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Trophic interactions mediate the response of predator populations to habitat change

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ABSTRACT

Identifying the mechanisms by which globally pervasive changes in habitat affect predators is a central, yet challenging, endeavor in applied ecology. Cryptic shifts in trophic interactions are potentially important but widely underappreciated mechanisms shaping predator population response to habitat change. Here, we assessed the extent to which variation in trophic interactions explained differences in predator populations at both local and landscape scales. We integrated stable isotope analyses, GPS tagging, and long-term territory occupancy information to characterize the trophic ecology of spotted owls in the Sierra Nevada, California, USA where population trends and densities vary among forest landscapes with contrasting land uses and disturbance regimes. Trophic interactions appeared to influence spotted owl space use and territory occupancy rates with emergent consequences for landscape-scale patterns in population abundance and trends. Specifically, consumption of woodrats and pocket gophers, which varied with habitat conditions, was associated with smaller home ranges and lower territory extinction probabilities. Moreover, spotted owls consumed significantly more woodrats and pocket gophers in landscapes with stable (national parks) and high-occupancy (private lands) populations than in landscapes with declining owl populations (national forests). Collectively, our results suggest that trophic responses to local habitat conditions can affect predators at multiple spatial scales and that managing for important prey species habitat may benefit predator populations. Because trophic interactions mediate species' responses to anthropogenic pressures in many ecological systems, our approach to integrating stable isotopes with behavioral, fitness, occupancy, and demographic data offers a tractable avenue for researchers elsewhere to quantify such relationships.

1. Introduction

As human-driven extinctions accelerate, understanding the factors that cause population declines is a central, yet challenging, goal in applied ecology (Ceballos et al., 2017). It is increasingly recognized that interspecific interactions play an important role in shaping the response of species to anthropogenic habitat loss and degradation (Stier et al., 2016). Trophic interactions (i.e., consumer-resource relationships) in particular may affect whether and to what degree habitat alterations lead to changes in population trends, given that resource consumption can influence key aspects of species' life histories (Elton, 1927). Indeed, resource use can modify individual space-use behavior (and thus energetic budgets; Schoener, 1968), fine-scale demographics (Moss et al., 2016b), and broad-scale patterns in abundance (Chamberlain et al., 2005). Thus, understanding the interplay among habitat changes, trophic interactions, and population trends may be an important prerequisite to reversing species declines, conserving biodiversity, and restoring functional relationships to ecosystems (Stier et al., 2016).

Predators are particularly prone to diet-mediated responses to habitat change because of their higher trophic position and dependence on spatially and temporally variable prey resources (Elton, 1927; Moss et al., 2016b). Because predator diets are often relatively plastic (Darimont et al., 2009), local shifts in habitat structure and abundance that alter resource availability may lead to concomitant changes in trophic interactions between predators and their prey. In some cases, trophic plasticity may allow predators to exploit novel resources in

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highly impacted ecosystems (Moss et al., 2016a). Yet, individuals may also incur fitness consequences when bottom-up shifts in resource availability result in reliance on low-quality resources (Heiss et al., 2009). Thus, for predators, local-scale variability in trophic interactions may cause both positive and negative responses to anthropogenic habitat changes.

Local, individual-level variation in trophic interactions may have emergent consequences for predator populations at broad spatial scales (Levin, 1992). In landscapes where predators consume high-quality (i.e., large-bodied and/or high-density) prey, elevated fitness can promote positive population growth (Benton et al., 2006) and smaller home ranges can increase population densities (McNab, 1963). However, because consumptive patterns are logistically challenging to quantify, they are seldom evaluated alongside habitat factors as drivers of predator population change over broad extents (Rosado et al., 2016). This constraint has contributed to the viewpoint suggested by some ecologists that interspecific interactions may be unnecessary to consider at coarse grains and large spatial scales (Soberón and Nakamura, 2009). Thus, despite the importance of predation to ecosystem processes (Estes et al., 2011), the role that trophic interactions play in mediating predator population response to anthropogenic habitat change is poorly understood.

Here, we assessed whether trophic interactions mediate the response of predator populations to anthropogenic habitat alteration, focusing on a territorial old-forest species, the California spotted owl *Strix occidentalis occidentalis* (hereafter "spotted owl"). In the Sierra Nevada, USA, spotted owl population status varies among forested landscapes that differ in structure owing to contrasting human land use practices on national parks, national forests, and private lands (e.g., Collins et al., 2017). Populations are declining on national forest-dominated landscapes, where selective logging and a century of fire suppression have created dense, homogeneous forests with a large-tree deficit (Jones et al., 2018). By contrast, populations appear stable or increasing on national parks, where timber harvest restrictions and the partial restoration of frequent-fire regimes have promoted more heterogeneous forests dominated by large trees (Collins et al., 2017). Finally, spotted owl territory occupancy is unexpectedly high in landscapes dominated by private lands managed for timber production that contain a mosaic of younger, even-aged forest stands (Hobart et al., 2019). Although patterns of spotted owl population status are well-described, the ecological mechanisms linking forest management and conditions to such patterns remain uncertain (Peery et al., 2017).

