

RESEARCH ARTICLE

Dynamic occupancy modelling reveals a hierarchy of competition among fishers, grey foxes and ringtails

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Abstract

1. Determining how species coexist is critical for understanding functional diversity, niche partitioning and interspecific interactions. Identifying the direct and indirect interactions among sympatric carnivores that enable their coexistence is particularly important to elucidate because they are integral for maintaining ecosystem function.
2. We studied the effects of removing nine fishers (*Pekania pennanti*) on their population dynamics and used this perturbation to elucidate the interspecific interactions among fishers, grey foxes (*Urocyon cinereoargenteus*) and ringtails (*Bassariscus astutus*). Grey foxes (family: Canidae) are likely to compete with fishers due to their similar body sizes and dietary overlap, and ringtails (family: Procyonidae), like fishers, are semi-arboreal species of conservation concern. We used spatial capture–recapture to investigate fisher population numbers and dynamic occupancy models that incorporated interspecific interactions to investigate the effects members of these species had on the colonization and persistence of each other's site occupancy.
3. The fisher population showed no change in density for up to 3 years following the removals of fishers for translocations. In contrast, fisher site occupancy decreased in the years immediately following the translocations. During this same time period, site occupancy by grey foxes increased and remained elevated through the end of the study.
4. We found a complicated hierarchy among fishers, foxes and ringtails. Fishers affected grey fox site persistence negatively but had a positive effect on their colonization. Foxes had a positive effect on ringtail site colonization. Thus, fishers were the dominant small carnivore where present and negatively affected foxes directly and ringtails indirectly.
5. Coexistence among the small carnivores we studied appears to reflect dynamic spatial partitioning. Conservation and management efforts should investigate how intraguild interactions may influence the recolonization of carnivores to previously occupied landscapes.

KEYWORDS

Bassariscus astutus, dynamic occupancy model, Jolly-Seber, *Pekania pennanti*, source community, spatial capture–recapture, translocation, *Urocyon cinereoargenteus*

1 | INTRODUCTION

Carnivores are integral members of ecological communities. The top-down pressures they exhibit on sympatric species structure ecosystems and their absences can trigger trophic cascades and effect changes in ecosystem integrity (Estes et al., 2011; Ripple et al., 2014; Ritchie & Johnson, 2009). The interactions among carnivore species can also be important drivers of carnivore community dynamics. Competitive, antagonistic behaviours among large carnivores can result in kleptoparasitism (Périquet, Fritz, & Revilla, 2015), spatial or temporal segregation (Dröge, Creel, Becker, & M'soka, 2017) and, at its most extreme, intraguild predation (Creel, 2001; Palomares & Caro, 1999). Subordinate species have adapted to occupy environments with their dominant competitors by partitioning space, time and resources to pre-empt and mediate conflicts (e.g. Bischof, Ali, Kabir, Hameed, & Nawaz, 2014; Kamler, Ballard, Gilliland, Lemons, & Mote, 2003; Swanson et al., 2014). While a large body of research has accumulated on the many mechanisms for large-carnivore coexistence, interspecific interactions governing coexistence among small carnivores are less well-studied.

Interspecific interactions within small-carnivore guilds may differ from those observed within large-carnivore guilds. Many small-carnivore guilds include numerous generalist species of similar body sizes whose members overlap in range, diet and habitat requirements (Lesmeister, Nielsen, Schaubert, & Hellgren, 2015; McDonald, Nielsen, Oyana, & Sun, 2008; Remonti et al., 2012). In addition to competing with carnivores of the same guild, smaller carnivores are also subject to top-down pressures from larger, dominant carnivores, and live in a "Landscape of Fear" (Laundré, Hernández, & Ripple, 2010). The structure and dynamics of these small-carnivore guilds have also changed over time due to decreases in the numbers of apex carnivores (i.e. "mesopredator release"; Estes et al., 2011; Prugh et al., 2009; Ripple et al., 2014) and changes in habitat (e.g. Ritchie & Johnson, 2009). The effects on species remaining in ecosystems following such mesopredator releases can include broad-scale decreases of small mammal and songbird populations (e.g. Crooks & Soulé, 1999; Johnson, Isaac, & Fisher, 2007), increases in disease prevalence (e.g. Levi, Kilpatrick, Mangel, & Wilmsers, 2012) and economic consequences in developing nations (e.g. Taylor, Ryan, Brashares, & Johnson, 2016). Limited research has examined how changing population numbers of smaller carnivores affect the dynamics of small-carnivore guilds. Investigating the effects that changing numbers of one small carnivore on the populations of other members of its guild is important to understand niche partitioning and coexistence in complex environments. A North American species that is a member of several small-carnivore guilds and that is also a species of conservation concern in the western portions of its range is the fisher (*Pekania* [formerly *Martes*] *pennanti*).

