IBIS
BOU international journal of avian science

Ibis (2021), **163**, 253–259 doi: 10.1111/ibi.12832

Short Communication

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

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

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

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

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

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

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

METHODS

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

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

For owls with GPS data (n = 25 owls from 23 territories), we used nightly locations to quantify 95% kernel density estimate (KDE) territory polygons. For owls without GPS data (n = 16 owls from 13 territories), we defined territories as circular buffers (1.92 km radius) centred on nests or roosts with areas equal to the mean area of KDE polygons for owls with GPS data. Quantifying conditions within territories approximated by buffers has previously proven effective for both occupancy- (e.g. Jones *et al.* 2016) and diet-based (e.g. Hobart *et al.* 2019) research. Within owl territories (either KDE polygons or circular buffers), we quantified fire history based on two data sources over four overlapping time steps: 5-year (2012–16), 10-year (2007–16), 20-year (1997–2016) and 33-year steps (1984–2016; see Table S1 for a summarized description of each variable). Our first data source was CAL FIRE's Fire and Resource Assessment Program (FRAP; https://frap.fire.ca.gov/mapping/gis-data/), from which we downloaded perimeter data for fires over 10 acres in size (the minimum fire size monitored by FRAP). For each time step, we calculated the number and area of wildfires and prescribed fires that overlapped each owl territory. Our second data source was the Monitoring Trends in Burn Severity (MTBS; https://www.mtbs.gov/) programme, from which we downloaded fire severity information (low: <25% overstorey mortality; moderate: 25–75% overstorey mortality; and high: >75% overstorey mortality) for fires larger than 1000 acres (Eidenshink *et al.* 2007). We calculated each severity class by time step, resulting in 12 time-step burn-severity categories. If a single location burned more than once, the calculated area was cumulative and included all fires. For each owl territory we calculated (i) the proportional area in each time-step burn-severity, (ii) the Shannon diversity index of fire severity within a burned area and (iii) the Shannon diversity index of fire severity within a burned area in addition to unburned area (identical to i, except including unburned as a fourth category). All spatial analyses were performed using ArcMap 10.5.1 (ESRI, Redlands, CA, USA).

For isotopic analysis, we rinsed feathers 3× with 2 : 1 chloroform : methanol to remove contaminants, homogenized them with scissors, and dried them at 55 °C for ≥72 h. We first soaked prey bones in 0.5 N HCl for ≥48 h to remove inorganic carbon. Second, because dietary proteins, but not lipids, are typically routed to feather keratin (Bearhop *et al.* 2002), and lipid-based carbon differs isotopically from protein-based carbon (Post *et al.* 2007), we soaked prey bones 3× in 2 : 1 chloroform : methanol for 24 h to extract lipids. Third, we dried bones at 55 °C for ≥72 h and crushed them with scissors. Samples were weighed in tin capsules for $\delta^{13}C$ and $\delta^{15}N$ analysis at the University of New Mexico Center for Stable Isotopes on a Thermo Scientific Delta V mass spectrometer connected to a Costech 4010 elemental analyser and a high-temperature conversion elemental analyser. Results were expressed as parts per mil (‰) ratios relative to the international standards Vienna Peedee Belemnite (C) and atmospheric nitrogen (N).

We corrected for trophic discrimination ($\delta^{13}C \pm$ sd: 1.88‰ ± 0.04; $\delta^{15}N \pm$ sd: 4.12‰ ± 0.26) based on Snowy Owl *Bubo scandiacus* captive-feeding trials (Robillard *et al.* 2017). After trophic correction of prey isotopic signatures, nearly all owl isotopic signatures fell within the mixing space, suggesting that we had adequately sampled prey and applied appropriate trophic discrimination factors. To estimate proportional Spotted

