

REPLY

Spotted owls and forest fire:
ReplyDEREK E. LEE †

In response to US Fish and Wildlife Service and USDA Forest Service planning documents that emphasized fire as a primary threat to spotted owl (*Strix occidentalis*) population persistence (e.g., USFWS 2017, USDA 2018), I performed a detailed multifaceted meta-analysis of all published studies of spotted owls and forest fire (Lee 2018). I found significant positive effects on foraging habitat selection and recruitment from mixed-severity forest fires, and significant positive effects on reproduction from high-severity fire. My meta-analysis examined key life history parameters in response to fires as they have burned through spotted owl habitat in recent decades under existing forest structural, fire regime, and climate conditions, including multiple “megafires” with large patches of high-severity burn. The absence of any widespread, consistent, and significant negative fire-induced effects and the presence of significant positive effects indicated forest fire is not a serious threat to owl populations. Therefore, fuel-reduction treatments intended to mitigate fire severity in spotted owl habitat are unnecessary and perhaps counterproductive to the species’ recovery. Planning documents claiming that forest fires currently, or will in future, pose the greatest risk to owl habitat and are a primary threat to population viability are either outdated or highly speculative in light of the Lee (2018) review.

Jones et al. (2020; hereafter Jones et al.) agreed with my most important assumptions, findings,

and conclusions from Lee (2018), namely: my characterization of western US forests inhabited by spotted owls as generally burning in mixed-severity fires where 5–70% of burned area is in high-severity patches with >75% mortality of dominant vegetation; that spotted owl responses to recent mixed-severity fires are variable; that severe fire has not resulted in substantial declines in spotted owl populations; and that fire has not been an overriding driver of recently observed long-term spotted owl population declines. Even though Jones et al. agreed with me that severe fire has not resulted in range-wide spotted owl population declines, and that fire has not been an overriding driver of recently observed long-term spotted owl population declines, Jones et al. questioned the results of my meta-analyses that illustrated why declines are not linked to fire.

The aim of Lee (2018) was to provide forest managers and decision-makers with a clear and concise summary of all evidence for mixed-severity fire effects on spotted owls in order to better inform forest management. Forest Service planning documents assume (paraphrasing): fire can harm owls and therefore owl territories and other owl habitat must be logged to protect owls from fire (e.g., USDA 2019). Jones et al. (2016), a reference often used to justify logging (e.g., USDA 2019), represent 1 fire, 30 burned territories, and 9 radio-tracked owls. Lee (2018) presented management guidelines based on a quantification of all available evidence including more than 20 fires, 425 burned territories, and 37 radio-tracked owls. The much larger dataset in Lee (2018) found mixed-severity fire, including several megafires with large high-severity patches, has mostly neutral effects, but also provides significant benefits to spotted owls.

The strength of meta-analysis as an evidence-based decision support tool is that it enables managers and decision-makers to justify management decisions using patterns and trends from all available data rather than making decisions based on a portion of a single study. I say “a portion of” because Jones et al. (2016) showed both negative and positive effects from a megafire, but typically only the negative effects are

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Biology Department, Pennsylvania State University, University Park, Pennsylvania, USA.

† E-mail: dereklee@psu.edu

used to justify management actions while fire-induced positive effects are ignored (e.g., USDA 2019). Similarly, Jones et al. advocate for what they call “context-specific” interpretation of owl responses to fire and emphasize only a few specific results from a few papers to inform forest management against fire while discounting the majority of evidence that indicates fire is neutral or beneficial and could be encouraged.

The observed variation in effects among studies and sites can be considered noise around a mean overall signal. The mean overall signal indicates all fires’ effects on all spotted owls everywhere. Given the Forest Service must manage an enormous area of forest lands for multiple uses, their management must consider mean overall effects as the most parsimonious description of a phenomenon. The evidence synthesized in Lee (2018) indicating that fire is not a grave and immediate threat to owl populations, and has some beneficial outcomes, directly supports management decisions that prioritize allocating wildfire management and suppression resources toward human communities rather than spotted owl habitat. Wildfires can pose a serious threat to human life and property, and wildfire never imparts benefits to human structures. There are limited resources available to protect homes and communities from wildfire (Schoennagel et al. 2017), and treating backcountry forested lands such as in owl habitats has no impact on community safety (Cohen 1999, 2000), so forest fire mitigation resources should be focused on home fire resistance and protection (Schoennagel et al. 2017).

