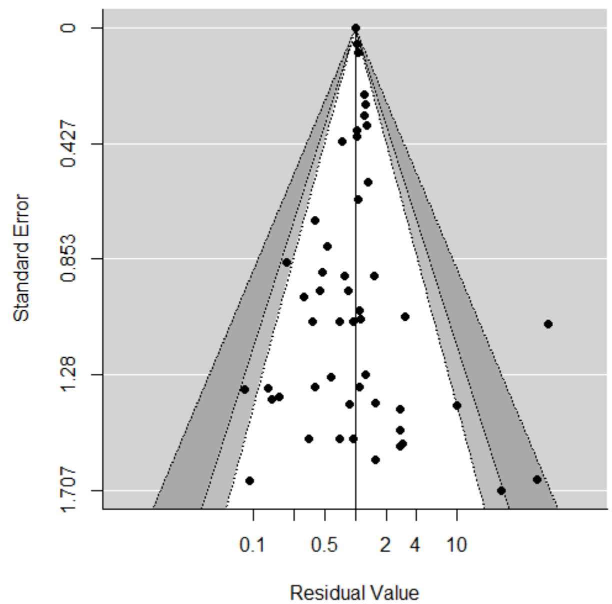

Figure S1. Funnel plot of all reported effects of mixed-severity fire on Spotted Owl (*Strix occidentalis*) parameters illustrating no publication bias or unusual heterogeneity exists.

Descriptions of papers

1. Bond et al. (2002) was an examination of survival, reproduction, and site and mate fidelity of northern (*S. o. caurina*), California (*S. o. occidentalis*), and Mexican Spotted Owls (*S. o. lucida*) 1 year after fire. Short-term (1-year) postfire survival of 21 color-banded Spotted Owls was reported from four separate study areas encompassing all subspecies: in northwestern California, southern California, New Mexico, and Arizona. All nest and roost areas were burned, and no post-fire logging had occurred before owls were surveyed the year after fire. Vegetation burn severity maps were available for 8 of the 11 breeding sites, with each breeding site defined as a circle approximately 150–400 ha, depending on study area. Half of the breeding sites where fire severities were mapped burned at low to moderate severity, and the other half burned 36–88% at high severity. The authors found that 18 of 21 (86%) individual owls were resighted after fire. These survival rates are higher (+0.03) than the mean from unburned sites. Sixteen of 18 (89%) surviving owls (of all subspecies) were in the same breeding sites after fire (-0.01),

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and all pairs were faithful to their pre-fire breeding site and mate. Productivity of burned Spotted Owl sites was higher (+0.26) than mean annual rates of reproduction for long-unburned sites.

2. Jenness et al. (2004) reported pre- and post-fire occupancy of 64 Mexican Spotted Owl sites in four national forests in New Mexico and Arizona. The authors selected owl breeding sites in fires that burned from 1993 to 1996 and compared levels of occupancy (single, pair, failed reproduction, and successful reproduction) in 1997 in 33 burned and 31 unburned sites, including 29 paired burned and long-unburned sites within 12 km of each other. Post-fire logging was minor in most of the fires. Post-fire occupancy rates were not significantly different between burned and unburned sites and did not statistically differ with time since fire. The percent of high-severity fire in a burned site had no significant influence on whether the site was occupied. The number of successfully reproducing Mexican Spotted Owl sites did not differ between burned and unburned forests. Non-significant effects included lower occupancy (-0.14) and lower reproduction (-0.07) in burned sites.

3. Bond et al. (2009) quantified roosting and foraging habitat selection by Spotted Owls in a burned landscape. The authors banded and radiomarked 7 California Spotted Owls occupying the McNally Fire in the southern Sierra Nevada, California 4 years after fire. Effects of high-severity fire were not confounded with post-fire logging because <3% of the foraging ranges of these owls had been post-fire logged. The probability of an owl using a site for foraging was significantly greater in low- (+0.33), moderate- (+0.42), and high-severity (+0.42) burned forests than unburned forest. In this study, California Spotted Owls roosted in all fire intensity classes. Owls selected roost sites burned at low severity (+0.29) and avoided unburned sites and sites burned at moderate (-0.13) and high severity (-0.28).

4. Bond et al. (2010) documented 3 of 5 radiomarked California Spotted Owls that occupied the McNally Fire in the southern Sierra Nevada during the breeding season 4 years post-fire, roosted within the burned landscape during the following winter.

