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COMMENT

Spotted owls and forest fire: Comment

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Western North American forest ecosystems are experiencing rapid changes in disturbance regimes because of climate change and land use legacies (Littell et al. 2018). In many of these forests, the accumulation of surface and ladder fuels from a century of fire suppression, coupled with a warming and drying climate, has led to increases in the number of large fires (Westerling 2016) and the proportion of areas burning at higher severity (Safford and Stevens 2017, Singleton et al. 2018). While the annual area burned by fire is still below historical levels (Taylor et al. 2016), some forest types in the west are burning at higher severities when compared to pre-European settlement periods (Mallek et al. 2013, Safford and Stevens 2017). As such, they face an increased risk of conversion to non-forest ecosystems (e.g., shrublands, non-native grasslands) following large, severe fires because of compromised seed sources, post-fire soil erosion and loss, high-severity re-burn, and climatic thresholds (Coppoletta et al. 2016, Stevens et al. 2017, Rissman et al. 2018, Shive et al. 2018, Wood and Jones 2019). Restoration methods such as mechanical thinning and prescribed and managed wildland fire that reduce accumulated surface and ladder fuels (e.g., removal of small- and medium-sized trees, especially non-fire adapted species) may reduce the spatial extent of severe fires and increase forest resilience to fire in a changing climate (Agee and Skinner 2005, Stephens et al. 2013, Hessburg et al. 2016, Tubbesing et al. 2019) and, in doing so, promote key ecosystem services (Hurteau et al. 2014, Kelsey et al. 2017, Wood and Jones 2019).

Proposals to increase the pace and scale of fuel reduction in frequent-fire forests, however, have been controversial for three main reasons. First, some stakeholders view such "forest restoration" activities as a euphemism for logging remnant large trees (Gutiérrez et al. 2015), and decades of logging throughout western forests have already created a deficit of large, old trees with undesirable ecological consequences (Safford and Stevens 2017, Jones et al. 2018). Second, some stakeholders have expressed concern that scientific or ecological justification for management activities intended to reduce fuel buildup is limited, stating that (1) current wildfire activity (including the patch size and proportional composition of high-severity fire) in frequent-fire forests is within the natural range of variation (Baker 2015) and (2) fuel treatments will be ineffective in reducing severe fire extent in a warming/drying climate (Schoennagel et al. 2017). Third, landscape-level fuel reduction projects have the potential to remove key habitat elements required by old-forest associated species (e.g., spotted owl *Strix occidentalis*) and thus exacerbate ongoing and long-term population declines (Stephens et al. 2014). The strength of this final argument against increasing the pace and scale of restoration hinges on what scientific research can tell us about which factor poses a

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greater relative threat to old-forest species: fuel reduction activities or changing climate and wildfire characteristics.

To better understand effects of wildfire on spotted owls, Lee (2018) conducted a quantitative meta-analysis synthesizing 50 empirical effects from 15 published studies investigating various responses (occupancy, demography, foraging habitat use) by spotted owls to wildfire. He concluded that wildfire—regardless of severity—did not adversely affect spotted owls and thus does not pose a threat to any of the three subspecies. Moreover, based on these results, Lee (2018) asserts that fuel reduction activities are unnecessary and that planning documents (USFWS 2011, 2012, 2017, Gutiérrez et al. 2017, USDA 2019) claiming that forest fires are a primary threat to owls are no longer relevant.

We appreciate the attempt made by Lee (2018) to provide a quantitative synthesis of fire effects on spotted owls, which until this time had been lacking. However, as a group representing authors from many of the spotted owl studies included in the Lee (2018) meta-analysis, as well as forest and fire scientists with extensive research experience in western forest ecosystems, we disagree with its central conclusions that high-severity (or stand-replacing) fire does not affect or threaten spotted owls. We also disagree with the assertion that the meta-analysis supersedes previous spotted owl-fire research and planning documents, and we argue below that it therefore is an improper challenge to previous work and conservation efforts. Rather, our interpretation of the scientific research to date is that the way spotted owls respond to fire is highly variable and context specific. Depending on the extent of and severity of wildfire, studies have shown negative fire effects on California (*S. o. occidentalis*) and northern (*S. o. caurina*) spotted owls (Rockweit et al. 2017, Jones et al. 2016, 2020), positive effects on the California and Mexican (*S. o. lucida*) subspecies (Bond et al. 2009, Ganey et al. 2014), or neutral effects on California spotted owls (Roberts et al. 2011, Lee et al. 2012). To distill this variability down to a conclusion of "no effect" vastly oversimplifies the complex demographic responses of the species (and potentially varied responses by each subspecies) to habitat disturbance. As we describe throughout this comment, a more ecologically relevant interpretation of the meta-analysis by Lee (2018) is that fire appears to have neutral or positive effects on owls in some contexts and at certain scales, but that fire *can also* pose serious threats to owls.