Jones et al.’s comment on Lee (2018) included several suggestions for technical modifications to the meta-analyses (Table 1). Some of these same suggestions for how Lee (2018) could be improved also appeared in Peery et al. (2019). In summary, Jones et al. and Peery et al. (2019) suggested my meta-analyses in Lee (2018) should have: (1) not focused my conclusions on mean effects because of the variation in effects across studies, nor used P values < 0.05 to determine significance; (2) excluded all studies with post-fire logging; (3) accounted for or eliminated data duplication; (4) analyzed subspecies separately; and (5) used different effect sizes and sample sizes for certain papers.

To test whether my original results in Lee (2018) were robust to the above-listed technical criticisms, I reanalyzed the data according to all their suggestions. Details are given below, but to summarize, none of their suggestions changed the results reported in Lee (2018). Regarding criticism 1, Lee (2018) did not focus on mean effects, in fact I thoroughly described and explored the variation among studies by presenting: (1) a random-effects meta-analysis of overall and parameter-specific mean effect sizes; (2) a two-step mixed-effects meta-regression to explain heterogeneity in mean effect sizes that included accounting for among-study and regional variation, time since fire, percent of high-severity fire in the study area, and parameter type (occupancy, survival, reproduction, recruitment, and foraging); and (3) a random-effects meta-analysis of variation to examine differences in parameter variances due to fire. My reporting of mean effect sizes and using $\alpha = 0.05$ for statistical significance are well-established norms for presenting ecological evidence. Many researchers have criticized null hypothesis significance testing using $\alpha = 0.05$, and many have defended it as well (Balluerka et al. 2005). In addition to the technical considerations, Jones et al. also offered their opinions on the ecological and inferential context of Lee (2018). A summary of Jones et al.’s issues with Lee (2018) along with my brief responses to each are found in Table 1.

For my reanalyses here addressing each of Jones et al.’s technical issues, I followed the same methods detailed in Lee (2018). I used: appropriately weighted and standardized effects (to account for different sample sizes and variances among studies); and random-effects and mixed-effects models (to account for non-independence of effects reported in the same study, partially duplicated datasets in a few studies, and other realities of meta-analyses to provide an inference about the average effect in the entire population of studies from which the included studies are considered to be a random selection). For comparison, the original Lee (2018) overall random-effects model standardized mean difference between unburned and burned sites was: -0.095 (95% CI: -0.537 to 0.348), a non-significant, slightly negative effect of mixed-severity forest fire (Fig. 1).

Table 1. Summary of Jones et al.'s issues related to Lee (2018) and responses.

General description	Issue	Response by Lee
Ecological		
Overgeneralization of historical fire regimes within forests inhabited by owls	Forest types and resulting fire regimes vary considerably across the geographic ranges of the three spotted owl subspecies analyzed	Geographic variation was accounted for in Lee (2018). Each parameter (e.g., occupancy) was modeled with effects of each study (e.g., Bond et al. 2009) within geographic region (e.g., Sierra Nevada) as multi-level random effects to properly estimate study site and region-specific variation and to account for repeated measurements (pseudo-replication) within a study or region. Subspecies-specific differences were also empirically tested for and no significant effects were observed. This was clearly stated in Lee (2018)
Statistical/technical		
Focus on the summary (mean) effects in the presence of high among-study variability	There was extremely high variation in effects across studies, including strong negative and positive in addition to neutral effects. In the presence of such high variability, the "average" effect is meaningless	Lee (2018) thoroughly explored and presented heterogeneity in effects, including 1) a random-effects meta-analysis of mean effect sizes including 10 sub-stratifications to specific parameters; 2) a 2-step mixed-effects meta-regression to explain heterogeneity in mean effect sizes that included 17 sub-stratifications accounting for among-study and regional variation, time since fire, percent of high-severity fire in the study area, and parameter type (occupancy, survival, reproduction, recruitment, and foraging); and 3) a random-effects meta-analysis of variation to examine differences in parameter variances due to fire
Selected data and representation of high-severity fire resulted in reduced variability in ecological effects	Spotted owls respond to fire at the territory level. Using the average value eliminates all variation in severe fire effects among territories that likely mediates spotted owl response within a given study	In meta-analyses such as Lee (2018), each included study can be thought of as a single sample from the population of all possible studies with relevant results (e.g., mean occupancy before and after a fire) and those results can be associated with some study-specific covariate values such as mean proportion of territories burned high severity or time since fire. Meta-analysis summarizes the results from many different studies and looks for patterns in results relative to covariates, but cannot be expected to have access to or use raw data from every study. Lee (2018) followed well-established accepted methods of meta-analysis. Jones et al. are setting an impossibly high standard for meta-analyses
Inaccuracies in reported fire effect sizes	A requirement for meta-analysis is the ability to obtain accurate and standardized effect sizes from different studies	Reanalysis using Jones et al.'s suggested effect parameters and sample sizes (see Fig. 1) resulted in no change in the results as reported in Lee (2018). Removing problematic studies also resulted in no change to the results reported in Lee (2018)
Transparency in reporting and treatment of studies with confounded salvage logging and fire effects	Studies with confounded fire-logging effects (i.e., when those effects could not be separated) should be treated in the same way: included or excluded. Moreover, we could not reproduce results by Lee (2018) regarding mean salvage logging effects	Lee (2018) removed 3 studies, all from the same study area, where post-fire logging was reported by the authors as so widespread and complete in areas of high-severity fire that essentially no unlogged high-severity patches remained. Reanalysis after removing all studies with any amount of post-fire logging made the overall effect of mixed-severity forest fire on spotted owls positive but not significantly so (Fig. 1)