Fishers are small forest-dwelling carnivores whose range decreased substantially after the mid-1800s (Aubry & Lewis, 2003; Krohn, 2012; Powell, 1993). Fishers are members of diverse small-carnivore guilds that can share environments with up to seven other terrestrial mammalian carnivores of their size or slightly smaller (e.g. grey foxes [*Urocyon cinereoargenteus*], spotted and striped skunks

[*Spilogale gracilis*, *Mephitis mephitis*], ringtails [*Bassariscus astutus*], martens [*Martes americana*, *Martes caurina*], raccoons [*Procyon lotor*] and opossums [*Didelphis virginiana*]). Although previous research has investigated range overlap and co-occurrence of some of these species (Campbell, 2004; Gompper, Lesmeister, Ray, Malcolm, & Kays, 2016; Sweitzer & Furnas, 2016), the strength and directionality of interspecific interactions influencing abundances and distributions are not well understood. Fishers are also a species of conservation concern in the western United States, as aside from successful translocations, this species has not recolonized many previously occupied habitats (Lewis, Powell, & Zielinski, 2012). Studying their interactions with other small carnivores may lend additional insight into any mechanisms that may be influencing recolonization.

Here, we investigated the intraguild dynamics among fishers, grey foxes and ringtails over 8 years using a planned translocation of fishers as an experimental removal. There is strong potential for competitive interactions within this small-carnivore guild because of their similar body sizes, and overlapping functional niches, diets and habitat requirements (Simberloff & Dayan, 1991). Very limited evidence exists showing that carnivores of this size engage in intraguild predation and, as such, spatial and temporal partitioning appears to play a large role in reducing their ecological overlap in space and time (de Satgé, Teichman, & Cristescu, 2017). We hypothesized that a hierarchy within small-carnivore guilds influences the distribution of its members on the landscape. We tested three predictions of this hypothesis, that (1) there would be a dominant carnivore within this small-carnivore guild that would limit the presence of subordinate carnivores, (2) subordinate carnivores would increase in their occurrence when the dominant carnivore is removed from the environment, and (3) there would be indirect effects of the dominant carnivore on other members of the guild that may mediate their occurrence.

2 | MATERIALS AND METHODS

2.1 | Study site

We monitored small carnivores in a portion of the Klamath-Siskiyou Ecoregion in northern California and southern Oregon, USA (henceforth, "Klamath"; Figure 1). Land cover was predominantly conifer forest (53%), along with mixed conifer/broadleaf (21%), broadleaf forest (5%) and open areas (11%; determined using Gradient Nearest Neighbour structure maps; Ohmann, Gregory, Henderson, & Roberts, 2011). Elevation ranged from 472 to 2269 m.

We conducted non-invasive surveys annually between 2006 and 2013 from mid-September to early December. The fisher population in Klamath served as one of several sources for a translocation of fishers to the northern Sierra Nevada and southern Cascade Mountains in winter 2009 and 2010 after our surveys in those years (Facka et al., 2016). A total of nine fishers (4F, 1M in 2009 and 3F, 1M in 2010) were removed from Klamath. We used the removal of these individuals with high reproductive value (Facka et al., 2016; Lewis et al., 2012; Powell et al., 2012) as an experimental manipulation to evaluate changes in the distribution of sympatric small carnivores.