We hypothesized that trophic interactions mediate spotted owl population response to habitat differences among national forests, national parks, and private landscapes. Spotted owls consume a diverse array of small mammals and other taxa, but flying squirrels *Glaucomys oregonensis* and woodrats *Neotoma* spp. dominate their diet by biomass in our study region (Verner et al., 1992). Whereas flying squirrels are associated with mature, closed-canopy forests (Waters and Zabel, 1995), woodrats utilize a wider range of forest conditions. Dusky-footed *N. fuscipes* and big-eared woodrats *N. macrotis* are relatively abundant in younger forests with ample hardwoods at lower elevations (Innes et al., 2007) but bushy-tailed woodrats *N. cinerea* reside in both young and mature forests – often near rocky features – at higher elevations (Carey et al., 1999). All three woodrat species also occupy riparian forests and utilize cavities in old trees, snags, and downed debris (Innes et al., 2007). Given their habitat associations, it is possible that anthropogenic changes to forest structure (e.g., fire suppression, restoration, and timber extraction) have altered the distribution and abundance of flying squirrels and woodrats in the Sierra Nevada. Moreover, although both are important prey for spotted owls, woodrats are higher-density (up to 40 acre^{-1} versus ~1 acre^{-1}; Williams et al., 1992) and provide more energy per prey (1205 kJ versus 592 kJ; Weathers et al., 2001), and thus may be more energetically profitable prey when present (i.e., higher-quality). Thus, because prey availability may vary among landscapes and with owl population status in the Sierra Nevada, this system offers a valuable opportunity to investigate whether trophic interactions mediate population response to anthropogenic habitat change and, in the process, resolve a longstanding uncertainty for a model species in population and landscape ecology.

We integrated stable isotope analyses with individual movement, territory occupancy, and remotely-sensed vegetation data to test three predictions related to our central hypothesis. First, at the local (territory) scale, we predicted that the prevalence of hardwoods, degree of forest heterogeneity, and presence of young forest would promote consumption of woodrats by owls, whereas medium-aged and older forest would promote consumption of flying squirrels. Second, we predicted that consumption of woodrats by owls would be associated with (i) smaller home range sizes and (ii) lower territory extinction rates. Third, at the landscape scale we predicted that spotted owls would consume primarily woodrats on private lands, flying squirrels on national forests, and an intermediate mixture on national parks. Thus, we predicted that consumption of woodrats would roughly positively correspond with landscape-scale population status. By testing these predictions across landscapes with different management strategies and ecological conditions, we offer insights into the role of trophic interactions as mechanisms that shape the response of predator populations to anthropogenic habitat change.

2. Methods

2.1. Study system

We studied spotted owls across the Sierra Nevada bioregion, USA (Fig. 1) as part of ongoing research (e.g., Atuo et al., 2019; Hobart et al., 2019; Jones et al., 2018). We surveyed for spotted owls on all major landownerships in the region, including national parks (Yosemite and Sequoia-Kings Canyon), national forests (Lassen, Plumas, Tahoe, Eldorado, Stanislaus, and Sierra), and private lands (primarily land owned by Sierra Pacific Industries). Generally, private lands occurred at lower elevations, national forests at intermediate elevations, and national parks at higher elevations (Table S1). National parks also occurred, on average, at lower latitudes than both national forests and private lands (Table S1).

2.2. Field and laboratory methods

We captured 142 adult spotted owls using established methods (Franklin et al., 1996) early in the breeding seasons (April–July) of 2017 and 2018. At the time of capture, we sampled 1–2 growing or recently grown body feathers per owl for isotopic analysis. Because feather is an inert tissue that reflects the diet for the period it was synthesized (Hobson and Clark, 1992) and spotted owls molt body feathers during the breeding season (Forsman, 1981), our samples reflected the diet for the current breeding season. We affixed GPS transmitters to a subset of 49 owls to quantify home range sizes (see Atuo et al., 2019 for details). We also opportunistically collected regurgitated spotted owl pellets to obtain count-based diet estimates and process prey bones for isotopic analysis. All animal research was approved by the University of Wisconsin institutional animal care and use committee and permitted by the necessary state and federal agencies.

