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RESPONSE

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Megafire effects on spotted owls: elucidation of a growing threat and a response to Hanson et al. (2018)

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Abstract

The extent to which wildfire adversely affects spotted owls (*Strix occidentalis*) is a key consideration for ecosystem restoration efforts in seasonally dry forests of the western United States. Recently, Jones et al. (2016) demonstrated that the 2014 King Fire (a "megafire") adversely affected a population of individually-marked California spotted owls (*S. o. occidentalis*) monitored as part of a long-term demographic study in the Sierra Nevada, California, USA because territory occupancy declined substantially at territories burned at high-severity and GPS-tagged spotted owls avoided large patches of high-severity fire. Hanson et al. (2018) attempted to reassess changes in territory occupancy of the Jones et al. (2016) study population and claimed that occupancy declined as a result of post-fire salvage logging not fire *per se* and suggested that the avoidance of GPS-marked owls from areas that burned at high-severity was due to post-fire logging rather than a response to high-severity fire. Here, we demonstrate that Hanson et al. (2018) used erroneous data, inadequate statistical analyses and faulty inferences to reach their conclusion that the King Fire did not affect spotted owls and, more broadly, that large, high-severity fires do not pose risks to spotted owls in western North American dry forest ecosystems. We also provide further evidence indicating that the King Fire exerted a clear and significant negative effect on our marked study population of spotted owls. Collectively, the additional evidence presented here and in Jones et al. (2016) suggests that large, high-severity fires can pose a threat to spotted owls and that restoration of natural low- to mixed-severity frequent fire regimes would likely benefit both old-forest species and dry forest ecosystems in this era of climate change. Meeting these dual objectives of species conservation and forest restoration will be complex but it is made more challenging by faulty science that does not acknowledge the full range of wildfire effects on spotted owls.

Introduction

The spotted owl (*Strix occidentalis*) has become an icon of conservation in North America because of conflicts amongst citizens, conservation groups, the timber industry, natural resource agencies and politicians arising over the best way to protect its economically valuable old-forest habitats (Simberloff 1987, Gutiérrez et al. 1995; Gutiérrez 2015). This basic conflict has expanded in recent years to include disputes that weigh the potential degradation of owl habitat from restoration projects in dry forest ecosystems that seek to reduce severe fire risk (e.g. logging, thinning, prescribed burning) against the potential risk posed to owl habitat by the increasing number of large, high-severity fires (Lehmkuhl et al. 2007, 2015; Collins et al. 2010; Tempel et al. 2014, 2015, 2016). A second element of this conflict relates to the nature of current and historical conditions and fire regimes. On the one hand, much research has shown that tree densities are higher now than they were prior to the beginning of fire suppression efforts in the early 20th century (e.g. Collins et al. 2017; Hagmann et al. 2017; Safford and Stevens 2017). Under this paradigm, lower tree densities and fuel loadings in historical dry forests were maintained by a frequent low- to moderate-severity fire regime (including smaller patches of high-severity fire), but modern fire suppression has allowed an increase in tree densities and fuel loadings that have, in turn, led to an increase in the frequency of large, high-severity fires (e.g. Calkin et al. 2005; North et al. 2015; Steel et al. 2015; Stevens et al. 2017). On the other hand, some researchers have suggested that larger patches of high-severity fire were relatively common in historical post-fire landscapes in dry forest types (Hanson et al. 2009, Williams and Baker 2012, Hanson and Odion 2014, Odion et al. 2014, Baker and Hanson 2017), although the validity of inferences from these studies has been contested (Spies et al. 2010, Fulé et al. 2014, Safford et al. 2015, Stevens et al. 2016, Hagmann et al. 2018). Hence, under the first paradigm, fuels reduction and forest restoration treatments are needed to reduce tree density and return forests ecosystems to the lower-severity fire regimes that were historically typical. Under the second paradigm, fuels reduction and forest restoration treatments are not necessary because current fire regimes in dry forests are consistent with historical ecosystem processes. The second paradigm also predicts that owls should not be negatively impacted by large, high-severity fires. However, if they are negatively impacted by large, high-severity fires, then it lends some support to the need for forest restoration. Therefore, knowing how high-severity fires affect spotted owls is pivotal to the management of dry forests in western North America.

There are two important questions for conservation scientists to address: (1) do management actions, intended to decrease risk of high-severity fire by reducing tree densities and surface fuels (e.g. thinning, prescribed fire), cause more or less harm to spotted owls than high-severity fire itself; and (2) how do owls respond to large, high-severity fires given they appear to be adapted, at least, to low- to moderate-severity fire regimes? Regarding the first question, we know that owls can be negatively impacted by restoration efforts in the short-term (Ager et al. 2007, Stephens et al. 2014, Tempel et al. 2014, 2015, 2016), but we do not know the extent to which these short-term impacts might mitigate loss of habitat or other impacts caused by high-severity fires. Regarding the second question, while there is unanimous empirical support that predominately low-severity fires have little negative impact on owls (Bond et al. 2002, Bond 2016, Ganey et al. 2017), there are two general alternative findings about the effect of large, high-severity fires on owls: neutral/beneficial effects (e.g. Bond et al. 2009, 2016; Lee et al. 2012; Lee and Bond 2015; Hanson et al. 2018) and negative effects (Comfort et al. 2016; Jones et al. 2016; Eyes et al. 2017; Ganey et al. 2017; Rockweit et al. 2017) (see also below the section "The science of spotted owls and fire"). Determining which of these results is correct will influence how forest restoration proceeds within the range of the spotted owl.