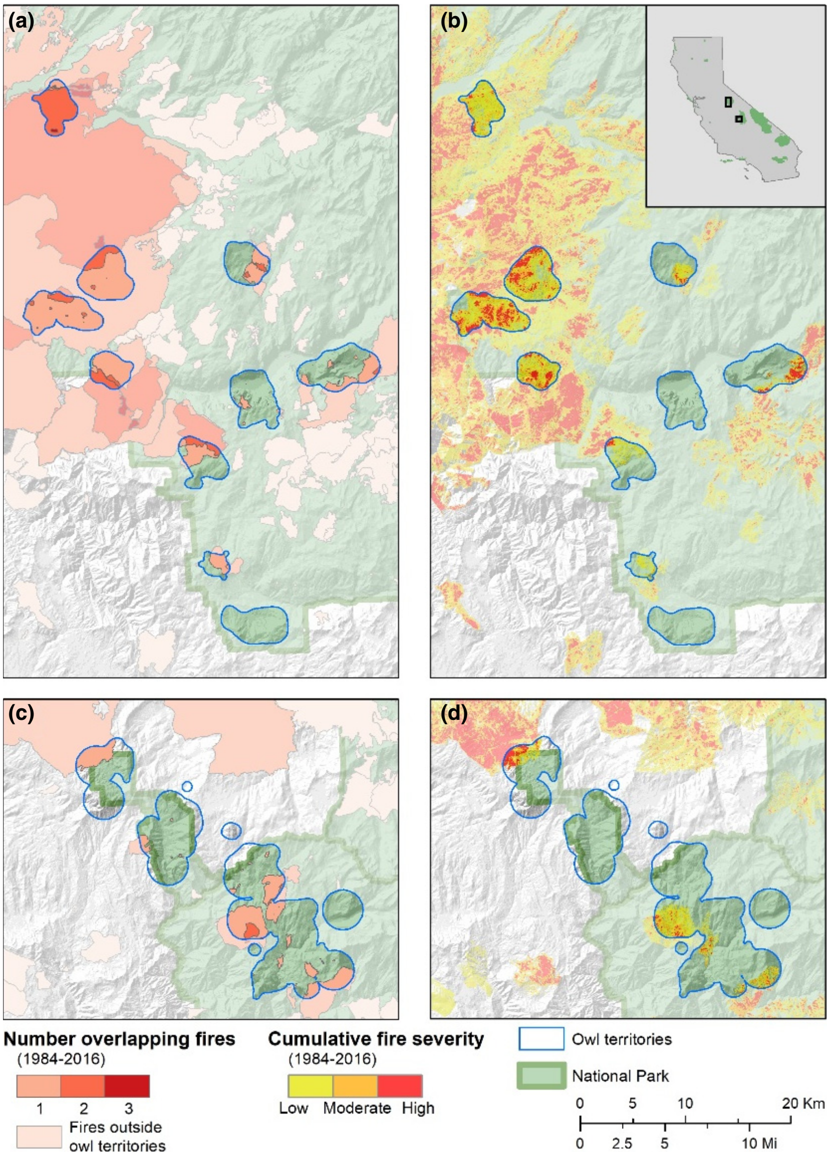

Figure 1. Map of the study areas in Yosemite (a, b) and Sequoia and Kings Canyon (c, d) National Parks, showing the distribution of fire perimeters and perimeter overlap (a, c) and cumulative fire severity (b, d) from all fires that burned between 1984 and 2016.

Owl diet, we employed Bayesian mixing models using the package MixSIAR, which quantifies the contribution of sources (prey) to mixtures (predators) while allowing for the incorporation of covariates, priors and flexible error structures (we point interested readers to Stock *et al.* 2018 for a comprehensive overview of model formulation and assumptions). We specified generalist ('uninformative') priors and ran three Markov chains (length = 300 000; burn-in = 200 000; thinning rate = 100), yielding an effective sample size of 3000 (calculated using the R package 'coda'; Plummer *et al.* 2006). We specified process × residual error structure for all models (Stock *et al.* 2018). We considered Gelman–Rubin diagnostic ($\widehat{R}$) values <1.05 to indicate model convergence. Although the diet of male and female owls differed (~10% proportional difference), such variability was modest enough that we chose to include both sexes in mixing models. We were, however, precluded from including sex as a categorical independent variable by model structure limitations. We included 14 MTBS-based and 16 FRAP-based fire variables in a set of MixSIAR models where each model had one continuous covariate (Table 1; see Stock *et al.* 2018 for model-fitting details). We used leave-one-out (LOO) cross-validation to rank the relative predictive capability of FRAP and MTBS variables and considered models ranked above a null model (i.e. no covariate included) to be plausible descriptions of Spotted Owl diet (i.e. ‘supported’). We did not include owl territory as a random effect because models with a random effect for territory did not converge and, in this context, the isotopic signatures of a pair of owls occupying the same territory can be assumed to be independent (see Appendix S1 for details).

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

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

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

RESULTS

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

DISCUSSION

Stable isotopes revealed consistent relationships between fire history and Spotted Owl diet in national parks with restored fire regimes. Although Woodrats and Pocket Gophers were the predominant prey, Spotted Owls consumed an increasing proportion of Flying Squirrels when their territories experienced more extensive and frequent fire. This result was opposite to our *a priori* predictions and, indeed, could be considered unexpected given previous work suggesting that partially restored fire regimes in national parks increase Woodrat abundance (Roberts *et al.* 2015). However, because isotopic mixing models estimate proportional consumption, the positive association observed between fire and Flying Squirrels could have been driven by increased consumption of Flying Squirrels with a smaller increase (or no change) in Woodrat and Pocket Gopher consumption. It is also important to recognize that fire-associated changes in the proportional consumption of the two prey groups could have occurred because of shifts in accessibility (e.g. reduced search times) independent of changes in the abundance of either prey group. Below we explore potential ecological mechanisms that may have driven the observed results, discuss implications for Spotted Owl conservation, and provide directions for future research.

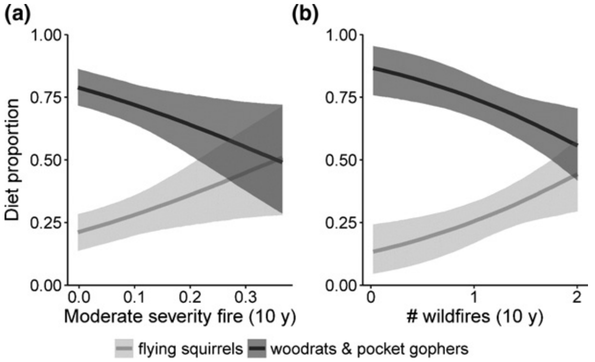

Figure 2. Relationships between California Spotted Owl diet and (a) the proportion of moderate-severity fire within owl territories in the last 10 years; and (b) the number of wildfires within owl territories in the last 10 years.

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

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

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

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

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

We thank R. J. Gutiérrez, Ceeanna Zulla, Danny Hofstadter, William Berigan, Tom Munton, Sarah Stock and Stephanie Eyes for logistical support with fieldwork and data collection. We are also grateful to Rebecca Kimball, Jesus Martínez-Padilla and an anonymous reviewer for their valuable feedback on our manuscript. This work was funded by Sierra Pacific Industries, the USDA Forest Service Region 5 and the Forest Service Pacific Southwest Research Station.

DATA AVAILABILITY STATEMENT

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

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Received 16 August 2019;
revision accepted 18 March 2020.
Associate Editor: Jesus Martínez-Padilla

SUPPORTING INFORMATION

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

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

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

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

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

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

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

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

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