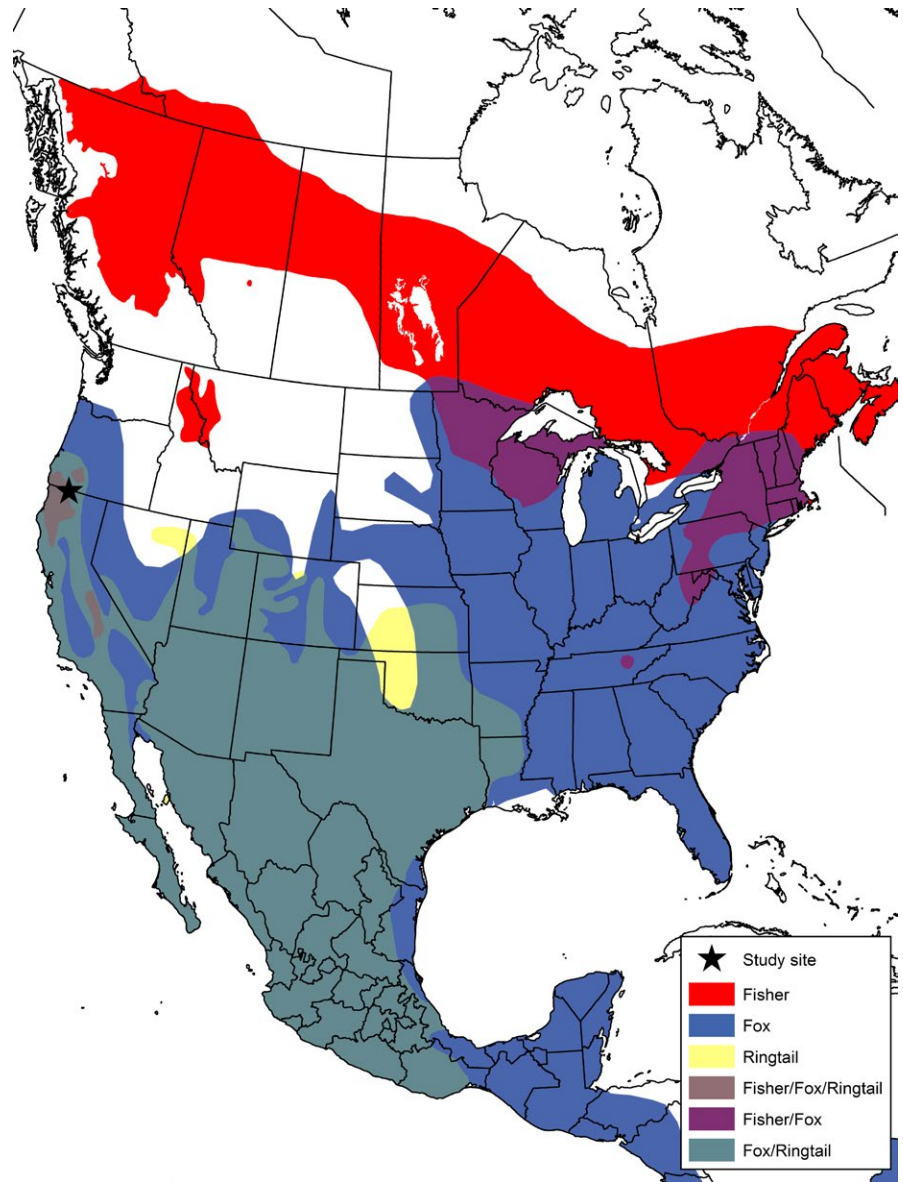


FIGURE 1 The location of our study site and the spatial overlap of fishers, grey foxes and ringtails in North America (Helgen & Reid, 2016; Reid et al., 2016; Roemer et al., 2016) [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Non-invasive sampling techniques

We surveyed 78 sites in Klamath for 4 to 6 weeks in 2006 and 100 sites in 2007 through 2013, using the same locations each year. We spaced sites 1.3 ± 0.4 km ($M \pm SD$) apart. Each sampling site consisted of a box made of corrugated plastic (Zielinski, Schlexer, Pilgrim, & Schwartz, 2006) baited with a raw chicken leg and a can of wet cat-food. The back of the box was closed with $\frac{1}{2}$ inch (1.3 cm) galvanized hardware cloth and the front was partially obstructed with three wooden slats (Zielinski et al., 2006). We fixed a strip of non-poisonous glueboard (Catchmaster 72MB, USA) to the underside of the bottom wooden slat, so that mammals coming into the box were likely to leave hair with follicles, hereafter “hair samples,” attached to the glue strip to be used for genetic analyses. Boxes were open and functioning for 2708 ± 439 ($M \pm SD$) sampling days per year. Henceforth, we refer to our study area in Klamath as the minimum convex polygon encompassing all of our sampling locations (465 km²).