We suggest that Lee (2018) arrived at the conclusions he did because a series of ecological, statistical/technical, and inferential issues that we detail below (Table 1). *Ecological issues* include an overgeneralization of the historical fire regimes of forests inhabited by spotted owls. *Statistical/technical* issues include a focus on the summary (mean) effects in the presence of high among-study variation, data selected for analyses and representations of high-severity fire and its ecological effects, inaccuracies in reported effect sizes of fires, transparency with reporting and treatment of studies with confounded effects, the use of identical data from multiple studies ("duplicate study effects"), and use of data from several studies that underestimated or miscalculated the potential effects of fire. *Inferential issues* include the lack of recognition of changing wildfire trends and contention that meta-analyses necessarily solve complex conservation issues and supersedes existing and widely accepted understanding based on studies examining specific mechanisms.

Ecological Issues

Overgeneralization of historical fire regimes within forests inhabited by spotted owls

Lee (2018:1–2) provided the following statement about natural fire regimes within the range of the spotted owl: "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, Baker 2015)." While this statement may be technically correct when applied to the entire geographic range of the spotted owl, it does not properly acknowledge that the natural range of variability (NRV) in fire regimes shows strong geographic variation according to forest type and climate (Brown and Smith 2000, Stephens et al. 2019). Indeed, the term "mixed-severity" tends to encompass such

Table 1. Summary of key issues related to Lee (2018).

General description†	Summary	Why this is a problem	Implication for meta-analysis
Ecological			
Overgeneralization of historical fire regimes within forests inhabited by owls	Lee (2018) characterized the fire regime within the range of the spotted owl as "mixed-severity," with 5-70% stand-replacing effects within fires	Forest types and resulting fire regimes vary considerably across the geographic ranges of the three spotted owls subspecies analyzed	Disconnect between analysis/inference and understanding of the types of fire regimes and fire effects to which each subspecies is likely to be adapted (or not adapted)
Statistical/ technical			
Focus on the summary (mean) effects in the presence of high among-study variability	Lee (2018) made the case that spotted owls showed a neutral response to fire because effects averaged across all studies was not statistically different from zero	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) did not adequately investigate potential factors driving among-study variability in spotted owl response to fire (e.g., patch sizes), or made decisions in the analysis that biased meta-regression results toward zero (i.e., no effect); see other sections
Selected data and representation of high-severity fire resulted in reduced variability in ecological effects	Lee (2018) computed an average value of the high-severity burned area across all territories (or alternatively from the whole fire) to represent the effects of severe fire within a study for meta-regression analysis	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	The elimination of territory-level variability in fire effects leads to a loss of information about how the scale/extent of severe fire affects spotted owls in an ecologically meaningful way
Inaccuracies in reported fire effect sizes	Lee (2018) used inconsistent, non-reproducible, or demonstrably incorrect estimates of effect sizes and group sample sizes	A requirement for meta-analysis is the ability to obtain accurate and standardized effect sizes from different studies.	Key inferences from Lee (2018) may be weakened if incorrect estimates of fire effects on owls from individual studies were used, or if effects were incorrectly weighted
Transparency in reporting and treatment of studies with confounded salvage logging and fire effects	Lee (2018) did not report the analytical method used for evaluating post-fire salvage logging effects and used an inconsistent framework for inclusion/exclusion of studies with confounded fire-logging 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	The *ad hoc* approach used by Lee (2018) for incorporating confounded fire-logging effects from individual studies into the meta-analysis appears to have biased fire effects toward zero
Inclusion of duplicated data from multiple studies	Several studies used by Lee (2018) included duplicated data; that is, multiple papers included in the meta-analysis used the same underlying spotted owl occupancy datasets	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) did not appear to take appropriate remedial measures to deal with duplicate study effects
Underestimation and miscalculation of negative effects of fire on occupancy from individual studies	Several studies included in the meta-analysis have been shown to contain analytical errors affecting effect size estimates and/or biases in the effects of fire or severe fire on spotted owls	Some of the underlying data included in the meta-analysis of fire effects on owls contain errors or biases and thus may be unreliable	Typically, the directional bias associated with these studies was positive, such that they systematically underestimated the effects of fire on spotted owls. These biases were propagated into the meta-analytical framework used by Lee (2018)

a broad range of fire effects that it does not adequately describe ecologically meaningful variation in fire regimes (Collins et al. 2017).

Certainly, portions of spotted owls range in the western Cascades in Oregon and Washington, and the California Coast Range, where

(Table 1. Continued.)