A paper published recently in *Nature Conservation* (Hanson et al. 2018) attempted to reverse the growing scientific consensus that large, high-severity fires *can* negatively impact spotted owl populations (Comfort et al. 2016, Jones et al. 2016, Eyes et al. 2017, Ganey et al. 2017, Rockweit et al. 2017), claiming instead that post-fire salvage logging–not high-severity fire–poses the key threat to owls in post-fire landscapes. While the analysis performed by Hanson et al. (2018) included data from several recent large fires, a large portion of the discussion section of Hanson et al. (2018) was devoted to re-interpreting and criticising our study published in *Frontiers in Ecology and the Environment* (Jones et al. 2016). Jones et al. (2016) demonstrated unambiguous negative effects of a large (~40,000 ha) high-severity fire, the 2014 King Fire, on a study population of spotted owls in the central Sierra Nevada, CA. This large fire occurred partly within the boundary of our long-term, demographic study area containing individually-marked California spotted owls. In addition, we (Jones et al. 2016) found no effect of salvage logging on the owls, but Hanson et al. (2018) claimed that the negative effects of the King Fire on spotted owls was due to salvage logging, not severe fire. Therefore, we developed this paper for two reasons. First, the conclusions reached by Hanson et al. (2018) lacked scientific merit because their inferences were negatively influenced by factual errors (owing to a lack of understanding of our data and our study population), errors in their data and inadequate statistical approaches. Second, there could be negative repercussions for species conservation, forest restoration and fire management in the western United States if the conclusions of Hanson et al. (2018) are not corrected. We begin by contextualising the Hanson et al. (2018) and Jones et al. (2016) papers within the current state of science of spotted owls and fire and then proceed to document the inaccuracies and mistakes in Hanson et al. (2018).

The science of spotted owls and fire

Spotted owls are adapted to low- to moderate-severity fire regimes as evidenced by no research revealing a negative response to these types of fires (Gutiérrez et al. 1995, 2017; Bond et al. 2002, Bond 2016, Ganey et al. 2017). Yet, literature reviews have revealed that spotted owls show a wider range of responses to high-severity fire (Bond 2016, Ganey et al. 2017, Lee 2018). One research group has inferred generally neutral or positive effects of high-severity fire on occupancy rates and owl foraging behaviour (Bond et al. 2009, 2016, Lee et al. 2012, 2013; Lee and Bond 2015, Lee 2018). In contrast, four other research groups, working independently of each other, have reported negative effects of high-severity fire on both owl population dynamics and foraging behaviour (Comfort et al. 2016, Jones et al. 2016; Eyes et al. 2017, Rockweit et al. 2017). Thus, a disparity exists that requires resolution because conservation decisions to restore forests or protect owl habitat are somewhat dependent on knowing the manner in which owls are expected to respond to high-severity fire.

We offer two possible explanations for the above contrasting results. First, variation in results from field studies can often be explained by differences amongst study systems and unique patterns and intensities of wildfires. For example, we know that the Rim Fire studied by Lee and Bond (2015) showed a different pattern of burning than the King Fire we studied (Jones et al. 2016); the former exhibiting more variability in intensity and pattern of burning and the latter being more uniformly intense with very large patches of high-severity burn (e.g. one contiguous patch was >13,500 ha) (see Stevens et al. 2017). Thus, it is logical to expect fires having different patterns of burn severity to affect a species differently.

Second, study methods influence data quality. We had an extensive individual history of owls affected by the King Fire because we had colour-marked and re-sighted birds in our study area for the 22 years preceding (1993–2014) as well as annually after the King Fire. Knowing the identity of individuals allowed us to associate individuals with places and, more importantly, allowed us to exclude false positive detections in survey/location histories of birds (Berigan et al. 2018). Interestingly, studies by Lee et al. (2012, 2013), Lee and Bond (2015) and Hanson et al. (2018) on occupancy dynamics of spotted owls showed no negative effects of high-severity fire but relied primarily on night-time detections of unmarked owls to assign the occupancy status, which suggests false positive detections could have been included in analysis (Berigan et al. 2018). It has been shown that even low rates of false positive detections result in positive biases that inflate occupancy rate estimates (Royle and Link 2006, Miller et al. 2011, Sutherland et al. 2013). We also knew from GPS-tag-based studies of spotted owls that owls frequently move amongst unoccupied (and sometimes occupied) territories (Berigan et al. 2018, Blakey et al. 2019). Therefore, we were able to exclude false positive detections from our owl detection database because we knew which owls were present at a given historical territory owing to our observation of their colour bands, both before and after the King Fire. In contrast, Hanson et al. (2018) and others (e.g. Lee and Bond 2015) were unable to do this because they relied on night-time observations of unmarked owls collected by others or otherwise did not have access to survey metadata that contained information regarding individual owl identity (see below). Therefore, we believe the quality of data in Jones et al. (2016) was higher than the data used by Hanson et al. (2018) in their re-analysis.