Starting in 2007, we also fixed to the bottom of the sampling box a metal track plate covered with contact paper and dispersed printer toner to capture track impressions from visiting animals (Belant, 2003; Zielinski & Truex, 1995). By collecting hair samples and track plates from our sampling units, we were able to investigate trends of the fisher population via individual identifications and trends in the occupancy of members of the small-carnivore guild. Units were checked weekly and every hair sample was analysed for the presence of fisher DNA, and all track plates were analysed for the presence of tracks by fishers, grey foxes and ringtails.

We focused on these three species because fishers and foxes are most likely to be the dominant small carnivores in this environment based on their body sizes. Furthermore, previous research has indicated distributional overlap of these three species (Figure 1; Helgen & Reid, 2016; Reid, Schipper, & Timm, 2016; Roemer, Cypher, & List, 2016), but the interactions that govern their partitioning at finer spatial scales are unknown.

2.3 | Individual identification of fishers with genetics

DNA was extracted from hair samples and genotyped using the multi-tube approach recommended for non-invasive samples (Tucker, Schwartz, Truex, Wisely, & Allendorf, 2014). All samples were amplified twice at each locus, and some were amplified a third time if the initial amplifications resulted in a lack of consensus scores (Schwartz & Monfort, 2008). Samples were discarded as being of insufficient quality for genetic analyses if these three scores did not prove to be consistent. We used DROPOUT to screen for any potential errors in genotyping for samples of sufficient DNA quality (McKelvey & Schwartz, 2004; Schwartz, Cushman, McKelvey, Hayden, & Engkjer, 2006). Samples identified to contain putative errors were re-amplified an additional three times.

2.4 | Spatial Jolly-Seber open population model

We evaluated the effects of removing fishers on population dynamics in Klamath with a spatial Jolly-Seber open population model (Jolly, 1965; Seber, 1965). Traditional sampling for these models results in data from secondary sampling periods (e.g. weeks) across >1 primary sampling periods (e.g. years), often referred to as the “robust design” (Pollock, 1982). Recently developed Jolly-Seber models fit with spatial capture-recapture integrate the movements of individuals directly into their formulation to provide spatially explicit estimates of population density (Gardner, Reppucci, Lucherini, & Royle, 2010; Royle, Chandler, Sollmann, & Gardner, 2014). Spatial Jolly-Seber population models have the capacity to improve the precision of parameter estimates (e.g. Ergon & Gardner, 2014; Whittington & Sawaya, 2015).

In these models, the spatially explicit sampled locations of each individual i are assumed to be a function of the distance to its latent activity centre s_i (Efford, 2004; Royle & Young, 2008). Locations of each s_i are then calculated by estimating individual-specific encounter probabilities and the distribution of activity centres in the defined state-space (S). The number of estimated s_i of individuals observed or unobserved in the state-space equates to the population size. We defined S as a continuous state-space bounded by the outside of a rectangular 9-km buffer around our sampling units, greater than three times the size of the estimated movement parameter (σ ; Royle et al., 2014). Initial models were run using a discrete state-space to investigate if elevation or canopy cover affected the distribution of fishers in Klamath, but these covariates were not significant (95% credible intervals overlapped 0); we reparametrized the model using a continuous state-space.