General description†	Summary	Why this is a problem	Implication for meta-analysis
Inferential			
Context of changing wildfire trends	Lee (2018) concludes that "mixed-severity fire" does not threaten spotted owls, without the critical context of well-documented directional changes in severe wildfire activity in the range of the spotted owl that are predicted to pose a serious threat	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	Lee (2018) claims that the meta-analysis renders existing forest planning documents outdated, when in fact these documents are forward-looking in terms of considering documented and predicted increases in severe fire within the range of the spotted owl
The use of meta-analysis to solve complex conservation issues and superseding of existing understanding	Lee (2018) implies that the meta-analysis resolves confusion about the effects of fire on spotted owls and supersedes conclusions reached by individual studies	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	Results from individual studies, particularly those that use before-after control-impact natural experimental designs, and those that explore demographic mechanisms, remain the strongest pieces of evidence regarding how spotted owls respond to fire

† Descriptions correspond to in-text section headings.

forests experience natural "mixed-severity" to stand-replacing fire regimes, are at the upper end of Lee's (2018) representation of NRV in percentage area burned at high severity (Arno 2000, Brown and Smith 2000). NRV in percentage area burned at high-severity in frequent-fire forests, however, which occur throughout a large portion of the range of the spotted owl—such as in the Sierra Nevada in California, the eastern Cascades in Oregon and Washington, and parts of the southern Rockies in Arizona and New Mexico—is at the lower end of the range provided by Lee (2018) according to extensive published research (Sudworth 1900, Show and Kotok 1923, Kilgore 1973, Agee 1993, Skinner 1995, Skinner and Chang 1996, Brown and Smith 2000, Keeley and Stephenson 2000, van Wagtendonk and Lutz 2007, Miller et al. 2009, 2012, Mallek et al. 2013). For example, NRV for percentage area burned at high severity in the forest types used by the California spotted owl in the Sierra Nevada is generally 5–15% in yellow pine-mixed conifer and 5–20% in red fir forest, with characteristic patches of 10–100 ha (Safford and Stevens 2017). While Lee (2018) cited several studies suggesting that NRV in high-severity burned area is greater for frequent-fire forests, the data and analyses used in these studies have been questioned and their conclusions are not widely accepted by the scientific community (Brown et al. 2008, Safford et al. 2008, 2015, Fulé et al., 2014, Collins et al. 2015, Stephens et al. 2015, Stevens et al., 2016, Hagmann et al. 2017, 2018, Levine et al. 2017, Miller and Safford 2017). We refer readers to Safford and Stevens (2017) for an extensive discussion of disagreements in the literature about NRV of fire regimes in yellow pine-mixed conifer forests in California, USA, which is a subject of relevance to the assessment of fire effects on spotted owls.

The overgeneralization of the proportion of high-severity fire within the range of the spotted owl leads to a misunderstanding of the types of post-fire effects to which spotted owls in, for example, frequent-fire forests are likely to be adapted (or not adapted). Attention to historical fire regimes within the frequent-fire forests that dominate most of the range of the California spotted owl is particularly important here, as the majority of studies (80%; 12 of 15) and specific effects (80%; 40 of 50) used in the Lee (2018) meta-analysis were conducted in this region. Indeed, area burned at high-severity has been steadily increasing since 1984 with "mega-fires" such as the King Fire in the central Sierra Nevada that burned at 50% high-severity (Jones et al. 2016) now substantially exceeding NRV within frequent-fire forest as a result of fuels buildup, climate change, and other human legacies (Miller et al. 2009, Steel et al. 2015, Safford and Stevens 2017, Stevens et al. 2017, Keyser and Westerling 2019).

As such, spotted owls in some frequent-fire forests now appear to be experiencing novel post-fire forest conditions characterized by larger, high-severity patches that convert forests used for nesting and roosting habitat to either foraging habitat or vegetation types that are unsuitable for these critical events of spotted owl life history (Ganey et al. 2017, Lesmeister et al. 2019, Jones et al. 2016, 2020). Thus, where forests provide nesting and roosting habitat, thresholds in area burned likely exist at which high-severity fire creates novel conditions that adversely affect spotted owl demographic rates (Jones et al. 2016, Rockweit et al. 2017). The magnitude of effects is likely dependent on a combination of the sizes, distribution, and amount of (1) high-severity patches that occur in a territory and (2) nesting, roosting, and foraging habitat remaining within a territory post-fire (Jones et al. 2016, 2020). The magnitude of measured effects of severe fire also likely depends on how "severe fire" is defined. Lee (2018) notes that there is evidence that some owl territories experiencing high-severity fire across 100% of their territory area can remain occupied post-fire. However, severe fire is typically defined as >75% tree mortality – meaning that some patches of live trees can remain for nesting and roosting in such cases (Lee and Bond 2015*b*). In territories experiencing 100% tree mortality, it is biologically intuitive that a shade-adapted species like the spotted owl will be unlikely to persist even over the short term (Jones et al. 2016).

Even when owls persist in severely burned territories in the shorter term, individual fitness can be reduced creating sink habitats such that population declines may occur over the longer term (Rockweit et al. 2017). Recovery of critical and limited nesting/roosting habitat following a stand-replacing fire event can take from decades to over a century, and the potential conversion to foraging habitat does not compensate for long-term loss of nesting/roosting habitat (Ganey et al. 2017, Lesmeister et al. 2019). Loss of nesting and roosting habitat is likely to become more frequent in light of projections of increases in severe fire within frequent forests and the climate become warmer and drier (Jones 2019, Wan et al. 2019), a factor not considered by Lee (2018).