(Table 1. Continued.)

General description	Issue	Response by Lee
Inclusion of duplicated data from multiple studies	This is referred to as “duplicate study effects.” It is recommended that duplicate study effects be either pooled or discarded from meta-analyses to avoid inferential errors	Lee (2018) accounted for duplicated data in all analyses. The inclusion of all papers, including those with repeated data, is common practice in meta-analyses, and the random-effects and mixed-effects models I used explicitly account for duplicated data. To test Jones et al.’s assertion that data duplication was a problem in Lee (2018), I removed all studies that used some or all of the dataset from another study and reanalyzed. Removing all studies with data duplication made the overall effect of mixed-severity forest fire on spotted owls positive but not significantly so (Fig. 1)
Underestimation and miscalculation of negative effects of fire on occupancy from individual studies	Some of the underlying data included in the meta-analysis of fire effects on owls contain errors or biases and thus may be unreliable	Reanalysis after removing Lee and Bond (2015a), Hanson et al. (2018), and the positive effect of < 50% high-severity burned territories in Jones et al. (2016) resulted in no change to Lee (2018) results (Fig. 1)
Inferential		
Context of changing wildfire trends	A sizeable body of literature suggests that severe fire activity in the spotted owl’s range will continue to increase and will possibly result in the loss of a majority of critical spotted owl nesting habitat by the end of the 21st century	There is considerable uncertainty surrounding recent and prehistoric patterns and trends in fire size and severity in spotted owl habitats. Jones et al.’s narrative was biased and highly speculative. Jones et al. agreed with me that severe fire has not yet resulted in substantial declines in spotted owl populations, and fire has not been an overriding driver of recently observed long-term spotted owl population declines. The years that produced the studies in Lee (2018) were among the biggest fire years in 40 years, so they accurately represent owl responses to fires within an already warmed and changed climate milieu
The use of meta-analysis to solve complex conservation issues and superseding of existing understanding	Meta-analyses are not replacements for studies that explicitly test mechanisms. Moreover because they are considered a “gold-standard” of evidence synthesis, meta-analyses yielding erroneous inferences can lead to further confusion of complex topics	Meta-analyses are powerful tools for synthesizing results from numerous studies and are designed to deal with heterogeneity and complex varied effects. Lee (2018) found consistent, significant patterns in how owls respond to mixed-severity fire by synthesizing available studies. Namely: a positive effect on recruitment immediately after the fire, with the effect diminishing with time since fire; reproduction positively correlated with the percent of high-severity fire in owl territories; and positive selection for foraging in low- and moderate-severity burned forest while high-severity burned forest was used in proportion to availability but not avoided. Reanalyses did not support any of Jones et al.’s criticisms, and confirmed the results from Lee (2018). Meta-analysis will always be superior to cherry picking one or a few studies to justify “context-specific” management decisions