We fit our models using data augmentation methods (Royle & Dorazio, 2008; Royle & Young, 2008). We introduced 550 all-zero encounter histories (nz) to our population of observed individuals (n) to prevent any truncation of the number of fishers with activity centres in S . We also introduced the partially latent variable z_{it} indicating population membership for observed or unobserved individual i in year t . Following Gardner et al. (2010), $z_{i1} \sim \text{Bernoulli}(\Psi_{\text{pop}})$ for year $t = 1$ and $z_{it} \sim \text{Bernoulli}(\mu_{it})$ for all years $t > 1$, where:

$$\mu_{it} = (z_{it-1} \times \Phi_{t-1}) + (A_{it-1}\gamma_t)$$

Here, the probability that an individual is estimated to be in the population in years $t > 1$ is a function of survival (Φ_{t-1}) from the previous year if already present (z_{it-1}) or of the probability that an individual is recruited (γ_t) into the population if not already present (A_{it-1}). In the latter part of this equation, we used the term A_{it-1} to ensure that individuals can only be recruited into the population once such that:

$$A_{it-1} = 1 - \text{step}(a_{it-1})$$

$$a_{it} = \text{sum}(z_{1:t}, t)$$

We defined a positive detection y of individual i in year t at sampling site j in week w as the Bernoulli-distributed random variable: $y_{itjw} \sim \text{Bernoulli}(p_{itjw}g_{itj}z_{it}m_{tjw})$. In this equation, p_{itjw} was the probability of detecting individual i in year t at site j in week w . The detection function g_{itj} described how the encounter rate of individual i decreased as a function of the distance between its activity centre in that year (s_{it}) and the location of sampling site j . The previously described latent variable z_{it} indicated population membership and m_{tjw} was a binary variable indicating whether or not in year t sampling box j was deployed in week w .

We hypothesized that there would be sex-specific detection probabilities and an increased probability of visitation following an initial detection as has been shown in previous studies (Linden, Fuller, Royle, & Hare, 2017; Popescu, de Valpine, & Sweitzer, 2014; Sweitzer, Furnas, Barrett, Purcell, & Thompson, 2016). We also hypothesized that time of year may influence detection, and predicted that individuals would be more likely to visit sampling locations closer to winter due to decreased food availability. We modelled the logit-linear mean encounter rate (p_{itjw}) as:

$$\text{logit}(p_{itjw}) = \alpha_0 + \alpha_1 \times \text{sex}_i + \alpha_2 \times \text{previousdetection}_{itjw} + \alpha_3 + \text{week}_w$$

where the mean encounter rate was a function of an intercept (α_0), a sex effect (α_1), an effect of a binary variable indicating whether or not the individual had visited this site in a previous week of that year (α_2), and a week-specific effect to estimate the effect of seasonality (α_3). Initial models varied α_0 by year, but there were no significant differences among α_0 in this parametrization (95% credible intervals overlapped each other) and this parameterization was ultimately dropped.

We modelled the detection function (g_{itj}) from a Gaussian encounter probability such that:

$$g_{itj} = e^{(-d_{itj}^2 / 2\sigma_k^2)}$$

where d_{itj} is the Euclidean distance between the sampling units where an individual was located and the location of its activity centre that year (s_{it}), and σ_k is the SD of a bivariate normal distribution reflecting space-use, also called the “movement parameter”, and was calculated independently for each sex (k). Sex was estimated as the Bernoulli-distributed random variable: $\text{Sex}_i \sim \text{Bernoulli}(\Psi_{\text{sex}})$. Data were collected during the fisher dispersal season (Arthur, Paragi, & Krohn, 1993; Matthews et al., 2013), but the movement parameter is robust to violations of stationary movement around the latent activity centres (Royle, Fuller, & Sutherland, 2016). We

modelled activity centres independently each year for every individual as a homogeneous Poisson point process in S (Royle et al., 2014). Population size and density were calculated as a function of the number of estimated activity centres located within the Klamath study area.

2.5 | Assessment of fisher translocations

We performed an analysis of the spatially explicit fisher densities to investigate how the removal of individuals for translocation affected the distribution of fishers in Klamath. We did this post hoc because we (1) wanted to know if the spatial capture–recapture model would identify a decrease in fisher numbers around the removal sites without censoring individuals beforehand, and (2) we were surprised that the overall fisher density did not change in our study area while a known quantity of individuals were removed for translocations. To investigate if the number of fishers declined in areas around the removal sites, we overlaid our study area with a 1×1 -km grid and calculated the estimated number of fisher activity centres per km^2 in this grid. We used a generalized linear model for this analysis such that:

$$\Delta \frac{\text{fisher}}{\text{km}^2} = \beta_0 + \beta_1 \times \text{distance} + \beta_2 \times \text{age} + \beta_3 \times \text{sex} + \beta_4 \times \text{distance} \times \text{sex}$$