Statistical/Technical Issues

Focus on the summary (mean) effects in the presence of high among-study variability

A key conclusion reached by Lee (2018:1) was that "Spotted Owls were usually not significantly affected by mixed-severity fire" and most studies "found no significant impact of fire on mean owl parameters." Lee (2018) makes this claim because mean effects were not "statistically significant" at the $\alpha = 0.05$ level, even though this is increasingly recognized as an arbitrary threshold on which to base inference (Wasserstein and Lazar 2016, Dushoff et al. 2018, Amrhein et al. 2019). In conservation science, accepting a false null hypothesis can be particularly costly with negative consequences for species persistence and recovery (Fidler et al. 2006). More important is the question of whether effects are ecologically meaningful. As an example, the p-value for the mean standardized effect size (Hedges d) for the occupancy parameter was $P = 0.072$ (and therefore was not deemed to be significant). Lee (2018) does go on to discuss its potential ecological significance, but argues that the mean effect size for the occupancy parameter (−0.060) is negligible because it is smaller than average annual declines in unburned forest reported by Jones et al. (2016).

We believe this interpretation is incorrect for two reasons. First, the mean effect size for the occupancy parameter (−0.060) was not, as Lee (2018) noted, smaller than mean annual occupancy declines in unburned forest. In fact, it was approximately three times larger than the average annual decline in occupancy derived from Jones et al. (2016) (−0.021; pre-fire average of annual raw changes in occupancy, 1993–2014), suggesting that indeed the measure was ecologically meaningful. Lee (2018) calculated the "typical annual declines in occupancy rates" in unburned forest as the average of raw changes in occupancy *only for those years with a negative sign*. This calculation yielded a value of −0.068. By definition, however, the approach used by Lee (2018) would always be expected to result in an overestimated decline that does not reflect the observed downward trend. By correctly averaging raw changes in occupancy from all years with both positive and negative annual changes (which would be considered standard practice in population ecology), a value of −0.021 is obtained. Thus, the average effect of fire on owl occupancy derived from the Lee (2018) meta-analysis (−0.060) exceeded background rates of annual occupancy declines in unburned forest (−0.021), indicating that the average negative effect of fire on occupancy was biologically meaningful.

Second, interpreting the mean effect was problematic because of high among-study variability. Specifically, meta-analyses that focus on summary (mean) effects and deemphasize among-study variability likely lead to conclusions that are incorrect (Bailar 1997, Borenstein et al. 2009). For example, Figure 2 in Lee (2018) shows considerable variability in positive and negative effect sizes that average out to either a neutral or close to neutral mean. As noted by Peery et al. (2019), among-study variability in the estimated effect size of fire across all parameters examined by Lee (2018) (i.e., occupancy, demography, foraging) was high by meta-analytical standards as quantified by the overall I^2 value (95.5%), which is a measure of among-study dispersion (Higgins et al. 2003). The I^2 values in Lee (2018) were similarly extreme for each individual grouping of parameters examined (occupancy = 97.72%; demography = 84.04%; foraging = 84.42%). Indeed, meta-analytical standards suggest that generalizations should be avoided when I^2 values exceed 50-75% (Higgins and Thompson 2002, Higgins et al. 2003). Borenstein et al. (2009:378) writes: "If there is substantial dispersion, then the focus should shift from the summary effect to the dispersion itself. Researchers who report a summary effect and ignore heterogeneity *are indeed missing the point of the synthesis* [emphasis added]." Moreover, variability in estimated fire effects among studies was greater at burned than unburned territories, which makes generalizations about how owls respond to fire difficult.

The putatively meaningful reduction in occupancy in burned territories coupled with the high level of variability in effect sizes contradicts the conclusion that fire does not threaten owl populations. Rather these findings support the conclusion that wildfire effects on spotted owls can be positive, neutral, or negative depending on the specific context, likely related to patch size and spatial patterns of severe fire (Ganey et al. 2017, Rockweit et al. 2017, Lesmeister et al. 2019, Jones et al. 2016, 2020). In the meta-regression portion of the paper, Lee (2018) explored how high-severity burned area within territories could have explained some of this variation and found a "nearly significant" negative effects across all parameters ($\beta = -0.044$; $P = 0.062$), but did not discuss or interpret the potential meaning of this result. Rather, Lee (2018) split the meta-regression of high-severity fire effects into parameter-specific regressions (occupancy, demography, and foraging) leading to small sample sizes that likely contributed to non-significant and inconclusive results. The only significant effect related to high-severity fire was a positive effect on reproduction ($\beta = 0.234$, $P = 0.032$), which was a regression through four data points (Lee 2018, Fig. 5; only three points are visible because two of the data points are identical, see *Inclusion of identical data used in multiple studies* below), highlighting potential issues with small sample sizes across multiple parameters (Lee 2018, Figs. 4 and 5). The occupancy effect, in contrast, had a reasonably good sample size ($n = 20$ effects) and was found to be negative ($\beta = -0.036$) but non-significant at $\alpha = 0.05$ ($P = 0.1$). However, as we describe below, this analysis used erroneous occupancy data that would be expected to bias the effect toward zero and was therefore insufficient to answer the question addressed.