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 calcium and associated 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. Feather and bone 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

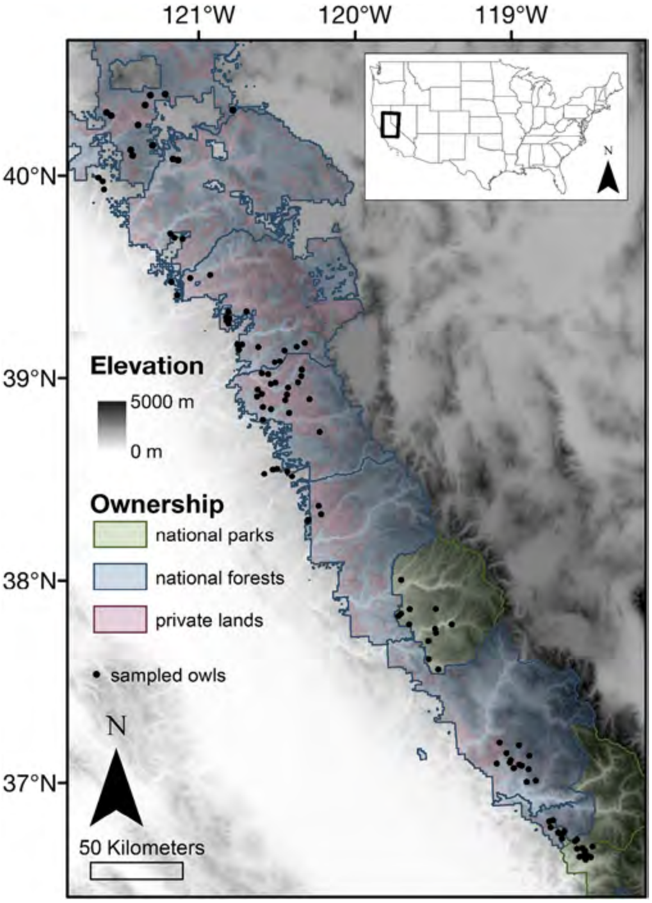

Fig. 1. Map of the Sierra Nevada, USA depicting locations where spotted owl feathers were sampled for isotopic analyses. Thick lines denote federal administrative boundaries and colored shading denotes ownership within such boundaries. Territories outside federal boundaries occurred on private lands.

Scientific Delta V mass spectrometer connected to a Costech 4010 elemental analyzer and a high-temperature conversion elemental analyzer. Results were expressed as parts per mil (‰) ratios relative to the international standards Vienna Peedee Belemnite (C) and atmospheric nitrogen (N).

2.3. Quantifying owl territory characteristics

We modeled owl diet as a function of habitat covariates (Table 1). We included elevation and latitude of owl territory centers because both variables are associated with prey species distributions. We included four forest age class covariates (open, young, medium, and old), as well as Shannon's diversity index (H) of such classes to estimate forest heterogeneity. We also included the mean basal area of hardwoods within owl territories. We calculated forest covariates using gradient-nearest-neighbor (GNN) maps (2012, lemma.forestry.oregonstate.edu) within 1270.5 ha circular buffers around owl territory centers (roosts and nests). Buffer size corresponded to the mean home range area (95% kernel density estimate [KDE]) of GPS-tagged owls calculated using the R package adehabitatHR (Calenge and Fortmann-Roe, 2013). We confirmed that forest cover (open, young, medium, and old forest) covariate values within circular buffers of GPS-tagged owls did not differ from values calculated within corresponding KDE polygons (paired t-tests, all $p > 0.05$, Table S2).

Using federal boundary maps, we classified landownership of territories entirely within national parks, national forests, or private lands accordingly. Remaining territories occurred on two ownerships; after calculating the ratio of landownership at such territories, those with a ratio between the first and third quartiles (0.31 and 0.76, respectively) were classified as "mixed-ownership". Territories with a ratio outside the quartiles were classified as the dominant owner. Thus, owl territories were assigned one of five ownership categories: national parks (n = 35), private lands (n = 25), national forests (n = 36), national park–national forest mixed ownership (n = 6), and private–national forest mixed ownership (n = 40).

Table 1
Definition and ranking of covariates included in isotopic mixing models to quantify spotted owl habitat–diet relationships. "QMD" abbreviates quadratic mean diameter. "LOO" abbreviates leave-one-out cross-validation results, where lower values indicate higher predictive capability.

Covariate	Definition	LOO
Hardwoods	Mean basal area of live hardwoods in a buffer	460.8
Elevation	Elevation (m) of territory center	472.6
Latitude	Latitude (°) of territory center	487.7
Medium forest[A]	Forest with QMD 30–61 cm and canopy cover > 40%	491.1
Forest heterogeneity[B]	Shannon's index calculated for the four cover types: $H = \sum_{i=1}^{s} (p_i) \times \ln(p_i)$	493.4
Young forest[A]	Forest with QMD < 30 cm and canopy cover > 40%	495.2
Null	No covariate included	496.4
Old forest[A]	Forest with QMD > 61 cm and canopy cover > 40%	498.3
Open area[A]	Land cover with canopy cover < 40%	498.8

[A] Unit is proportion of pixels in territory buffer.
[B] Unitless index.