REMOVING EFFECTS CONFOUNDED BY SALVAGE LOGGING RESULTS IN AN OVERALL POSITIVE EFFECT OF FIRE

When all studies known to have any amount of post-fire salvage logging were excluded from the analysis, I was left with four papers (Bond

et al. 2002, Roberts et al. 2011, Lee and Bond 2015a, Eyes et al. 2017). The overall difference in effect size between unburned and burned sites in the absence of salvage logging was +0.24 (95% CI: −0.94 to 1.43). Therefore, removing all studies with any amount of post-fire logging made the overall effect of mixed-

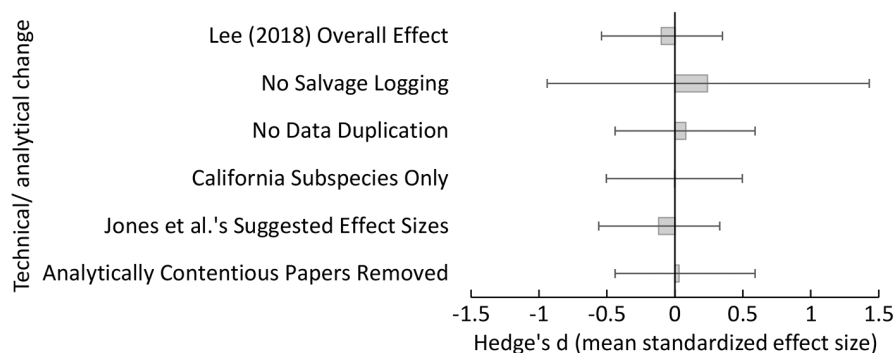


Fig. 1. Results from reanalyses of data used in Lee (2018) meta-analysis of spotted owl responses to mixed-severity forest fire, as suggested in Jones et al. (2020). Whiskers indicate the 95% confidence interval. Jones et al.'s speculations that various changes in data would alter results were not empirically supported.

severity forest fire on spotted owls positive but not significantly so (Fig. 1). No further analyses could be done because the sample of papers was so reduced by removing those with any salvage logging. All of the published peer-reviewed papers on owls and fire that examined salvage logging found negative effects from salvage logging on spotted owls (Lee 2018). Salvage logging has strong negative effects on many aspects of forest ecology and biodiversity (Lindenmeyer et al. 2012, Thorn et al. 2018), so a negative effect of post-fire logging on spotted owls is not surprising.

REMOVING DUPLICATE DATASETS RESULTS IN AN OVERALL POSITIVE EFFECT OF FIRE

The inclusion of all papers, including those with repeated data, is common practice in meta-analyses, and the random-effects and mixed-effects models I used explicitly account for this practice. To test Jones et al.'s assertion that data duplication might be a problem in Lee (2018), I removed studies that used some or all of the dataset from another study. I eliminated older studies and kept the more recent study. I removed Hanson et al. (2018), Roberts et al. (2011), Tempel et al. (2016), the occupancy component of Tempel et al. (2014), Lee et al. (2013), and Lee et al. (2012). The mean difference between unburned and burned sites in the absence of data duplication was +0.08 (95% CI: -0.44 to 0.59). Therefore, removing all studies with data duplication

made the overall effect of mixed-severity forest fire on spotted owls positive but not significantly so (Fig. 1). Removing all studies with data duplication also did not change the results of meta-regression analyses.

ANALYZING SUBSPECIES SEPARATELY IS EMPIRICALLY UNSUPPORTED

My methods to explain heterogeneity in effects included accounting for among-study and regional variation (Table 1). For northern and Mexican subspecies, there was only 1 paper each presenting subspecies-specific data (Jenness et al. 2004, Rockweit et al. 2017). The terms for subspecies in my meta-regression were not significant (Lee 2018), so there was no empirical evidence from these two papers that the Mexican or northern subspecies have responses to fire that are substantially different from the California subspecies. The most parsimonious hypothesis given these data is that subspecies responses to fire are similar. Analyzing the California subspecies data alone did not change the results of overall effects or meta-regression analyses (Fig. 1).