Selected data and representation of high-severity fire resulted in reduced variability in ecological effects

Lee (2018) reported the "percentage of high-severity fire in burned territories" in his Table 2 (pp. 10–11) for each of the 50 effects from the 15 studies used in the meta-analysis. This reported value was meant to represent the "amount of high-severity fire in the total fire perimeter and/or within the owl territory core areas examined" (Lee 2018:4) for the sample group representing the effect. For example, if a group contained 10 territories, the value reported in Table 2 (Lee 2018) was supposed to represent the mean percent high severity across those 10 territories. If the territory-specific values were not reported in the original papers, the percent of the total fire area containing high-severity fire was recorded. These data were used as inputs to the meta-regression analysis in which Lee (2018) explored the potential for high-severity fire to explain variability in standardized mean effects. We think there are at least two problems with this approach that individually and collectively indicate that the conclusion drawn from the meta-analysis that severe fire does not threaten spotted owls is not supported.

First, mixing territory- and fire-level estimates of severe burn extent is problematic because fire-level estimates have the potential to systematically bias the extent of severe fire experienced by individual territories. An important example illustrating this problem comes from Jones et al. (2016), where Lee (2018) estimates the high-severity value to be 64% for a group of n = 14 severely burned territories (Lee 2018:11, Table 2, line 2). The 64% value comes from an appendix from Jones et al. (2016; WebTable 1) that represents the percentage of the entire study area affected by high-severity fire. The actual mean value across territories in this group was 89% (noted by Kelsey 2019), with individual territories containing between 71 and 100% severe fire. Underestimating severe fire extent within this group alone likely altered results of the meta-regression analysis focused on occupancy (see Lee 2018:16, Fig. 4). Hence, using a fire-level average may consistently underrepresent high-severity fire extent experienced by spotted owl territories if those territories burn at higher severities than the broader landscape.

Second, using a single, fire-level average value of high-severity fire extent eliminates all variation in severe fire effects among territories that likely mediates spotted owl response within a given study. That is, whether fire has a positive or negative effect on a given parameter (e.g., occupancy) will depend on variation in the amount of severe fire that occurred within individual territories, and such an effect is likely to include thresholds and/or may be non-linear. Thus, there was a hierarchical elimination of variation in fire severity, first within study areas (see above) and second among study areas. Indeed, distilling this variation into a single mean value that applies to all territories leads to a loss of information about how the scale/extent of severe fire affects spotted owls in an ecologically meaningful way.

Inaccuracies in reported fire effect sizes

A requirement for meta-analysis is the ability to obtain accurate and standardized effect sizes from different studies on exactly the same scale (Koricheva et al. 2013). We found several instances where effect sizes and/or group sample sizes (n) reported by Lee (2018) were either demonstrably incorrect or non-reproducible.

Using the same example study group from the above section (Jones et al. 2016), Lee (2018) reported a raw effect size (mean difference) of −0.49, meaning that occupancy probability, or proportion of sites occupied, was 0.49 lower in the burned group (0.08) than the control group (0.57) (see Lee 2018:11, Table 2, line 2). However, Lee (2018) used the wrong set of territories as the control group. Specifically, he used the pre-fire (2014) estimate of occupancy from the entire study area (including burned and unburned territories) the year prior to the fire (2014) as the control group (0.57) when he should have used the reported pre-fire (2014) estimate of occupancy from the burned group (0.72) (see Jones et al. 2016:304). He thereby underestimated the raw effect size, which we would have computed as −0.64 not −0.49, a notable difference.

In other cases, we could not reconstruct values presented in Table 2 (Lee 2018). For example, the two effect groups corresponding with Hanson et al. (2018), Table 2 of Lee (2018) indicates the control (unburned) group consisted of n = 201 territories. However, Hanson et al. (2018) only reported parameter estimates (in this case, occupancy) from n = 54 territories, all of which experienced fire (Table 3 from Hanson et al. 2018). Thus, it is unclear from where the control group values reported in Table 2 of Lee (2018) for this study came, and how a sample size of n = 201 was calculated. An improperly specified large sample size would more heavily weight results from this study in the meta-analysis.

Another example comes from Table 2 of Lee (2018) where a positive, significant effect of fire (the 2013 Rim Fire) on occupancy (+0.175) from Lee and Bond (2015*b*) was reported; this positive effect was also the largest standardized effect obtained from any study, as shown in Figure 2 of Lee (2018). However, this effect was not reported anywhere in the text of Lee and Bond (2015*b*), and we were unable to reproduce the value (+0.175) using any information available within that paper. The only modeled effects of fire on occupancy reported by Lee and Bond (2015*b*) were either neutral or negative; no positive effects were reported in their analysis. Moreover, for this specific effect, Lee (2018) reported a sample size for unburned sites of n = 145 in Table 2 (only 45 sites were included in Lee and Bond 2015*b*), which would heavily weight its positive effect in the meta-analysis. For the negative and neutral effects of fire on occupancy reported from this same study (Lee and Bond 2015*b*), Lee (2018) reports n = 45 for both the unburned (control) and burned groups, although there were only 45 sites in the entire study. The inclusion of a large positive effect of fire on spotted owl site occupancy that could not be verified and appears to have been improperly weighted, along with incorrect group sample sizes for other effects from Lee and Bond (2015*b*), likely influenced the inferences made in the Lee (2018) meta-analysis.