Jones et al. (2016) tested the effects of high-severity fire on owls using a "natural" Before-After Control-Impact (BACI) design

Hanson et al. (2018:101) criticise a central finding of a decline in owl occupancy following the King Fire, reported by Jones et al. (2016), as "not sound" while also providing alternative explanations for other results in Jones et al. (2016). So we here summarise the salient points of Jones et al. (2016), which we follow with an exposition of the errors in Hanson et al. (2018) that led to their spurious conclusions. The 2014 King Fire partially occurred within the 23-year Eldorado spotted owl demographic study used by Jones et al. (2016), but the fire only impacted about half of the study area. Thus, the King Fire created an ideal structure for a natural Before-After Control-Impact study (BACI; Popescu et al. 2012) in which half the area was "treated" by fire and the other half was not "treated." Moreover, we had over two decades of pre-fire data, colour-marked individual owls and temporally consistent, standardised robust (i.e. repeated surveys within and amongst years) survey data for the owls that were either potentially affected or not affected by the King Fire (Jones et al. 2016). Due to the long-standing conflicts surrounding the conservation of the spotted owl (Gutiérrez et al. 1995, Gutiérrez 2015), these survey methods have been peer-reviewed many times (e.g. Franklin et al. 2004, Blakesley et al. 2010).

The King Fire occurred in September and October 2014, but Jones et al. (2016) began assessing effects of the fire on owls the following spring breeding season (2015). Of the 45 long-term territories – defined as 1100-m radius circles centred on nests and roosts – monitored in the above-described density study area, 14 burned with > 50% high-severity fire over the entire territory, 16 burned with < 50% high-severity fire over the entire territory and 15 experienced no fire. We assessed the potential for fire effects on spotted owls separately from potential effects of salvage logging in our modelling, but only a relatively small amount of salvage logging occurred on private land prior to the conclusion of our owl surveys at the end of the 2015 breeding season (see also below for specific comments on potential effects of salvage logging). Moreover, our survey design, with multiple surveys conducted per territory every year, allowed for the rigorous modelling of detection probabilities within a multi-season occupancy modelling framework (MacKenzie et al. 2003). Finally, at the same time territory occupancy was being assessed in 2015, we deployed nine GPS tags on spotted owls that had persisted around the periphery of the large patch of forest burned at high-severity to characterise how fire affected patterns of owl foraging habitat selection.

Our key findings in Jones et al. (2016) were:

(1) The likelihood of a territory that was *occupied* in the breeding season prior to the King Fire (i.e. 2014) becoming extinct the year following the fire (i.e. 2015) was strongly and positively associated with the proportion of the territory that burned at high severity.

(2) Seven of eight territories that were *occupied* during the breeding season prior to the King Fire (i.e. 2014) and that also experienced > 50% high severity fire became

"extinct" after the fire (i.e. 2015). The estimated territory extinction rate at high-severely-burned territories after the fire (0.88) was ~7 times greater than average annual extinction rates (0.12) for the same territories or any other group of territories–*well* beyond the range of variability estimated for the previous 22 years (Tempel et al. 2016).

(3) In some cases, both high-severity fire and salvage logging occurred within owl territories, but high-severity fire was predominant in its spatial extent by an order of magnitude. At 1100 m and 1500 m scales, the area affected by high-severity fire was ~17 and ~12 times greater, on average, than salvage logging (where salvage logging actually occurred). We (Jones et al. 2016) explicitly modelled effects of salvage logging, which explained negligible variation; we therefore inferred salvage logging to be an uninformative parameter (*sensu* Arnold 2010).

(4) None of the 6 territories that were *unoccupied* during the breeding season prior to the King Fire (i.e. 2014) and experienced > 50% high severity fire was recolonised (i.e. became occupied) by new birds in 2015.

(5) Collectively, (2) and (4) resulted in only 1 of 14 territories that experienced > 50% high-severity fire remaining occupied the year after the King Fire. The single occupied territory contained a pair of owls (although a "turnover" occurred with a new male pairing with the same female who was present pre-fire) that shifted their activity centre > 1,300 m to the east – from within their severely-burned historical nest stand into a stand that experienced predominately low-severity fire.

(6) The King Fire resulted in the largest negative rate of change in population occupancy (λ) observed for a single year (22% decline from the previous year) in territory occupancy over the 23-year Eldorado study.

(7) Three instances of breeding dispersal by individually-marked owls out of the high-severity-burned territories and into the surrounding and low- to moderate- severity burned landscape were documented, even though breeding dispersal in California spotted owls is relatively rare (Gutiérrez et al. 2011).

(8) We observed one apparent adult mortality associated with the King Fire, as evidenced by our finding of the scorched remains of an owl carcass with its United States Geological Survey (federal government) aluminium locking leg band near a high-severity-burned nest site. Band numbers corresponded with an individual that we observed to be alive at this site several weeks prior to the King Fire.

(9) GPS-tagged owls persisted in less severely burned territories around the large high-severity burned patch, but showed strong avoidance of the large high-severity burned area for foraging (even when the central place foraging behaviour of spotted owls was accounted for; see below).

Collectively, these results indicated that the King Fire had a major negative effect on both spotted owl habitat and the local spotted owl population. Moreover, the 13% decline in absolute territory occupancy (22% rate of change in occupancy) from 2014 to 2015 in the Eldorado density study area likely did not represent the full impact of the King Fire to the local population because territories that experienced large amounts of high-severity fire have likely been rendered unsuitable to spotted owls for nesting and roosting for decades. The loss of territories, then, will reduce carrying capacity and will limit the growth of the population. In support of this hypothesis, all of these unoccupied territories have remained unoccupied in 2016, 2017 and 2018 (M. Z. Peery, *unpublished data*).