2.4. Data analyses

2.4.1. Proportional diet

Based on remains in regurgitated pellets, flying squirrels, woodrats, and pocket gophers *Thomomys* spp. were the only prey that each constituted > 5% of biomass-corrected owl diet, and collectively constituted ~94% of biomass-corrected owl diet (Table S3). These prey were the only groups included in isotopic analyses because including infrequently consumed resources can bias proportional diet estimates (Phillips et al., 2014). We implemented K-nearest-neighbor randomization tests (Rosing et al., 1998) to establish that prey isotopic signatures did not vary regionally (all $p > 0.05$). Additional KNN tests indicated that woodrats (n = 35) and pocket gophers (n = 30) were isotopically indistinguishable (p = 0.50) but were distinct from flying squirrels (n = 35) individually and when grouped ($p < 0.001$), resulting in two isotopically distinct prey groups: (i) woodrats and pocket gophers and (ii) flying squirrels. We note, however, that between woodrats and pocket gophers, owl consumption of the former is more spatially variable and, at times, accounts for a majority of owl diet (e.g., Munton et al. (2002) found that whereas pocket gophers consistently accounted for 10–15% of biomass-corrected owl diet, woodrats represented > 80% in some landscapes and < 10% in others). Thus, we had a priori evidence that observed variability in the woodrat–pocket gopher prey group was largely due to woodrats.

We employed MixSIAR Bayesian mixing models (Stock et al., 2018) to quantify proportional diet. We corrected for trophic discrimination (δ^{13}C ± sd: 1.88‰ ± 0.04; δ^{15}N ± 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 adequately sampled prey and applied appropriate trophic discrimination factors (Fig. S1A). For each model, we specified generalist ("uninformative") priors and ran three Markov chains (length = 300,000; burn-in = 200,000; thinning rate = 100). We specified process × residual error structure for all models except those containing factors with 1 level (the individual model, see below), for which only process error was estimated (Stock et al., 2018). We considered Gelman-Rubin diagnostic ($\widehat{R}$) values < 1.05 to indicate model convergence.

To assess habitat–diet relationships, we included habitat covariates in a set MixSIAR models (one covariate per model; Table 1; see Stock et al., 2018 for model-fitting details). We used leave-one-out (LOO) cross-validation to identify which covariate(s) better-predicted proportional diet than a null model.

We also included individual and territory as fixed factors in MixSIAR models and calculated medians of posterior distributions for subsequent analyses. Although this approach ignored uncertainty associated with each posterior distribution, the high Pearson correlations between median values and both upper ($r_{\text{ind}} = 0.76$, $r_{\text{terr}} = 0.85$) and lower ($r_{\text{ind}} = 0.92$, $r_{\text{terr}} = 0.94$) credible interval bounds indicated that resulting estimates of diet were largely unbiased and subsequent relationships would hold at the bounds of credible intervals.

Finally, we included territory ownership as a fixed factor in a MixSIAR model and tested for dietary differences using two-sided pairwise measures of overlap between posterior distributions of mixing model solutions (see Hopkins et al., 2014 and Manlick et al., 2019 for details). Such tests are analogous to *t*-tests; significance was evaluated at $\alpha = 0.05$.

2.4.2. Diet–space use associations

We used least-squares regression to model home range size (95% KDE polygon area [ha]) as a function of individual diet (proportion of woodrats and pocket gophers). Before interpreting model output, we ensured that assumptions of linear regression were met (i.e., normal residuals, constant variance, no influential points [all Cook's distances < 1.0]).

2.4.3. Occupancy models

We used a simple multi-season occupancy model (MacKenzie et al., 2003) to assess whether diet – and proxies for diet (prey habitat, elevation) – could explain territory occupancy dynamics. Using the best-available spotted owl detection histories across a range of landownerships and ecological conditions ($n = 73$ territories with occurrence data for various intervals between 1993 and 2017; see Appendix 2 for details), we first determined that detection probability (p) varied among surveys within years ($w = 0.99$) but not among years ($w \leq 0.001$). Then, holding initial occupancy (ψ_1) constant and colonization (γ) in a year-varying structure, we modeled territory extinction probability (ε) as a function of (i) hardwoods, (ii) elevation, and (iii) dietary proportion of woodrats and pocket gophers (all covariates were z-standardized). We used AIC to evaluate support for models relative to each other and to a null model.

3. Results

We found strong evidence that spotted owl diet was related to local habitat conditions: six covariates outperformed a null model, the best of which was the mean basal area of hardwoods in an owl territory (Fig. 2, Table 1). This variable (hardwoods) was positively associated with the estimated dietary proportion of woodrats and pocket gophers (Fig. 2A) and tended to be more abundant within territories on private lands than national forests and parks (Table S1). Elevation, latitude, medium forest, young forest, and heterogeneity of forest types also outperformed the null model (Table 1, Fig. 2).