CHANGING DISPUTED EFFECT SIZES TO THOSE SUGGESTED BY JONES ET AL. DID NOT CHANGE RESULTS

The Jones et al. commentary suggested alternative effect sizes and sample sizes for four papers for which analytical issues were raised,

Jones et al. (2016), Lee and Bond (2015a,b), and Hanson et al. (2018). Using Jones et al.'s new effect and sample sizes, the overall mean difference between unburned and burned sites was -0.12 (95% CI: -0.56 to 0.33). Changing effect sizes following suggestions by Jones et al. did not change the overall mean effect results (Fig. 1). I also reanalyzed only the occupancy data subgroup using Jones et al.'s suggestions and found no significant mean effect of fire on occupancy (effect = -0.75 , 95% CI: -1.52 to 0.03), the same finding as in Lee (2018). When the four papers for which analytical issues have been raised were simply removed from the analysis, the overall mean difference between unburned and burned sites was $+0.03$ (95% CI: -0.44 to 0.59). Removing studies with analytical issues made the overall effect of mixed-severity forest fire on spotted owls positive but not significantly so (Fig. 1). Neither changing effect sizes nor removing these papers changed the meta-regression results from what was reported in Lee (2018).

THERE WAS NO FOCUS ON MEAN EFFECTS IN LEE (2018), HETEROGENEITY WAS THOROUGHLY EXAMINED, AND GEOGRAPHIC VARIATION WAS ACCOUNTED FOR

Far from ignoring the heterogeneity in effects among studies, in Lee (2018) I used multiple analytical tools (weighted effect sizes, random-effects models, multi-level mixed-effects meta-regressions of Hedge's d against percent of study area burned at high severity and time since fire, and meta-analysis of variation) to describe and examine patterns in the variation of effects among studies. I made 10 sub-strata analyses of mean effects, and 17 sub-strata analyses within the meta-regression. Lee (2018) presented: (1) a random-effects meta-analysis of mean effect sizes that included overall effect, parameter type sub-stratification (occupancy, demography, and foraging), and parameter-specific sub-stratification (reproduction, survival, recruitment, and foraging in low-, moderate-, and high-severity burn); (2) a 2-step multi-level linear mixed-effects meta-regression to explain heterogeneity in mean effect sizes that included accounting for among-study and regional variation, time since fire, percent of high-severity fire in the study area, and

parameter type (occupancy, survival, reproduction, recruitment, and foraging in low-, moderate-, and high-severity burn); and (3) a random-effects meta-analysis of variation to examine differences in parameter variances due to fire.

In addition to finding no significant negative mean effects of fire on owls, Lee (2018) reported multiple significant effects of fire covariates on specific owl parameters. These effects were as follows: a negative correlation of occupancy with time since fire; a positive effect on recruitment immediately after the fire, with the effect diminishing with time since fire; a positive correlation between reproduction and the percent of high-severity fire in owl territories; and positive selection for foraging in low- and moderate-severity burned forest, with high-severity burned forest used in proportion to its availability, but not avoided.

In the meta-regression portion of my paper, I explored how high-severity burned area within territories explained this variation and found a "nearly significant" negative effect across all parameters. I did not discuss the potential meaning of this "nearly significant" result because the more detailed meta-regression of high-severity fire effects partitioned into parameter-specific regressions (occupancy, demography, and foraging) had "clearly significant" results.

Jones et al. also criticized my formulation of the proportion burned at high-severity covariate, but my methods were transparent, used all data available in the published studies that were examined, produced study-specific covariate values representative of the variation among studies, and found numerous significant results. Jones et al. suggested I should have used data from every individual territory ever burned in my meta-regressions, an impossibly high standard for meta-analyses when raw data were not published with every paper. Until all studies make their raw data publicly available, researchers will continue to rely on the methods of meta-analyses and meta-regressions with study-specific covariates to synthesize the results from different studies as a sample of all possible studies.

Jones et al. also claimed the examination of heterogeneity in Lee (2018) was inadequate because I did not examine high-severity patch size as a covariate. This is surprising given that

one of the co-authors (M. P. North) published a paper acknowledging that high-severity patch size is highly correlated with the proportion of fire area burned at high severity (Collins et al. 2017 citing Miller et al. 2009, Harvey et al. 2016). Because high-severity patch size is highly correlated with the proportion of fire area burned at high severity, my meta-regression analysis of effects in relation to high-severity burned area was also an examination of high-severity patch size. Again, the assertions of Jones et al. were not supported by the empirical evidence.

With $\alpha = 0.05$, the criteria most commonly employed in ecological decision making, $P > 0.05$ is not statistically significant. I adhered to the convention of not emphasizing non-significant results, particularly since there were numerous clearly significant results that required discussion. I did discuss the biological significance of the non-statistically significant occupancy result (see *Fire-induced change in occupancy is not greater than annual changes in occupancy in unburned forest* below).