where the change in the estimated fisher density between the year before (2009) and after the first removal (2010) per km^2 was modelled to vary by an intercept (β_0), the distance between the grid cell centre and the nearest removal site (β_1), the age of the nearest individual removed (β_2), a binary variable indicating the sex of the individual removed closest to this grid cell centre (β_3), and an interaction between distance and sex of the individual removed (β_4). We included age, sex and an interaction between distance and sex to test the hypothesis that removals of females and older individuals would have a larger effect on fisher density. Only one adult male was removed in 2009, so we were unable to investigate an interaction between age and sex. We performed this analysis on the difference between 2009 and 2010 to isolate this perturbation from any other lag-effects that may be present following the second year of removals. We also only included grid cells within 6 km of a removal site for this analysis because this was twice as large as the radius of a male home range and was likely to capture any variation stemming from the removals.

2.6 | Dynamic multi-species occupancy model with interspecific interactions

Estimating the occupancy of species while accounting for imperfect detection is a technique regularly used in ecology (MacKenzie et al., 2002). Many single season multi-species occupancy models have been developed to investigate spatial-temporal overlap and interspecific interactions among species (e.g. Cusack et al., 2017; MacKenzie, Bailey, & Nichols, 2004; Richmond, Hines, &

Beissinger, 2010; Rota et al., 2016). These single season models, however, do not explicitly test the direct effects of the occupancy of one species on the occupancy of another species at the same site in the future. Dynamic occupancy models account for changes in occupancy over time as a function of the probability of site colonization and persistence (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003). We developed a novel implementation of a dynamic multi-species occupancy model to investigate carnivore guild dynamics in Klamath following the parameterization of Royle and Kéry (2007). In this parameterization, a detection y of species s in year t at site j in week w (y_{stjw}) was modelled as the Bernoulli-distributed random variable:

$$y_{stjw} \sim \text{Bernoulli}(z_{stj} p_{sw} m_{tjw})$$

where z_{stj} indicates the occupancy of species s in year t at site j , p_{sw} is the probability of detecting species s in week w and m_{tjw} is a binary variable indicating whether or not in year t a sampling box was deployed at sampling site j in week w . Similar to the spatial capture–recapture model, we hypothesized that time of year influenced detection, and we predicted that individuals would be more likely to visit sampling locations closer to winter due to decreased food availability and an increased probability of a previous visit. We modelled the logit-linear mean probability of detection p_{sw} as:

$$\text{logit}(p_{sw}) = \alpha_{0s} + \alpha_{1s} \times \text{week}_w$$

where p_{sw} is a function of a species-specific intercept (α_{0s}) and a species-specific effect of the week of sampling on detection coded as a time-series variable (α_{1s}). We were unable to disentangle a behavioural effect of a repeat visitation vs. a seasonal effect in the occupancy analysis. Thus, the effect of week investigates both of these hypotheses.

In year $t = 1$ (2007), occupancy was modelled as a latent random variable. In years $t > 1$ (2008–2013), we modelled site occupancy as:

$$z_{sjt} \sim (z_{sj,t-1} \times \Phi_{sjt}) + (1 - z_{sj,t-1} \times \gamma_{sjt})$$

where Φ_{sjt} is the probability of a site occupied in the previous year remaining occupied in the following year (i.e. persistence) and γ_{sjt} is the probability of a site previously unoccupied becoming occupied in the following year (i.e. colonization). We did not include any habitat covariates in these analyses because we were primarily interested in the interspecific interactions among these species.