At the local scale, spotted owl home range size significantly decreased as individual consumption of woodrats and pocket gophers increased ($\beta_{\text{WR-PG}} = -3185.4$, 95% CI = -4855.30 to -1515.48; Fig. 3A). Territory extinction probability (ε) was also significantly lower when owl diet contained a greater proportion of woodrats and pocket gophers ($\beta = -0.47$, 95% CI = -0.76 to -0.18; Fig. 3B). Moreover, hardwoods (ΔAIC = 7.25) and elevation (ΔAIC = 9.19) poorly explained extinction probability relative to proportional diet ($w = 0.94$; Table S4). Home range size and extinction probability results based on proportional diet were corroborated by significant positive relationships between both response variables and raw isotopic values (δ^{13}C, i.e., consumption of flying squirrels; Fig. S2).

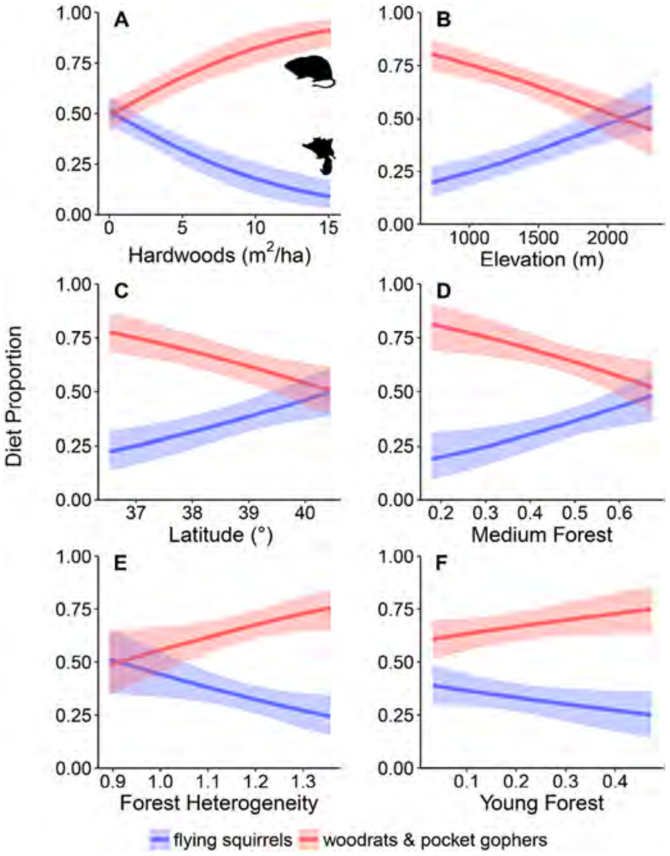

Fig. 2. Relationships between spotted owl habitat and proportional diet estimated by isotope mixing models. Only covariates that performed better than a null model based on leave-one-out cross-validation are included here. Forest class covariate units are proportions of owl territories.

At the landscape scale, spotted owls occupied divergent trophic niches among landownerships. Owls on national parks and private lands consumed significantly more woodrats and pocket gophers than did owls on national forests (Fig. 4). Moreover, comparison of diet at geographically paired national forests and national parks (Sierra NF and Sequoia-Kings Canyon NP) revealed strong trophic differences, where owls on the latter consumed significantly more woodrats and pocket gophers ($p < 0.001$; Fig. S3). Diet of owls with mixed-ownership territories generally fell intermediate to primary ownership groups (Fig. S4B).

4. Discussion

Our results suggest that trophic interactions contribute to spotted owl population differences among landscapes with contrasting land management and habitat conditions. Specifically, the consumption of presumably high-quality prey – which varied with habitat conditions – appeared to benefit spotted owls at both local and landscape scales. Although prey consumption has previously been linked to variation in spotted owl life-history traits (e.g., Zabel et al., 1995; Franklin et al., 2000), our findings are the first to show that it has consequences for territory occupancy dynamics and appears associated with landscape-scale population metrics such as density and trends in abundance. Our study also corroborates mounting evidence that (i) Eltonian niches are more plastic than previously recognized (Terry et al., 2017; Manlick et al., 2019) and (ii) trophic interactions can mediate species response to anthropogenic habitat changes (Narango et al., 2018), thus

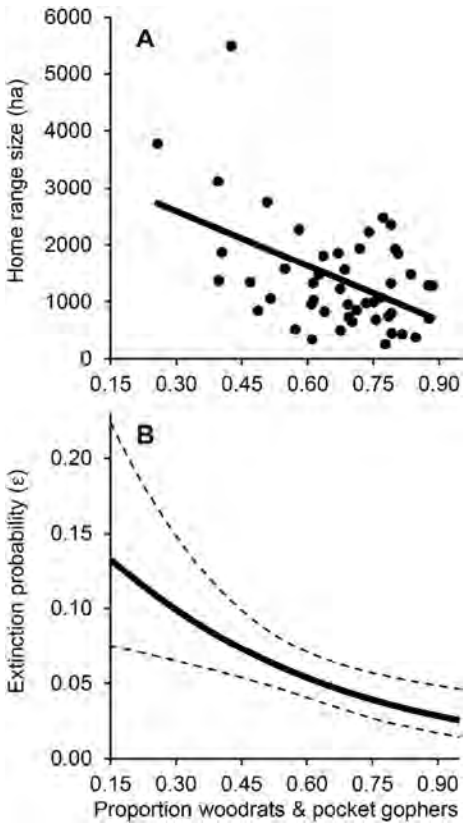

Fig. 3. Relationships between the proportion of spotted owl diet comprised of woodrats and pocket gophers and (A) home range size and (B) territory extinction probability. Thick lines indicate best fit, thin lines represent 95% CI bounds, and points indicate individual owls.