Hanson et al. (2018): error-fraught criticisms of Jones et al. (2016)

Given the results published by Jones et al. (2016), Hanson et al. (2018) attempted to compare the relative effects of high-severity fire vs. salvage logging on occupancy rates of California spotted owl territories. While this study included data from eight large fires in California occurring from 2002–2015, a key conclusion was that the 2014 King Fire did not negatively impact California spotted owls as inferred by Jones et al. (2016). Instead, Hanson et al. (2018:101) argued that the observed occupancy declines and high extinction rates in severely burned spotted owl territories reported by Jones et al. (2016) were due to post-fire salvage logging, not high-severity fire, stating that:

"…*the conclusion by Jones et al. (2016), that the King fire caused the loss of occupancy in these sites, is not sound.*"

We do not argue against Hanson et al.'s point that salvage logging *can* negatively impact spotted owls, particularly when such logging occurs in forests used by owls (e.g. fires burning in a mosaic pattern often leave areas suitable for owl use). In the case of the King Fire, however, the independent effect of high-severity fire on spotted owls was unambiguous. The claim made by Hanson et al. (2018) that declines in owl occupancy and foraging in forests burned at high-severity by the King Fire were the result of salvage logging, not high-severity fire, is without scientific merit and is the result of clear factual errors and erroneous inferences. Below, we describe seven issues, focusing on Hanson et al.'s inferences as they relate to the findings of Jones et al. (2016).

(1) Hanson et al. excluded the most severely-burned spotted owl sites from their analysis. A key reason why Jones et al. (2016) made strong inferences regarding the effects of severe fire on spotted owls is because they documented extinction in 7 of 8 territories that burned at high severity across > 50% of their territory area (62–99% high severity) that were occupied pre-fire (PLA0050, PLA0067, ELD0058, PLA0113, PLA0039, ELD0057, PLA0065 [see Suppl. material 1: Figure S1 for PLA 0113, Suppl. material 2: Figure S2 for PLA 0065 and Suppl. material 3–6: Figures S3–S6 for general views of the extent and relative severity of the King Fire] – these are unique codes corresponding to United States Forest Service [USFS]-delineated spotted owl management units). Of these seven territories, Hanson et al. (2018: 97) deliberately excluded the four most severely burned (91–99% high severity) from their analysis (i.e. PLA0050, PLA0067, PLA0113 and PLA0065; see supplemental materials for post-fire photos of PLA0113 and PLA0065) claiming, it appears, that including sites that burned at > 80% high severity fire would have apparently created an "analytical problem" for their analysis – "*Conversely, the effects of post-fire logging* *were not analysed for sites with > 80% high-severity fire because nearly all of these sites have ≥ 5% post-fire logging and there was not a sufficient number of such sites with ≥ 5% post-fire logging for the analysis"* – but we do not understand the rationale because their decision effectively removed from analysis many territories most likely to show a negative effect of high-severity fire. Additionally, using categorical rather than continuous variables (as we did in addition to categorical covariates) to represent fire and salvage logging effects provides less analytical power (Cottingham et al. 2005). Finally, from an ecological perspective, it is arbitrary to subdivide territories that burned at > 50% high-severity into two groups (50–80% and > 80%) and subsequently eliminate the > 80% category, as Hanson et al. did. By doing so, they deliberately eliminated from their analysis those territories most extensively affected by high-severity fire and, therefore, those territories which would most likely demonstrate high-severity fire effects on spotted owl territory occupancy. Thus, Hanson et al. (2018) included only three of the seven sites (ELD0058, PLA0039 and ELD0057) that actually became unoccupied ("went extinct") after the King Fire as we reported (Jones et al. 2016). The decision to exclude the most severely burned territories represented an egregious analytical flaw and part of the reason Hanson et al. (2018) erroneously concluded that salvage logging, not high-severity fire, was responsible for the considerable decline in territory occupancy post-fire.

(2) Hanson et al. incorrectly claimed that Jones et al. (2016) underestimated or dismissed the potential influence of salvage logging. Hanson et al. (2018: 101) stated that Jones et al. (2016) *"…dismissed post-fire logging as a factor in the reduced spotted owl occupancy that they reported one year after the fire."* In fact, we (Jones et al. 2016) explicitly tested for the effect of post-fire salvage logging using a model-selection framework and determined it was statistically uninformative (Arnold 2010) at the 1100-m spatial scale. An additional analysis, performed by G. M. Jones (G. M. Jones, unpublished results), confirmed the same result at the 1500 m scale. Hanson et al. further state that, based on their own methods of quantifying salvage logging in the King Fire, they found more salvage logging than was reported by Jones et al. (2016), implying that Jones et al. under-reported salvage logging. However, the two studies shared only six territories (of the 21 salvage-affected territories in Jones et al.) rendering a direct comparison inappropriate. It is noteworthy that, of these six territories, three became extinct after the King Fire (ELD0058, PLA0039 and ELD0057), yet experienced only 0%, 0% and 0.2% salvage logging, respectively and all experienced between 60–70% high-severity fire. Thus, one must consider the profound difference in spatial extent of high-severity fire vs. salvage logging and its likely relative influence; within the 21 territories studied by Jones et al. (2016), where both high-severity fire and salvage logging occurred, high-severity fire was *17 and 12 times more prevalent on average* than salvage logging at 1100-m and 1500-m scales, respectively.