5. Clark et al. (2011) examined the survival rates of northern Spotted Owls 3–4 years after fire and postfire logging in two fire areas in southwestern Oregon. Twelve (12) owls were radiomarked in unburned forest and 11 owls were radiomarked inside the burn perimeter where much of the forest (20–23%) had been post-fire logged. The authors found no significant effect of fire severity or quantity of forested habitat on Spotted Owl survival. Six of the owls monitored in unburned forest were known to have moved outside the fire perimeter after fire and salvage logging, but before survival monitoring took place. In the original paper, the authors considered the owls that moved similar to the owls inside the fire perimeter. I combined all outside-the-burn owls to compare with inside-the-burn owls. Non-significant effects: owls that resided within the post-fire logged landscape had lower survival rates (-0.07) than those residing in unburned unlogged forest.

6. Roberts et al. (2011) compared effects of wildfire and prescribed burns on occupancy of California Spotted Owls residing in burned (1 to 15 years since fire) and long-unburned forests in Yosemite National Park, central Sierra Nevada, California. This study compared occupancy in 16 randomly selected burned and 16 unburned 'owl survey areas,' each 3.75 km^2. A total of 19 owl pairs were monitored for a single year, and vegetation at owl sites was compared with sites that yielded no owl response to build detectability and occupancy models. The mean 'owl survey area' that burned at high severity was 14%, with the greatest amount of high-severity burn in a survey area being 52%. Because this study was conducted in a national park, no post-fire or recent pre-fire logging had occurred to confound results.

The authors found no support for a model of occupancy rates that distinguished between burned and unburned sites. Non-significant effects: occupancy from model based on canopy cover and basal area was lower at burned versus unburned sites (-0.26).

7. Lee et al. (2012) published an 11-year longitudinal study of California Spotted Owl occupancy on national forest lands in the Sierra Nevada, California. The authors used data collected by the U.S. Forest Service to compile occupancy survey histories at 41 breeding sites within six large mixed-severity fires that occurred from 2000 to 2007 throughout the Sierra Nevada and at 145 long-unburned control sites. Fires had no significant effect on occupancy probability. Non-significant effects: occupancy probability was higher in burned sites (+0.041) relative to unburned. Post-fire logging occurred in an unknown number of territories.

8. Bond et al. (2013) found Spotted Owls in the McNally Fire area, southern Sierra Nevada, California fed primarily on pocket gophers (*Thomomys* spp., 40.3% by biomass) and northern flying squirrels (*Glaucomys sabrinus*, 25.9% by biomass), whereas owls fed primarily on flying squirrel and woodrats (*Neotoma* spp.) in long-unburned study areas. The mean home-range sizes of the McNally Fire owls were 12% smaller than those recorded in unburned forests using similar time periods and methodology.

9. Clark et al. (2013) investigated the occupancy dynamics of northern Spotted Owls in burned and salvage-logged landscapes in three fire areas and an adjacent long-unburned demographic study area in the southern Oregon Cascade Mountains. The three fires all burned within 1 year of each other. Modeled occupancy rates of 103 Spotted Owl sites in the long-unburned area were compared with 40 burned sites before and after fire and post-fire logging occurred. Post-fire logging was prevalent, thus it was not possible to quantify the influence of fire alone on occupancy dynamics and survival. Occupancy probability declined more steeply after post-fire logging than in the unburned area (-0.39).

10. Lee et al. (2013) used Spotted Owl survey data from 97 long-unburned and 71 burned breeding sites over 8 years to examine the influence of fire and post-fire logging on local rates of extinction, colonization, and occupancy probability. Post-fire logging occurred on 21 of the burned sites. None of the fire and logging coefficients were statistically significant. Non-significant effects: model-averaged effect sizes suggested that high-severity fire that burned >50% of forest in the 203-ha core area was correlated with lower occupancy relative to unburned sites. Post-fire logging further increased extinction probability. The majority (75%) of sites burned below the 50% threshold. Non-significant effects: burned site occupancy -0.062 lower than unburned sites. Post-fire-logged sites occupancy -0.05 lower than unlogged burned sites.

11. Ganey et al. (2014) reported a sample of 4 radiomarked Mexican Spotted Owls in the Sacramento Mountains, New Mexico, moved to wintering areas that had burned 4–6 years earlier and that had 2–6 times greater abundance and biomass of small mammal prey than nest core areas associated with those owls.