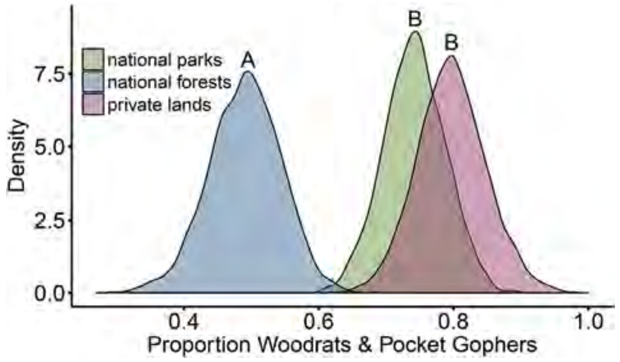

Fig. 4. Frequency distributions of proportional diet for spotted owls inhabiting the primary landownerships studied here. Letters above distributions indicate significant differences according to a two-sided test of overlap (α = 0.05).

supporting the concept that consideration of trophic interactions – in addition to habitat conditions – is important to the conservation of predator populations (Stier et al., 2016).

Our diet analyses were based on stable isotopes, which offer space- and time-integrated estimates of proportional biomass assimilation but depend on at least two key assumptions (Phillips et al., 2014). First, because consumers may utilize resources not included in mixing models, it is possible that our estimates of proportional diet are confounded with the consumption of other prey (Phillips et al., 2014). The direction and magnitude of any such biases depends on the functional roles, isotopic signatures, and dietary importance of prey not included in mixing models. In our study system, predation of primary consumers (e.g., chipmunks) by owls may result in the overestimation of woodrats and pocket gophers, predation of secondary consumers or mycophagous prey (e.g., voles) may result in the overestimation of flying squirrels, and predation of omnivorous prey with isotopic signatures intermediate to our two prey groups (e.g., *Peromyscus* spp.) may not introduce any biases in diet estimations. However, independent diet information (from regurgitated pellets) provided a measure of confidence that we included all major spotted owl prey groups in our isotopic analyses. Indeed, woodrats, pocket gophers, and flying squirrels constitute ~94% of owl diet by biomass (Table S3). Still, owls consume small amounts of other prey, so our dietary estimates of woodrats, pocket gophers, and flying squirrels must be considered relative. Nevertheless, we consider comparative differences and directional relationships to be meaningful. Second, processes other than food consumption may affect isotopic assimilation (e.g., body condition, prey digestibility, isotopic routing; Bearhop et al., 2002). However, our sample sizes were large and spanned a broad gradient of ecological conditions such that among-individual variability in such factors was unlikely to introduce a systematic bias in dietary estimates. Thus, stable isotopes appeared well-suited to quantify trophic interactions in our study system.

Isotopic mixing models provided strong evidence for relationships between habitat and prey consumption in spotted owls. In agreement with our predictions and earlier pellet-based analyses (Munton et al., 2002), owls consumed more flying squirrels in areas with prevalent medium-aged forest, at higher elevations, and at higher latitudes. Conversely, owls consumed more woodrats and pocket gophers at territories containing more hardwoods and young forest, higher forest heterogeneity, and at lower elevations – habitat features particularly important to the distribution of dusky-footed and big-eared woodrats. Thus, prey utilization varied predictably with habitat features important to flying squirrels and woodrats, but not pocket gophers (Waters and Zabel, 1995; Innes et al., 2007). This suggests that, in general, woodrats contributed more to spotted owl diets than pocket gophers (Munton et al., 2002; but see below). These findings also suggested that owls select woodrats and flying squirrels over other prey, but also that the relative consumption of these species varies, at least in part, according to availability. We recognize, however, that a lack of prey availability data precluded the distinction between selective versus proportional use of resources (Macarthur and Pianka, 1966). Regardless, our findings supported the notion that predators shift their diet in response to local habitat conditions which, in turn, may drive spatial variability in predator behavior and population status (Moss et al., 2016b).

At the individual-scale, consumption of high-quality resources leads to the utilization of smaller home ranges, which reduces energetic expenditures and predation risk (McNab, 1963). Here, we found that for the spotted owl, a central place forager, individuals that consumed more woodrats and pocket gophers had smaller home ranges (Fig. 3A). Past studies reported similar results (Zabel et al., 1995), suggesting that consumption of woodrats and pocket gophers – and particularly the former given they are large-bodied and locally high-density – may optimize foraging-related energetic expenditures. Although a formal assessment of optimal foraging in spotted owls is hampered by a lack of information on, for example, prey handling times (Macarthur and Pianka, 1966), variability in home range sizes may nonetheless be associated with energetic consequences for individual owls.