Conservation biology, in its mission to sustain ecological and evolutionary processes, typically espouses conservatism and the precautionary principle when considering unnatural anthropogenic actions such as logging relative to natural disturbances (Noss 1993). Therefore, because Lee (2018) showed there is not strong, widespread, and unequivocal evidence that fire is threatening spotted owl population persistence, it follows that unnatural anthropogenic actions such as logging intended to reduce fire but that can harm owls should not be considered on public lands that are not immediately adjacent to towns and infrastructure. Indeed, rather than high-severity fire, which has burned historically throughout the range of the spotted owl, the novel disturbance to the species is logging (Beardsley et al. 1999). Even the largest most intense fire leaves dead big trees standing for decades, providing many ecological goods and services to the dynamic forest ecosystems. Logging is the primary reason the spotted owl has declined (USFWS 2011, USFWS 2012), and additional logging, even logging which is called thinning, fuel reduction, or restoration, is unlikely to contribute meaningfully to owl conservation or recovery.

FIRE-INDUCED CHANGE IN OCCUPANCY IS NOT GREATER THAN ANNUAL CHANGES IN OCCUPANCY IN UNBURNED FOREST

In Lee (2018), I provided biological perspective regarding the observed non-statistically significant change in site occupancy probability due to fire (-0.06) by comparing this value to the observed stochastic declines in site occupancy between pairs of sequential years in the unburned Eldorado study area (-0.07). My estimate was based on Jones et al. (2016) time series of annual proportion of sites occupied from 1993 to 2015 (Fig. 2A). Each year the proportion of sites occupied could be the same relative to the previous year's occupancy (zero change), higher (a positive number), or lower (a negative number). So each year's stochastic change in occupancy relative to the previous year can be seen as a zero indicating no change, or a positive or negative departure from zero (Fig. 2B).

To describe the magnitude of annual departure from zero change in annual proportion of sites occupied ($\psi_t - \psi_{t-1}$) for the time series in the unburned Eldorado study area, I used the mean of all negative changes (-0.07), but I could also have used the mean of all positive changes (0.06), the mean absolute value of all changes (0.07), the mean proportional change (ψ_t / ψ_{t-1}) applied to mean occupancy (0.07), or the standard deviation of occupancy (0.15). For example, if occupancy over four years was 0.5, 0.6, 0.4, and 0.5, then annual changes in occupancy would be $+0.1$, -0.2 , and $+0.1$ (the results of: $0.6-0.5$, $0.4-0.6$, and $0.5-0.4$). Jones et al.'s proposed method of simple averaging would estimate the mean annual change in occupancy was 0.0, which is clearly not the case, whereas the absolute value method I described would estimate mean annual change in occupancy as 0.13, and the standard deviation of the four hypothetical occupancy values above is 0.08. Jones et al.'s method of averaging the positive and negative changes was wrong because any average of positive and negative random numbers will tend to have a mean of zero (Fig. 2B). The -0.02 overall mean reported by Jones et al. was actually the slope of the trend line through the time series of Eldorado owl occupancy with y -intercept at 1.0 (Fig. 2A).

To revisit the biological significance of the nearly statistically significant change in mean occupancy after fire (-0.06), I did the following: (1) detrended the Jones et al. (2016) occupancy data by subtracting the trend line estimate from each observation in the series; (2) calculated the mean and standard deviation of the detrended occupancy data; (3) computed the year-on-year change in occupancy for each year by subtracting occupancy in year $t-1$ from occupancy in year t (Fig. 2B); (4) computed the absolute value of each year's change in occupancy; and finally (5) calculated the mean of the absolute values of each year's change in occupancy. The mean of the absolute value of each year's change in occupancy in the unburned forests of Jones et al. (2016) is 0.063. Thus, the mean raw effect size of mixed-severity fire on occupancy (0.060) is less than the mean annual change in occupancy in unburned forest owl sites of the Eldorado study area (0.063), and less than the standard deviation of detrended occupancy probabilities (0.077). As reported in Lee (2018), the mean effect size of mixed-severity fire on spotted owl site

occupancy is neither statistically nor biologically significant.