12. Tempel et al. (2014) used data from a long-term (>20 years) demographic study of California Spotted Owls in the Eldorado and Tahoe national forests of the central Sierra Nevada, California to examine the influence of timber harvest and wildfire on reproduction, survival, and occupancy over a 6-year timescale using data from 74 breeding sites. Twelve (12) breeding sites experienced fire during the course of the study. Fire did not significantly affect survival, reproduction, or site extinction. The coefficient for the effect of fire on site colonization was negative, but the standard error of the

coefficient could not be estimated making this parameter estimate of low quality. The authors reported lower occupancy (-0.06) when fire frequency was doubled in simulations that assumed zero post-fire colonization. Post-fire logging occurred on public and private lands in the study territories, but was not reported.

13. Lee and Bond (2015a) examined California Spotted Owl site occupancy in the 2013 Rim Fire near Yosemite National Park, which was the largest fire in recent recorded Sierra Nevada history, burning more than 100,000 ha. The fires burned through 45 known Spotted Owl breeding sites in the Stanislaus National Forest and all sites were surveyed by U.S. Forest Service personnel the following year. For all detections, 100% severe fire surrounding nest and roost sites decreased occupancy probability (-0.04), but did not affect occupancy by pairs of owls. Single-season modeled occupancy rates 1 year after the Rim Fire were significantly higher (+0.175) than other previously published occupancy rates in long-unburned forests.

14. Lee and Bond (2015b) examined how the quality of a site influenced California Spotted Owl occupancy and reproduction after fire in southern California (using the same dataset as Lee et al. 2013). Site quality was measured by whether the site supported a single owl, pair of owls, or pair of owls with offspring the previous year. Amount of severe fire in a core use area was not a significant variable influencing reproduction. The influence of severe fire on occupancy was minor in sites that had been occupied and reproductive the previous year (high quality), and if a site remained occupied, severe fire did not affect the probability of reproduction compared with unburned sites. Occupancy of high-quality sites (previously reproductive) that burned was -0.02 lower than unburned sites. Occupancy of high-quality sites that were post-fire logged was -0.03 lower. Occupancy of low-quality sites (previously non-reproductive) was -0.19 lower in burned versus unburned sites, and -0.26 lower after post-fire logging.

15. Bond et al. (2016) analyzed foraging habitat selection by 8 radiomarked California Spotted Owls in the Slide Fire in the San Bernardino National Forest of southern California 3 and 4 years after fire. Habitat selection with sensitivity analysis at three spatial extents of available habitat showed owls used forests burned at all severities in proportion to their availability (no significant effects), with the exception of significant selection for moderately burned forest (+0.03) farther from core areas.

16. Comfort et al. (2016) examined foraging habitat selection by 23 radiomarked Northern Spotted Owls in the Timbered Rock Fire in southwest Oregon in relation to edges created by fire and post-fire logging. Because post-fire logging occurred immediately following fire on extensive private lands in the study area, and their remote-sensing methodology could not distinguish between fire and post-fire logged areas, the authors created a combined burned–logged variable called the 'disturbance severity.' The edges between forested habitats and burned–logged areas were defined as 'hard' edges. At smaller spatial scales (3.2 and 51.8 ha surrounding telemetry locations), increases in disturbance severity decreased the probability of use, but at larger spatial scales (829 ha), the opposite was true. The use of a location for foraging was maximized when about 20% of a 3.2-ha area surrounding the location was composed of hard edge. Owls avoided areas with larger amounts of hard edge, but selected smaller amounts of edge. Larger, more contiguous hard edges were described as intensively managed edges created by post-fire logging.

17. Jones et al. (2016) reported on breeding site occupancy dynamics from 15 unburned and 30 burned sites (14 of which burned >50% high severity), and foraging habitat selection for 9 owls, in the Eldorado National Forest, central Sierra Nevada, California after the King Fire of 2014. Occupancy declined in

burned sites relative to unburned, and >50% high-severity burn further reduced occupancy. Foraging habitat selection showed owls significantly avoided high-severity burn and a non-significant preference for low-severity burn.