We found a novel relationship between spotted owl occupancy dynamics and prey use: territory extinction probability was lower when owls consumed more woodrats and pocket gophers, indicating that owls were less likely to die at or abandon territories where such prey was readily consumed, presumably owing to energetic benefits. Of note, the extinction–diet relationship was strongly supported despite including diet as a static, site-level covariate in occupancy models, thus assuming that resource utilization did not vary temporally. Although this assumption was likely violated to some degree, we suggest that diet is more spatially than temporally variable because (i) we found that diet varies strongly as a function of habitat conditions, which themselves have remained reasonably stable over the course of our study (Jones et al., 2018) and (ii) pellet-based data suggest that dietary proportions were relatively stable over a 25-year window in the Eldorado National Forest (B.K. Hobart, *unpublished data*). Future research that includes trophic information as a dynamic covariate (i.e., year-varying) may provide new insights into the importance of temporal variability in trophic interactions for territory occupancy of spotted owls. Regardless, because extinction probabilities drive site occupancy for long-lived species with high site fidelity such as the spotted owl, this result suggests that future shifts in prey species distributions (e.g., with climate change; Moritz et al., 2008) may cause concomitant changes in spotted owl population abundance and occupancy dynamics (Jones et al., 2016). Our results and findings by others (e.g., Chamberlain et al., 2005; Garces-Restrepo et al., 2019) indicate that trophic interactions can be an important determinant of spatial variability in population status. Thus, failure to account for such interactions in applied ecological research may lead to knowledge gaps and, at worst, ineffective or detrimental conservation measures (Stier et al., 2016).

Long-term research of spotted owls has elucidated numerous associations between occupancy dynamics and habitat conditions but few of the mechanisms that underlie those observed patterns (reviewed in Roberts, 2017). In particular, the prevalence of old forest in national parks and young forest with hardwoods in private-dominated areas explained favorable population metrics in such landscapes relative to national forests (Jones et al., 2018; Hobart et al., 2019). However, our finding that owls consumed significantly more woodrats and pocket gophers in national parks and private lands than in national forests provides preliminary evidence that trophic interactions between spotted owls and their prey may be partly responsible for differences in population abundance and occupancy dynamics among these three landscapes.

Although the historical loss of nesting and roosting habitat is one factor limiting spotted owl populations on national forests (Jones et al., 2018), forest management leading to an overreliance on relatively low-quality flying squirrels may also contribute to and exacerbate downward population trends. It is possible that forest densification and homogenization resulting from fire suppression have increased the abundance of suitable habitat for flying squirrels but not woodrats and pocket gophers (Collins et al., 2017). Bottom-up shifts in prey communities may have then altered spotted owl trophic interactions, with consequences for home range size, occupancy dynamics, and population trends. We acknowledge the alternative explanation that such downward trends could also be due to declines in flying squirrel abundance from historical levels. However, owl consumption of flying squirrels increased with medium forest – which has likely become more common on national forests owing to large-tree logging and fire suppression – suggesting that reductions in flying squirrel availability may not limit owl populations in such landscapes. A second alternative hypothesis is that rodenticides originating at illegal marijuana growing operations – which could be more common on national forests than other ownerships – are poisoning owls in such landscapes, leading to lower survival, reproduction, and territory occupancy (Gabriel et al., 2018). However, flying squirrels, which rely heavily on lichens and hypogeous fungi (Meyer et al., 2005), likely experience lower exposure to rodenticides than woodrats and pocket gophers. Thus, it is unlikely that contaminant exposure explains the relatively estimated high extinction rates at territories where spotted owls consume high proportions of flying squirrels.

In contrast to national forests, a greater reliance on woodrats and pocket gophers by spotted owls in national parks and private lands may contribute to relatively high owl abundance and occupancy rates in such landscapes. On private lands, even-aged forest management may promote patches of young forest woodrat habitat (Sakai and Noon, 1993), particularly when landowners manage for the retention and recruitment of hardwood species (e.g., California black oak) and shrub cover (Innes et al., 2007; Gray et al., 2019). Although private lands have long been thought to provide only modest suitable habitat for spotted owls owing to active logging operations (Bias and Gutiérrez, 1992), such land management may benefit owls by providing key prey resources if younger forests with shrubs and hardwoods are juxtaposed with ample nesting and roosting habitat (older forest).