ECOLOGICAL AND INFERENTIAL CONTEXT OF LEE (2018) WAS APPROPRIATE

Jones et al. claimed I overgeneralized historical fire regimes within forests inhabited by spotted owls, and did not address changing wildfire trends due to global warming. In Lee (2018), I acknowledged both sides of the ongoing unsettled debate about whether fires in forests inhabited by spotted owls are becoming larger or more severe at evolutionary timescales, while Jones et al. present a narrower perspective. I assert that climate change is not a future event, but one we have been experiencing for decades (Westerling 2016, USGCRP 2017). The years that produced the studies analyzed in Lee (2018) were among the biggest fire years in 50 years, so they accurately represent owl responses to fires within an already warmed and changed climate milieu (Littell et al. 2009, Miller et al. 2009, Parks et al. 2015, Westerling 2016). Thus, the results from

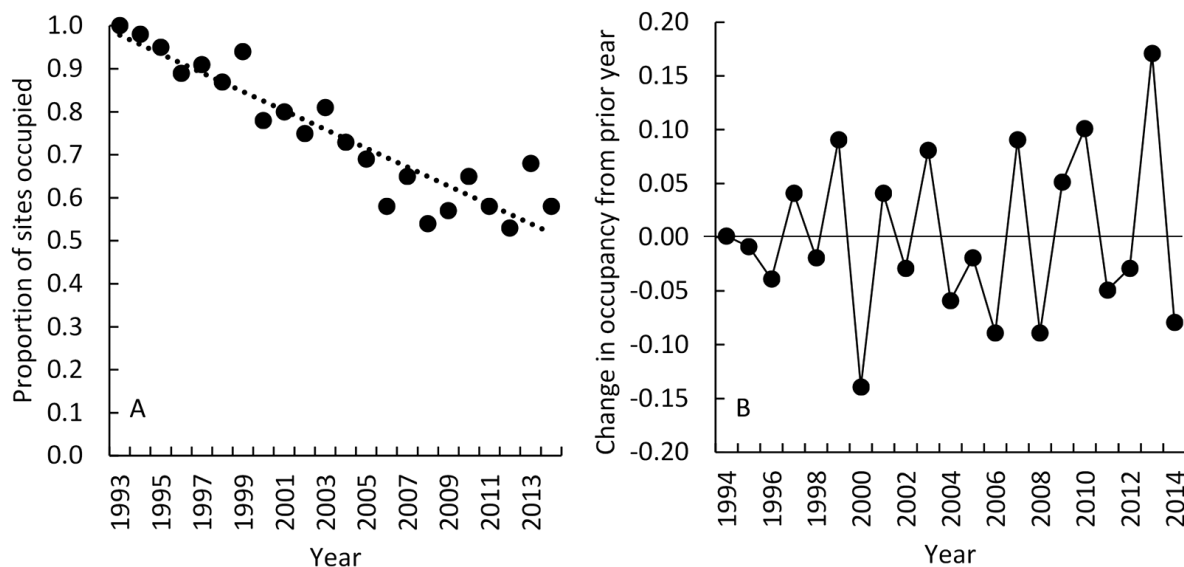


Fig. 2. (A) Annual estimates of spotted owl site occupancy (ψ) in Eldorado, California study area 1993–2014 (data from Jones et al. 2016: Fig. 3e). The dotted line represents a regression line fitted to the time series ($y = -0.02x + 1.0$). (B) Change in spotted owl site occupancy probability from year $t - 1$ to year t calculated using detrended occupancy data. Raw mean of changes is 0.0 (SD = 0.08). Mean of absolute value of changes is 0.063 (SD = 0.043).

Lee (2018) are directly applicable to climate change predictions for western forests.

The topic of fire regimes and natural range of variability is fraught with uncertainty, and tangential to my synthesis of published literature. In Lee (2018) I thoroughly accounted for regional geographic variation in my analyses. Each parameter (e.g., occupancy) was modeled with effects of each study (e.g., Bond et al. 2009) within geographic region (e.g., Sierra Nevada) as multi-level random effects to properly estimate study site and region-specific variation and to account for repeated measurements (pseudo-replication) within a study or region. Regions were defined as Sierra Nevada, southern California, national parks, not California, and the Eldorado density study area. Subspecies-specific differences were also empirically tested for and no significant effects were observed. This was all clearly explained in Lee (2018).