Transparency in reporting and treatment of studies with confounded salvage logging and fire effects

Lee (2018) reports in his Table 1 standardized effect sizes for salvage logging in studies where it was possible to distinguish between salvage and wildfire effects. In the final paragraph of the results section, Lee (2018:15) reports that "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)." However, the analytical method was not presented, and we were therefore unable to validate the estimated effect size of salvage logging on occupancy (−0.18) using the data from studies presented in Table 1 (the estimate for survival was based on a single study).

Perhaps more important than clearly reporting the methods used in the salvage logging analysis was the lack of consistency in how the confounding of salvage logging with fire effects from different studies were categorized and treated. As an example, two studies considered in the meta-analysis (Lee et al. 2012, Clark et al. 2013) were unable to distinguish between the effects of salvage logging and wildfire (i.e., the effects were confounded) on occupancy rates; this limitation was explicitly noted in the text of each respective study. However, in the meta-analysis (Lee 2018), the effect of salvage/fire on occupancy from Clark et al. (2013) was attributed exclusively to salvage logging (−0.39) and subsequently excluded from analyses of wildfire effect. Yet the salvage/fire effect from Lee et al. (2012) was attributed exclusively to fire (+0.041) and subsequently included the effect in the analysis of wildfire effects (see Lee 2018: Fig. 2 and Tables 1 and 2). To maintain consistency in the treatment of studies, both effects should be either included or excluded from wildfire analyses. Including the effect from Lee et al. (2012) and excluding the effect from Clark et al. (2013) would be expected to shrink the estimated mean effect of fire on occupancy (see Lee 2018: Figs. 2 and 3) and potentially influence inferences made from the meta-regression analysis (see Lee 2018: Fig. 4).

Inclusion of duplicated data from multiple studies

An assumption underlying meta-analysis is that effects measured from individual studies are independent. Violation of the independence assumption can produce a standard error on the mean effect that is too small (Gurevitch and Hedges 1999). Non-independence of study effects commonly arises in meta-analyses when data are collected from the same geographical region, or from the same laboratory group, such that effects may be more similar within regions/groups than among regions/groups. Such dependence can be accounted for in a meta-analytical framework using random effects structures (Gurevitch and Hedges 1999). A related, but potentially more serious problem arises when the exact same underlying data are used in multiple publications, and effects from those publications are subsequently summarized as different effects in a meta-analysis ("duplicate study effects"; Wood 2008). Possible remedial measures for dealing with data duplication in meta-analyses include aggregation of effects or eliminating duplicate effects from the meta-analysis (Wood 2008).

The Lee (2018) meta-analysis included effect sizes from multiple studies using the exact same underlying data, but no remedial measures were taken. Specifically, 4 of the 15 studies from which Lee (2018) used data for the meta-analysis contained data that were duplicate records from another study in the analysis. The level of duplication varied, ranging from identical occupancy histories shared by a subset of territories between studies (Jones et al. 2016, Hanson et al. 2018) to full dataset duplication (Lee et al. 2013, Lee and Bond 2015*b*). First, Hanson et al. (2018) used occupancy data from six of the 45 territories used by Jones et al. (2016) to assess the effects of severe fire on spotted owl site occupancy. Second, Lee and Bond (2015*a*) was a re-analysis of the exact occupancy dataset used by Lee et al. (2013), but the former used a multi-state occupancy model and the latter used a single-state occupancy model. How duplicate study effects might have influenced inferences made by Lee (2018) about the effects of fire on occupancy rates remains uncertain.

Underestimation and miscalculation of negative effects of fire on occupancy from individual studies

Following the Lee (2018) meta-analysis, three studies were published showing results from some papers used by Lee (2018) contained errors that led to the underestimation or miscalculation of the effect of fire on spotted owl site occupancy. First, Berigan et al. (2019) showed that failing to account for wide-ranging behaviors of individual unmarked spotted owls after the 2013 Rim Fire (which contained a considerable high-severity component) may have underestimated the effect of this fire on site occupancy by ~20% (Lee and Bond 2015*a*). Second, Jones and Peery (2019) showed that while Lee and Bond (2015*a*) suggested the negative effect of fire on site occupancy was smaller for breeding owls (−0.02) and larger for non-breeding owls (−0.19) in southern California, the modeled effect was actually the same for both breeding states; the odds of a site being unoccupied increased by a factor of 2.5 for both breeding states following fire. The conclusion reached by Lee and Bond (2015*a*) was based on a misinterpretation of covariate effects in a multi-state occupancy model. Third, Hanson et al. (2018) used inaccurate detection histories and excluded from their analysis of severe fire effects on occupancy the territories that experienced >80% high-severity fire (and thus were most likely to demonstrate an effect of high-severity fire) (Jones et al. 2019), which would be expected to underestimate potential negative severe fire effects. Although we recognize that the critiques of these papers and their data were not published until after Lee (2018), their inclusion in the meta-analysis affected the meta-analysis of variation and the meta-regression that found no statistically significant effects of fire in general, and severe fire specifically, on occupancy.