Spotted owls in national parks consumed a high proportion of woodrats and pocket gophers despite a relative paucity of habitat features (e.g., young forest and hardwoods at low elevations) that our stable isotope analyses suggested promoted consumption of these two species (Table S1). By using coarse remote-sensed landcover data, we may not have captured fine-scale habitat characteristics important to pocket gophers (e.g., small meadows) and woodrats (e.g., patchy understory brush) in national parks. Such conditions are likely promoted by the prescription of frequent, low-intensity fire regimes in the national parks studied here (Collins et al., 2017). Moreover, because bushy-tailed woodrats den in rocky areas like talus slopes (which are relatively common in the national parks studied here; S.L. Roberts *personal communication*) and in cavities of large trees, it is possible that naturally-occurring geological features and the protection of defect trees in national parks acted to increase the availability of woodrats to owls. Thus, although some uncertainties remain, our results provided a plausible mechanism to explain landscape-scale variability in spotted owl population measures and suggest that incorporating information about trophic interactions is an important prerequisite to understanding how predators respond to habitat differences among landscapes with contrasting land use histories and strategies.

Our results collectively suggest that restoration and management activities that promote key prey species may also benefit predator conservation, even if prey habitat does not necessarily reflect predator habitat (e.g., nesting areas). For example, forest management in the Sierra Nevada that produces woodrat and pocket gopher habitat may also benefit spotted owls. Specifically, promoting patches of brushy woodrat habitat and grassy pocket gopher habitat adjacent to closed-canopy forests could enhance foraging opportunities for spotted owls. Our results also point to linkages among forest management, restoration, and species conservation: the regeneration of hardwoods – which has slowed owing to fire suppression – following natural and anthropogenic disturbance may simultaneously benefit woodrats, spotted owls, and forest restoration. Moreover, all three woodrat species nest and den in tree cavities, underscoring the potential benefits of forest management and restoration that retain and promote snags and trees with cavities — key structural features that have declined significantly from historical levels owing to the selective harvesting of large trees (Collins et al., 2017). Thus, as is increasingly being recognized for a range of taxa in diverse ecosystems (Samhouri et al., 2017), our research on trophic interactions suggests that compatibility may exist between ecosystem restoration in the Sierra Nevada and the conservation of the spotted owl.

More broadly, our work highlights the importance of biotic interactions as drivers of species' responses to land use and management. Consider, for example, the dramatic and ongoing decline of woodland caribou *Rangifer tarandus caribou* in North America, driven by both bottom-up (loss of lichen food resources owing to logging; Bergerud, 1974) and top-down (expansion of predators following the construction of industrial linear features; Latham et al., 2011) trophic interactions. Thus, our research and that of others suggests that failure to incorporate information about trophic interactions into species management may lead to undesirable outcomes and conservation conflicts (Stier et al., 2016). Indeed, interactions among members of ecological communities (e.g., predation) shape the role and stability of populations in novel ecosystems. Considering biotic interactions is thus likely to be important to emerging conservation issues such as reintroduction (Carlson et al., 2014) and rewildling efforts (Alston et al., 2019), climate-driven spatial (Kudrna et al., 2008) and temporal (Jara et al., 2019) shifts, and species invasions (Larson et al., 2010). Because the consequences of novel or decoupled trophic interactions extend beyond populations to both communities and ecosystems (Estes et al., 2011), incorporating the Eltonian niche is broadly valuable to applied ecological research.

Our research provides both impetus and direction to quantify linkages between anthropogenic change, trophic interactions, and population processes in other ecological systems. Despite the historical difficulty of measuring trophic interactions (Rosado et al., 2016), our stable isotope approach offers a potentially tractable avenue to quantify such relationships more broadly for three reasons. First, isotopic analyses require small quantities of biomaterials that can generally be collected with relative ease as part of ongoing ecological studies, from museum collections, or from harvested individuals. Second, recent developments have provided flexible, robust statistical tools to analyze isotopic data (e.g., MixSIAR, used here) and well-documented best practices for isotopic research (Ben-David and Flaherty, 2012; Layman et al., 2012; Phillips et al., 2014). Third, isotopic information can be combined with additional, potentially preexisting data (e.g., behavioral, occupancy, fitness, or demographic) to improve and augment understanding of how biotic interactions affect species. Our two-step approach demonstrated that the benefits of modern isotopic analyses can be leveraged to (i) identify how trophic interactions vary with habitat conditions and (ii) identify the consequences of changes in trophic interactions for a focal species. However, this approach is not limited to questions about linkages among habitat, diet, and population processes, but could be used to study how trophic interactions mediate population responses to invasions, extinctions, light and noise pollution, disturbance, and climate change. Although such relationships are seldom tested explicitly, doing so could help elucidate previously unrecognized and cryptic mechanisms by which species respond to environment change.

Declarations of Competing Interest

The authors declare no conflicts of interest.

Data accessibility

The data associated with this paper have not been archived due to the sensitive legal and political circumstances surrounding the pending listing decision for the California spotted owl (*S. o. occidentalis*) under the U.S. Endangered Species Act.

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Author contributions

B.K.H. and M.Z.P. conceived the ideas and designed the study; all authors collected the data; B.K.H., G.M.J., and M.Z.P. drafted the manuscript with inputs from all authors. All authors contributed substantially to revisions and approved the final draft of the manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2019.108217.

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