I included the results from this paper in my review, however methodological difficulties in this study make their results unreliable. First, the Eldorado owl population that provided the data for Jones et al. (2016) has documented long-term trends of decreasing site colonization and increasing site extinction probabilities, as reported before the King Fire (Tempel and Gutiérrez 2013). However, Jones et al. did not account for these pre-fire trends in their site occupancy analyses. This omission of temporal trends means their results for 2015 could be due to the fact that this single year of post-fire data was the last year in the dataset, and should not be attributed unequivocally to the King Fire. Fig. 3f shows that the 2015 post-fire year of decrease in occupancy was not significantly different from the 10 previous instances of documented declines that occurred in the absence of fire. Second, Jones et al. (2016) used compositional analysis of foraging habitat selection, a method that is inappropriate for central place foragers like Spotted Owls (Rosenberg and McKelvey 1999). Compositional analysis relies upon an assumption of no spatial correlation among foraging locations (Rosenberg and McKelvey 1999, Manly et al. 2002). Central place foraging behaviour results in a clustered distribution of foraging points near the center of a territory which violates the assumption of no spatial correlation among foraging locations, a pattern that was apparent for most of the Spotted Owls in Web Figure 3 of Jones et al. (2016). The appropriate habitat selection analysis is a 'resource selection function', a mathematical function that accounts for the fact that Spotted Owls, as central place foragers, will return to their nest or roost trees many times during the night, so their probability of using habitats near the nest or roost core is much higher than the probability of using habitats farther away (Bond et al. 2009, Bond et al. 2016, Eyes et al. 2017). Third, Jones et al. (2016) reported extinction for a territory in WebFigure 4 when the owls shifted their location by a distance that was less than the diameter of a territory as defined by the authors, and less than mean foraging distance reported by the authors. This decision inflated their 'burned site' extinction probability by classifying a normal within-territory movement as site extinction. These methodological difficulties in their data analyses limit the utility of Jones et al. (2016) for guiding forest management, particularly when weighing the risks from management actions relative to risks from fire.

18. Tempel et al. (2016) examined occupancy dynamics in 43 burned breeding sites and 232 unburned sites in four study areas across the Sierra Nevada using 19 years of data. The authors found no significant effects of fire on occupancy, but their top ranked model for one study area (Sequoia Kings Canyon) included a covariate for proportion of the core area where canopy cover was reduced by >10% by wildfire. This covariate was negatively correlated with territory extinction probability, meaning more area burned reduced the site extinction probability, thereby increasing occupancy probability (+0.01).

19. Eyes et al. (2017) radiotracked 13 California Spotted Owls over 3 years and collected data on foraging habitat selection in Yosemite National Park, Sierra Nevada, California. The authors analyzed foraging by a sample of owls nesting in and near forest burned 1–14 years previously from a mix of wildfires and prescribed burns. Eyes et al. (2017) found no significant effect of burn severity on foraging habitat selection, but non-significant effects were reported that showed a decrease in probability of use for the most severely burned locations (-0.06), and moderately burned locations (-0.03), relative to unburned locations.

20. Rockweit et al. (2017) examined survival and recruitment rates of northern Spotted Owls in 70 unburned sites and 28 sites burned in four fires. The authors reported wildfires with different mixtures of burn severity resulted in different effects on survival and recruitment. Ten owl territory cores that were burned at mostly low severity (1987 and 1999 fires) were associated with no significant effects on survival or recruitment. When 14 territory cores burned with moderate amounts of high- and low-severity fire (2008 fire), the result was a significant reduction in survival (-0.17) and a significant increase in recruitment (+0.22). When 4 territory cores burned at predominantly high severity (2004 fire), there was a significant reduction in survival (-0.30). The burned territories were partially post-fire logged, although that was not reported by the authors (C. Hanson, pers. comm.).

21. Hanson et al. (2018) examined naïve site occupancy of California Spotted Owls in 54 sites that burned in one of 8 large fires between 2002 and 2015. All sites were occupied in the year immediately prior to the site burning, and comparisons were before-after fire and logging. Sites were classified into 4 groups based on amount of high-severity burn (20-49% or 50-80%) and amount of post-fire logging (<5% and ≥5%) in a 1500m-radius circle around the nesting roosting core area. Hanson et al. (2018) found no significant effect of fire severity on occupancy, but significant effects of post-fire logging. Mean amount of core areas burned at high severity was 63%. Results were: 80% occupancy in sites with 20–49% high-severity fire and <5% post-fire logging, 33% occupancy in sites with 20–49% high-severity fire and ≥5% post-fire logging; and 77% occupancy in sites with 50–80% high-severity fire and <5% post-fire logging, 20% occupancy in sites with 50–80% high-severity fire and ≥5% post-fire logging. Amongst the sites with ≥5% post-fire logging, the mean amount of such logging of the area within a 1500 m radius of site centers was 16.7% (SD = 8.7%).

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