Lee's (2018) calculation of the effects of fire on spotted owl territory occupancy in moderately burned territories (mean = 12% area burned at high-severity fire) within the King Fire studied by Jones et al. (2016) also may have contributed to his finding that fire did not affect spotted owls. Specifically, Lee (2018:11, Table 2, line 3) calculated a value of 0.07 for this effect, indicating that fire benefited owls at these sites. While it is certainly true that occupancy increased in this group of territories, the increase occurred because some of these sites—which were vacant before the fire—were colonized (and thus become occupied) by dispersing individuals that were displaced from nearby territories experiencing more extensive severe fire (mean = 89% area burned at high-severity fire; see WebFigure 4 from Jones et al. 2016). Attributing the increase in occupancy at territories experiencing a mean of 12% severe fire (note: Lee [2018] recorded that these territories experienced a mean of 19% severe fire) to the positive effects of fire does not reasonably capture the ecological processes by which fire influences individual behavior and its emergent effects on populations. Thus, attributing a positive effect of fire to occupancy at these sites may have biased the overall estimate of fire effects on occupancy in a positive direction in the meta-analysis. Moreover, this key insight about fire impacts on individuals was enabled by the detailed study of a banded population of spotted owls in Jones et al. (2016) and involved dynamics that were not possible to identify in many of the occupancy studies of unbanded owls used in Lee (2018).

Inferential Issues

Context of changing wildfire trends

Lee (2018:19) states that "forest fire does not appear to be a serious threat to owl populations and likely imparts more benefits than costs for Spotted Owls..." In support of this conclusion, Lee (2018) cites studies suggesting that mixed-severity fire typically affects "a very small portion (0.02–0.50%) of spotted owl nesting and roosting habitat per year..." We agree that severe fire has not yet resulted in substantial declines in spotted owl populations at regional or subspecies scales and rather that recent declines (Conner et al. 2016, Dugger et al. 2016, Tempel et al. 2016) have occurred for other reasons including competition with barred owls (Diller et al. 2016, Dugger et al. 2016, Mangan et al. 2019), potentially the loss of large trees and old-forest habitat (Jones et al. 2018), and potentially shifts in prey communities (Hobart et al. 2019). Certainly, severe fire has caused declines in spotted owl abundance at more local scales (e.g., 100s of km^2; Jones et al. 2016) and resulted in an enduring loss of nesting and roosting habitat, but fire has not been an overriding driver of recently observed long-term spotted owl population declines.

However, the conclusion that wildfire does not pose a threat to spotted owls does not take into account that wildfires will inevitably become larger and more severe in rapidly warming and drying forest ecosystems (Westerling and Bryant 2008, Stephens et al. 2013, Liu et al. 2013, Millar and Stephenson 2015, Abatzoglou and Williams 2016, Davis et al. 2017, Stevens et al. 2017, Littell et al. 2018, Wan et al. 2019), with Lee (2018) making no mention of climate change or its potential effects on future wildfire activity or spotted owls. Moreover, the only conclusion that can be drawn from the meta-analysis (Lee 2018) regarding the benefits of fire on owls was a positive effect to foraging-related parameters (see Lee 2018: Figs. 2 and 3). However, as noted above, any potential increase in foraging habitat resulting from mixed-severity fire will not compensate for a continued loss of nesting and roosting habitat, which is well-understood to be a key factor limiting spotted owl populations throughout their range (Ganey et al. 2017). High-severity fire effects across the range of all three subspecies of spotted owls are expected to increase over the coming decades (Wan et al. 2019), and in some regions, it has been shown that cumulative nesting habitat area that will experience >50% basal area mortality from wildfire over the next 75 yr may exceed the total existing nesting habitat amount available for California spotted owls (Stephens et al. 2016). Within the range of the northern spotted owl, fire regimes are expected to shift to more frequent-fire return intervals and higher prevalence of large forest wildfires as climate changes over the next century (Davis et al. 2017). These predictions make it clear that those interested in conserving old-forest species and their ecosystems must consider the future consequences of changing disturbance regimes.