(3) Hanson et al. used inaccurate data about the owl territory histories affected by the King Fire that were part of Jones et al. study area. The following errors likely stemmed from Hanson et al.'s lack of familiarity with our study area and using data they did not collect. The best example of data inaccuracy that led to inferential errors was Hanson et al. (2018) treating one territory (PLA0065) as unoccupied both before (2014) and after the fire (2015). However, this territory was unmistakably occupied by a banded pair of owls that fledged three young in 2014 and then became extinct after the King Fire (the burned remains of the territorial male were found near its nest site in 2015, see above). In a second example, Hanson et al. (2018) treated two spatially overlapping territories (PLA0039 and PLA0080) as being occupied both before (2014) and after (2015) the fire, even though these territories have not been simultaneously occupied by territorial owls during a single breeding season since 1996. However, because the two territories share a relatively large overlapping area (i.e. overlapping estimated territory areas based on average study area-wide nearest-neighbour distances), a single detection could occur within "both" territory areas (i.e. within the area of overlap). Thus, we assigned detections each year from PLA0039 and PLA0080 to a single territory where either nesting behaviour was observed during the breeding season or, if no nesting behaviour was observed, to the territory where the majority of detections occurred during that breeding season. Therefore, assigning the correct annual occupancy status to PLA0039 and PLA0080 required direct observational knowledge of both the study area and the behaviour of the birds in any given year - Hanson et al. (2018) lacked this critical information. As a result, Hanson et al. (2018) treated PLA0039 as occupied before and after the fire, but this territory actually became extinct after the fire. In this case, Hanson et al. assigned an owl detection to PLA0039 in 2015 that should have been assigned to an adjacent (and overlapping) territory (PLA0080) because PLA0080 represented the primary nest/roost area being utilised by colour-marked spotted owls in that year. By the same error, a detection that Hanson et al. assigned to PLA0080 in 2014 should have been assigned to PLA0039. Therefore, Hanson et al. assigned an incorrect pre- or post-fire occupancy status to 3 of 7 territories (43%) from the Eldorado study area and at least 3 of 10 (30%) King Fire-affected territories used in their analysis.

(4) Hanson et al. used partial datasets and inadequate analyses. Faulty inferences can easily occur when raw data are re-analysed without understanding the data collection process or the implications of one type of data versus another (e.g. the difference between a night-time location and a daytime location when assessing territory occupancy – see below). In contrast to Jones et al. (2016), Hanson et al. (2018) did not collect data on spotted owl occupancy themselves. Rather, they acquired data collected by the USFS and contractors. In the case of the King Fire, this information included summary data on spotted owl territory occupancy that we submitted to the USFS but did not include other information such as: (1) colour-band combination of owls at each territory; and (2) individual survey data. The USFS did not request the other information from us because they simply needed to know if any owls had been detected at a site, the pair status, presence of young and the exact location of the birds and nest (if present). As discussed above, without information on individual identity and time of detection during a survey, it was not possible for Hanson et al. to eliminate "false positive" detections resulting from owls using multiple territories during their nocturnal activities, which can lead to significant upwardly biased occupancy estimates (Sutherland et al. 2013, Berigan et al. 2018). As they did not have survey-specific data, Hanson et al. (2018) were unable to use standard occupancy modelling approaches that account for imperfect detection (i.e. the possibility that an owl is present even if not detected), an issue well-known to lead to biased estimates of site occupancy (MacKenzie et al. 2006). Finally, in contrast to Jones et al. (2016), who used a natural Before-After Control-Impact experimental design that accounted for imperfect detectability, Hanson et al. (2018) analysed only post-fire naive occupancy patterns without considering imperfect detection of owls, which does not provide a robust test of fire effects.

(5) Hanson et al. are incorrect in their claim that Jones et al. (2016) overestimated territory extinction rates. Hanson et al. (2018) argued that we (Jones et al. 2016) overestimated the effect of high-severity fire on owls by inferring the extinction of eight owl territories (PLA0007, PLA0065, PLA0015, PLA0109, PLA0102, ELD0060, PLA0049 and PLA0043) that were actually unoccupied pre-fire (and therefore could not have become extinct). With the exception of one territory where Hanson et al. (2018) had incorrect data (PLA0065, where three owlets were fledged in the summer 2014 [see above]), Hanson et al. were *correct* that the other seven territories were unoccupied pre-fire but *incorrect* in that we (Jones et al. 2016) treated them otherwise. Indeed, we (Jones et al. 2016) treated these seven territories as unoccupied pre-fire. As the territories were unoccupied pre-fire, they made no numerical contribution to our (Jones et al. 2016) estimate of high extinction rates in high-severity- burned owl territories. In this last case, we have concluded that Hanson et al. (2018) apparently misunderstood the nature of local extinction, which is a first-order Markov process where an extinction event occurring at time *t* is conditional on that same unit being occupied at time *t*–1.