I find it useful to consider the evolutionary past when contextualizing perceived threats to an ecosystem and its natural disturbances. Fire is a natural and widespread mechanism of changes in vegetation community structure and distribution (Pickett and White 1985, Sugihara et al. 2006). There is evidence that native plants and animals such as spotted owls are well adapted to take advantage of large patches of high-severity burn found in recent megafires, indicating that large high-severity patches are not novel conditions (Tingley et al. 2016, Downing et al. 2020). The spotted owl and the older forests it inhabits have experienced numerous very warm and dry periods during their evolutionary history that were likely similar to the current and predicted near-future climate (LaMarche 1974, Graumlich 1993, Stine 1994). Mixed-severity fires that included large patches of high-severity fire have likely often been found in western forests, and even if one is uncertain of exactly how much high-severity fire was on the landscape at different points in time, it is clear that at least a few times in the past few thousand years, there have been droughts and climate swings that likely led to more fire than is currently observed (Pierce et al. 2004, Power et al. 2008, Marlon et al. 2012). The spotted owl survived those episodes. I find this to be compelling evidence for built-in adaptation and resilience in the forest-owl system that the novel disturbance of logging could disrupt.

The notion that logging or thinning might somehow avert large, weather-driven, mixed-severity forest fires with large patches of high-severity burn is not well supported by the evidence (reviewed in Kalies and Kent 2016, Schoennagel et al. 2017). Approximately 90% of the forested acres burned at high severity occur each year in a few extreme climate- and weather-driven mixed-severity fire events that thinning treatments are unlikely to interact with, let alone slow or stop (Flanagan and Wotten 2001, Williams 2004, Lydersen et al. 2014, Kalies and Kent 2016). In fact, some evidence supports the observation that thinning and other logging can exacerbate fire severity (Raymond and Peterson 2005, Cram et al. 2006, Wimberly et al. 2009, Cruz et al. 2014, Bradley et al. 2016), while spotted owl nesting and roosting habitat (old-growth forest characterized by large trees and high canopy cover) is naturally more resistant to high-severity fire than younger forest (Weatherspoon and Skinner 1995, Odion et al. 2014, Lesmeister et al. 2019). Logging of green trees also can exacerbate competition between invasive barred owls (*Strix varia*) and spotted owls (Dugger et al. 2011).

Another aspect of thinning and other logging activities considered fuel reduction that is underappreciated is the genetic variation among trees that is the raw material for forest adaptation in a changing climate (Kolb et al. 2016, Prunier et al. 2016, Pinnell 2016, Six et al. 2018). Until foresters can identify exactly which individual trees are most genetically and epigenetically adapted to be resilient and resistant to drought, higher temperatures, fire, disease, and insects, and can use that genetic information to preserve those specific locally well-adapted individual trees, then random thinning and logging will inevitably impoverish the genetic variation of our forests and impair their natural processes of adapting to a changing climate.

CONCLUSIONS

None of the issues raised by Jones et al. regarding Lee (2018) were supported by reanalyses (Table 1). Most were not truly issues at all, but misunderstandings by Jones et al. about meta-analysis in general and the specific methods used in Lee (2018). Jones et al. espouse the belief, based on a small subset of available data, that because

mixed-severity fire with large patches of high-severity burn *can* sometimes harm some spotted owl territories or individual owls, thinning or other logging within owl habitat is justified if it can reduce fire severity. That is a highly questionable management recommendation, particularly when a different subset of the available data showed high-severity fire *can* be significantly preferred by foraging owls and more high-severity fire *can* increase reproduction. Crucially, thinning logging is rarely effective at mitigating fire severity during the large, climate- and weather-driven fires that burn 90% of burned area each year.

Given the known absence of consistent negative effects, and the significant positive effect of high-severity fire on spotted owls, I propose that the limited resources available for forest fire mitigation should be prioritized for human community protection in the wildland–urban interface rather than in remote spotted owl territories. When all available data are examined objectively in meta-analysis, the larger pattern is revealed that high-severity fire patches from climate-changed wildfire events are used by spotted owls for foraging in proportion to their availability, and more high-severity fire significantly increases reproduction, but no strong consistent negative effects are apparent. This is exactly why meta-analyses such as Lee (2018) are so valuable, because they provide decision-makers with the broader consistent patterns found among all studies so that decisions need not be based on single studies or so-called “biological intuition.”

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