Looking ahead is a fundamental principle of conservation biology, which is "concerned with the long-term viability of whole systems." (Soulé 1985:727). To discard evidence that the types of fires that threaten spotted owls are the same types of fires that are predicted to become more common in the future (e.g., large, severe fires; Littell et al. 2018, Wan et al. 2019) does not give full justice the risks posed by wildfire to this species. Of course, the meta-analysis (Lee 2018) was explicitly retrospective and therefore necessarily focused on owl responses to past fire events and the "current" threat of fire. However, Lee (2018) states that his meta-analysis has rendered existing planning documents outdated (USFWS 2011, 2012, 2017, Gutiérrez et al. 2017, USDA 2019). Beyond the concerns, we have described herein, several of the planning documents to which Lee (2018) refers (see below) do in fact consider how climate change is expected to increase severe fire activity and by extension affect spotted owls. As such, we do not universally consider them to be outdated and, rather, consider them forward-looking.

The use of meta-analyses to solve complex conservation issues and superseding of existing understanding

We raise two final questions regarding the claim in Lee (2018) that the meta-analysis indicates that forest fires pose little risk to spotted owls. First, is meta-analysis sufficient to settle complex conservation issues? While meta-analysis has helped to advance scientific understanding across a broad range of disciplines by offering tools for science synthesis (Gurevitch et al. 2018), its ability to lead to novel understanding is limited by the input data and decisions made by the meta-analyst. Moreover, we suggest that meta-analyses are not replacements for mechanistic ecological studies. In the case of spotted owls, intensive, long-term studies of marked individuals demonstrate that owls can be displaced by severe fire (Jones et al. 2016) and that severe fire can create sink habitats (Rockweit et al. 2017), both processes that are difficult capture within a meta-analyses framework and likely contributed to Lee's (2018) conclusion that severe fire does not adversely affect spotted owls. Yet, because meta-analyses are often viewed as a gold standard of evidence synthesis, meta-analyses that yield erroneous inferences are likely to further confuse already complex conservation issues and have the potential to lead to negative conservation consequences. As we have pointed out throughout this comment paper, Lee (2018) contains issues that have created more confusion and thus it did not resolve the complex issue of conserving spotted owls in fire-prone forests.

Second, shall the conclusions reached by Lee (2018) supersede the existing literature and current understanding of spotted owl responses to fire? What Lee (2018) has demonstrated is that responses of spotted owls to fire is varied, as we discussed above; a conclusion that is a well-supported by previous empirical studies and review papers (Ganey et al. 2017, Lesmeister et al. 2018, Wan et al. 2018). That is, there is no consistent way spotted owls respond to what Lee (2018) refers to as "mixed-severity fire," in either magnitude or direction. However, fires dominated by lower burn severities have minimal effects to owls, whereas fires with greater high-severity characteristics tend to yield mixed demographic responses by owls. Responses to high-severity fire specifically are likely to depend on severe fire patch size, spatial pattern, and extent (Ganey et al. 2017, Wan et al. 2018, Jones et al. 2016, 2020), but as we discussed above, the Lee (2018) meta-analysis was inadequate in assessing these nuances.

Individual studies based on long-term demographic studies of marked individuals and involving before-after-control-impact study designs have shown that large and uniform patches of high-severity fire have negative effects on owl parameters (Jones et al. 2016, Rockweit et al. 2017). In contrast, large but more complex patches of high-severity fire may have less negative effects by comparison (Lee and Bond 2015*b*). Moreover, there may be a threshold of high-severity effects within territories beyond which extirpation becomes more likely (Lee et al. 2013). Moreover, spotted owls may use severely burned forest for foraging when patches are relatively small (Bond et al. 2009, 2016, Jones et al. 2020) but tend to avoid larger patches and particularly the interior of large patches (Eyes et al. 2017, Jones et al. 2016, 2020). Certainly, questions related to the temporal scale of adverse severe fire effects have not been fully addressed in the literature. Nevertheless, conclusions about severe fire effects on spotted owls from previous studies need to be considered regardless of those made by the Lee (2018) meta-analysis and remain of critical importance to managers and conservation practitioners.

Conclusions

We appreciate the attempt made by Lee (2018) to provide a quantitative synthesis of fire effects on spotted owls, which until this time had been lacking. However, because of the ecological, statistical/technical, and inferential issues we have discussed above, this attempt did not provide clarity. In fact, the conclusions drawn are faulty and should not be taken to replace or supersede the existing body of literature demonstrating the highly variable ways in which spotted owls respond to different types of fire. Moreover, planning documents stating that changing wildfire regimes pose a considerable threat to spotted owls remain current despite the assertion of Lee (2018).

The existing body of evidence suggests that spotted owls respond largely in a neutral or positive manner to lower-severity fire and smaller patches of high-severity fire that fall within the historical range of variability but that spotted owls can respond negatively to larger patches of high-severity fire. Thus, management actions that can demonstrably reduce the extent of severe fire within spotted owl habitat in a changing climate may contribute to owl conservation if those actions do not remove critical structural habitat elements positively associated with spotted owl vital rates (e.g., large, old trees) (Jones et al. 2016, 2018, Jones 2019). It is critical that future analyses examining the effects of fire on spotted owls provide sufficient context and nuance to ensure they will be beneficial to scientists and managers seeking to understand how to minimize the loss of essential owl nesting and roosting habitat to the increasing threat of high-severity fire in a changing climate.

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