(6) Hanson et al. (2018) made incorrect or unsubstantiated claims about errors in the habitat selection analyses in Jones et al. (2016). We marked spotted owls with GPS backpacks and found that they avoided forests that burned at high-severity, but Hanson et al. claimed our inference was invalid for two reasons. First, Hanson et al. (2018: 101) stated that "*…Jones et al. (2016) did not account for distance from site centres for this central place forager…*" – that is, owls were less likely to use areas further away from their central nest/roost area. While many other studies of spotted owl foraging have not explicitly accounted for this effect (e.g. Carey et al. 1990; Ganey and Balda 1994; Ganey et al. 2005; Hamer et al. 2007; Bowden 2008; Williams et al. 2011; Forsman et al. 2015; Comfort et al. 2016; also see Singleton et al. 2010 for barred owl), we (Jones et al. 2016: 303) *did* because we eliminated foraging locations beyond the 95th percentile of foraging distances so that "*…distant areas rarely visited by owls in foraging bouts (Bond et al. 2009) were not counted as 'available' habitat. As a result, the analysis consisted of GPS locations that occurred within distance ranges used at relatively high frequencies….*" Moreover, our result held even when we re-analysed the data using a continuous distance-to-centre covariate (Figure 1), which indicated that owls were over 2.5× *less likely* on average to use high-severity-burned forest than any other forest type (Odds Ratio(β_{severe}) = 0.38, 95% CI = 0.28, 0.54). A simple visual inspection of foraging locations for our GPS-marked owls demonstrated the strong

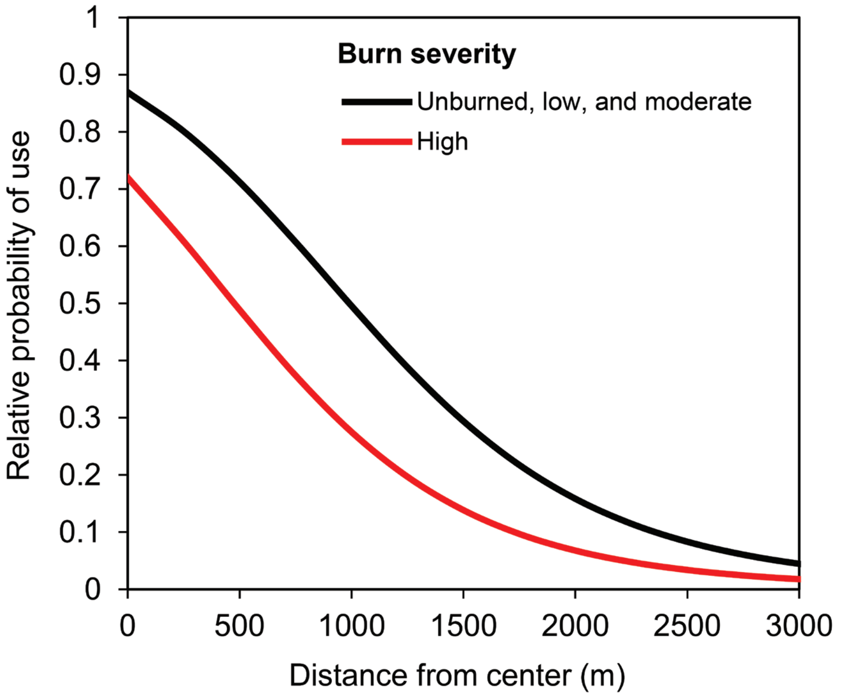

Figure 1. Mixed-effects logistic regression model showing foraging habitat selection (third order, use vs. available) by California spotted owls near or within the boundary of the 2014 King Fire. The model structure was $logit(y_i)=\beta_0+\beta_1*\text{distance}_i+\beta_2*distance_i^2+\beta_3*severity_i+\sigma_{individual}$, where the final term was a random effect for individual owls. The coefficient estimate for β_3 was –0.951 (95% CI = –1.28, –0.62) and the odds ratio was OR(β_3) = 0.38 (95% CI = 0.28, 0.54), indicating that owls avoided high-severity-burned forest relative to other severities and unburned forest.

avoidance of high-severity fire areas, particularly for owls whose activity centres were near the large, high-severity burned patch (Figure 2). Second, Hanson et al. claimed that spotted owls avoided high-severity-burned forest in Jones et al. (2016) because these areas included recent pre- and post-fire clear-cuts, suggesting spotted owls would have preferentially selected such areas had they not been logged. While spotted owls may indeed avoid such areas, data from Jones et al. (2016) unambiguously showed several clear examples of spotted owls avoiding large tracts of high-severity burn area that were *not* salvage logged (Figure 2). Without any specific analysis by Hanson et al., we conclude they were merely presenting assertions or unsubstantiated claims.

(7) Hanson et al. selectively referenced literature to support their conclusions. Hanson et al. (2018) either failed to cite, or cited but misinterpreted, research that supports negative effects of high-severity fire on spotted owls. First, Hanson et al. did not cite a recent paper by Rockweit et al. (2017) who also found a negative effect of high-severity fire on northern spotted owls (*S. o. caurina*) in north-western California.

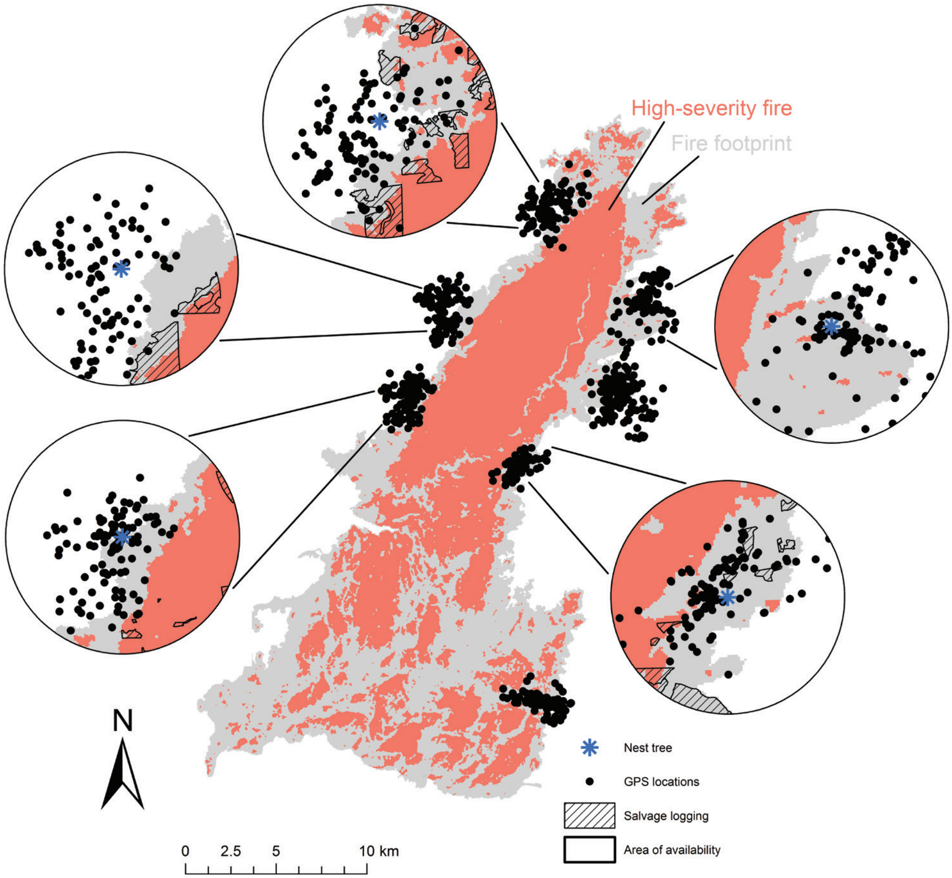

Figure 2. Spotted owl movement patterns in and around the 2014 King Fire. Locations of spotted owl foraging activities that were collected in 2015 are represented by black dots. The King Fire extent (footprint) is shown in grey and high-severity fire (> 75% canopy mortality) is shown in orange. The locations of known post-fire salvage logging operations on private lands that occurred prior to the end of data collection in 2015 are shown using black hatch marking (displayed in the inset examples). Large patches of high-severity-burned forest (orange) within spotted owl foraging ranges are clearly avoided. Data from Jones et al. (2016), but the graphical presentation here is different.

Although Rockweit et al. (2017) studied a different subspecies of owl, California and northern spotted owls have similar habitat associations and evolved in similar fire-adapted forests. Second, Hanson et al. (2018) did not cite Ganey et al. (2017), who reviewed the spotted owl-wildfire literature and concluded that the loss of spotted owl nesting habitat to high-severity fire was sufficiently widespread to constitute a threat to the species' persistence. Third, although Hanson et al. cited two recent studies in which habitat use patterns of northern and California spotted owls were investigated in relation to fire (Comfort et al. 2016, Eyes et al. 2017), they failed to acknowledge that these studies supported the patterns reported in Jones et al. (2016).

Conclusions

Here we have demonstrated that Hanson et al. (2018) used erroneous data, flawed statistical analyses, unsupported assertions and faulty inferences to reach their main conclusion that the King Fire did not negatively affect spotted owls and more generally that large, high-severity fires do not pose risks to spotted owls in dry forest ecosystems. While much remains to be learned about how and under what conditions high-severity wildfire affects spotted owl habitat and populations, research has provided a growing body of evidence that high-severity fire can have adverse effects on spotted owls. Territory occupancy declined immediately following the King Fire and GPS-tagged spotted owls avoided a large area of high-severity fire, independent of salvage logging (Jones et al. 2016); turnover rates were higher and survival lower for owls in territories affected by high-severity fires in north-western California (Rockweit et al. 2017); and owls avoided high-severity burned areas in both the Timbered Rock fire and fires in Yosemite National Park (Comfort et al. 2016, Eyes et al. 2017). Ignoring the potential for large, high-severity fire to affect spotted owls negatively could compromise the ability to conserve this species, particularly as climate change produces conditions that exacerbate the risk of high-severity fires (Abatzoglou and Williams 2016, Westerling 2016). As scientists we believe it is fundamentally more important to understand or acknowledge the negative effects of high-severity fires on spotted owls because failing to do so has the potential to impede forest restoration and efforts to reduce fire risk through management actions (Peery et al. 2019).

We do not recommend any particular management strategy because it is beyond our purview here, but we do suggest that forest ecosystem restoration activities that reduce the frequency and size of large, severe fires could benefit spotted owls if these activities are conducted properly (i.e. with consideration of spotted owl habitat and space use requirements), but we submit that the evidence is unambiguous that mega-fires can be a major threat to spotted owls and their habitat. Thus, we need to understand the nature of the threat(s) and how best to meet that threat through appropriate conservation strategies. We also do not profess to know the appropriate balance between retaining spotted owl habitat to promote viable populations in the short-term and implementing forest restoration activities to reduce large, severe fires in the long-term, but we must strive to find it or at least a range of conservation options. We believe that deriving such balance can best be achieved through an improved understanding of how wildfire affects spotted owls, how climate change affects future changes in wildfire regimes and forest conditions and by prospective modelling that links spotted owl dynamics to changing conditions. Forest ecosystem management, intended to reduce large, high-severity fires, is least likely to impact spotted owls in the short-term if they can be designed to retain forest structural characteristics known to be important to owls (Tempel et al. 2015, Jones et al. 2018). Clearly, meeting the dual objectives of spotted owl conservation and forest ecosystem restoration will be complex, but these objectives are not served by faulty science (Peery et al. 2019).

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Supplementary material 1

Figure S1

Authors: Gavin M. Jones, R. J. Gutiérrez, H. Anu Kramer, Douglas J. Tempel, William J. Berigan, Sheila A. Whitmore, M. Zachariah Peery

Data type: Representative photographs of two spotted owl nest areas burned at high fire severity during the King Fire (2014) and three general areas within the Eldorado Study Area in the central Sierra Nevada, California, USA that depict three general fire severity classes of this fire.

Explanation note: Nest site area within the spotted owl territory PLA0113 taken 7 months after being burned by the King Fire, central Sierra Nevada, California, USA. An estimated 90.7% of this owl territory (based on 1100 metre radius circle) burned at high-severity.

Link: https://doi.org/10.3897/natureconservation.37.32741.suppl1

Supplementary material 2

Figure S2

Authors: Gavin M. Jones, R. J. Gutiérrez, H. Anu Kramer, Douglas J. Tempel, William J. Berigan, Sheila A. Whitmore, M. Zachariah Peery

Data type: Representative photographs of two spotted owl nest areas burned at high fire severity during the King Fire (2014) and three general areas within the Eldorado Study Area in the central Sierra Nevada, California, USA that depict three general fire severity classes of this fire.

Explanation note: Nest site area within the spotted owl territory PLA0065 taken 7 months after being burned by the King Fire, central Sierra Nevada, California, USA. An estimated 95.5% of this owl territory (based on 1100 metre radius circle) burned at high-severity.

Link: https://doi.org/10.3897/natureconservation.37.32741.suppl2

Supplementary material 3

Figure S3

Authors: Gavin M. Jones, R. J. Gutiérrez, H. Anu Kramer, Douglas J. Tempel, William J. Berigan, Sheila A. Whitmore, M. Zachariah Peery

Data type: Representative photographs of two spotted owl nest areas burned at high fire severity during the King Fire (2014) and three general areas within the Eldorado Study Area in the central Sierra Nevada, California, USA that depict three general fire severity classes of this fire.

Explanation note: Example of a typical area within the contiguous >13,000 ha patch of high-severity fire that burned at high-severity on the Eldorado spotted owl study area located in the central Sierra Nevada, California, USA.

Link: https://doi.org/10.3897/natureconservation.37.32741.suppl3

Supplementary material 4

Figure S4

Authors: Gavin M. Jones, R. J. Gutiérrez, H. Anu Kramer, Douglas J. Tempel, William J. Berigan, Sheila A. Whitmore, M. Zachariah Peery

Data type: Representative photographs of two spotted owl nest areas burned at high fire severity during the King Fire (2014) and three general areas within the Eldorado Study Area in the central Sierra Nevada, California, USA that depict three general fire severity classes of this fire.

Explanation note: Example of a typical area within the contiguous >13,000 ha patch of high-severity fire that burned at high-severity on the Eldorado spotted owl study area located in the central Sierra Nevada, California, USA.

Link: https://doi.org/10.3897/natureconservation.37.32741.suppl4

Supplementary material 5

Figure S5

Authors: Gavin M. Jones, R. J. Gutiérrez, H. Anu Kramer, Douglas J. Tempel, William J. Berigan, Sheila A. Whitmore, M. Zachariah Peery

Data type: Representative photographs of two spotted owl nest areas burned at high fire severity during the King Fire (2014) and three general areas within the Eldorado Study Area in the central Sierra Nevada, California, USA that depict three general fire severity classes of this fire.

Explanation note: Example of an area burned at moderate-severity within a spotted owl nest stand used in 2015 (ELD0085) on the Eldorado spotted owl study area located in the central Sierra Nevada, California, USA. In this case, the original territory centre (i.e. 2014) was ~1 km from this new nest stand but was burned at high severity. In addition, this female paired with the male displaced from PLA0113 (see Figure S1) by high-severity fire.

Link: https://doi.org/10.3897/natureconservation.37.32741.suppl5

Supplementary material 6

Figure S6

Authors: Gavin M. Jones, R. J. Gutiérrez, H. Anu Kramer, Douglas J. Tempel, William J. Berigan, Sheila A. Whitmore, M. Zachariah Peery

Data type: Representative photographs of two spotted owl nest areas burned at high fire severity during the King Fire (2014) and three general areas within the Eldorado Study Area in the central Sierra Nevada, California, USA that depict three general fire severity classes of this fire.

Explanation note: Example of an area burned at low-severity on the Eldorado spotted owl study area located in the central Sierra Nevada, California, USA. This area had natural open areas of brush and rock with continuous patches of forest that incurred low tree mortality. This area contained no spotted owl territory.

Link: https://doi.org/10.3897/natureconservation.37.32741.suppl6