We modelled persistence and colonization as a function of the estimated occupancy of one or two other species to incorporate interspecific interactions within the small carnivore guild in one model. Interspecific interactions among carnivores are often determined by body size (Polis, Myers, & Holt, 1989). Fishers and grey foxes are similar in size (2–6 kgs), but ringtails are smaller (0.7–1.5 kgs). We developed hierarchical models in which the occupancy of foxes could influence the persistence and colonization of fishers, fishers could influence the persistence and colonization of foxes and both fishers and foxes could influence the persistence and colonization of ringtails, such that:

$$\begin{aligned}
\text{fisher persistence: } \text{logit}(\Phi_{\text{fisher},jt}) &= \beta_{0\text{fisher}} + \beta_{1\text{fisher}} \times Z_{\text{fox},jt-1} \\
\text{fisher colonization: } \text{logit}(\gamma_{\text{fisher},jt}) &= \delta_{0\text{fisher}} + \delta_{1\text{fisher}} \times Z_{\text{fox},jt-1} \\
\text{fisher persistence: } \text{logit}(\Phi_{\text{fox},jt}) &= \beta_{0\text{fox}} + \beta_{1\text{fox}} \times Z_{\text{fisher},jt-1} \\
\text{fisher colonization: } \text{logit}(\gamma_{\text{fox},jt}) &= \delta_{0\text{fox}} + \delta_{1\text{fox}} \times Z_{\text{fisher},jt-1} \\
\text{fisher persistence: } \text{logit}(\Phi_{\text{ringtail},jt}) &= \beta_{0\text{ringtail}} + \beta_{1\text{ringtail}} \times Z_{\text{fisher},jt-1} + \beta_{2\text{ringtail}} \times Z_{\text{fox},jt-1} \\
\text{fisher colonization: } \text{logit}(\gamma_{\text{ringtail},jt}) &= \delta_{0\text{ringtail}} + \delta_{1\text{ringtail}} \times Z_{\text{fisher},jt-1} + \delta_{2\text{ringtail}} \times Z_{\text{fox},jt-1}
\end{aligned}$$

where Φ_{ijt} and γ_{ijt} are functions of a species-specific intercept (β_0) and effects of the estimated occupancy of one or two other species at the same site in the previous year on site persistence (β_1 , β_2) and colonization (δ_1 , δ_2). Full model code is provided in Appendix S1.

2.7 | Model fitting and assessment

We fit our models using a Bayesian approach and the Markov-chain Monte Carlo (MCMC) methods of JAGS (Plummer, 2003) with the jagsUI package (Kellner, 2016) in R v. 3.2.3 (R Core Team, 2016). We used uninformative prior distributions for all parameters. Spatial capture-recapture parameter estimates were calculated from 4,000 MCMC samples, taken from four chains run for 3,000 iterations, thinned by three, following an adaptation and burn-in period of 1,000 iterations. The assessment of the fisher translocation on density and occupancy analyses parameters were calculated from 40,000 MCMC samples, taken from four chains run for 30,000 iterations, thinned by three, following a burn-in and adaptation period of 10,000 iterations. We assessed model convergence by examining trace plots and \hat{R} values for parameter estimates (Gelman & Hill, 2007; Gelman et al., 2014). Descriptive statistics are presented as yearly $M \pm SD$ and posterior parameter estimates are presented as medians and 95% credible intervals (CIs). Parameters for which the 95% CI did not overlap zero were considered to be statistically significant.

3 | RESULTS

We collected ($M \pm SD$) 226 ± 28 hair samples that were submitted for genetic analyses each year. Of these samples, 212 ± 20 (91 ± 6%) were of sufficient quality to identify species identity from 2007 to 2013. Hair samples identified not to be fisher in 2006 were not further analysed to species. For samples identified to be fisher, $84 \pm 8\%$ annually were of sufficient quality to determine sex and individual identification. The number of unique individuals sampled each year showed little variation; we identified 139 unique fishers from 2006 to 2013, with 27 ± 3 individual fishers detected annually. We genetically identified more males in 5 years, more females in 2 years, and an equal number in 1 year (number males:females annually = 1.2 ± 0.4). Fishers were detected at multiple boxes each year (number survey units that individuals visited = 1.7 ± 1.2) and re-detected across years (number of individuals sampled that were present in previous years = 16.6 ± 2.8). Between 2007 and 2013, we annually collected 210 ± 30 track plates, with fisher identified on 73 ± 16 (35 ± 8%), grey fox on 49 ± 18 (24 ± 10%) and ringtail on 47 ± 13 (23 ± 6%) of them.

The spatial capture-recapture model failed to detect any changes in the fisher population in Klamath stemming from the removals in 2009 and 2010 (Figure 2). Estimated locations of fisher activity centres, however, varied each year with a larger decrease in the number of activity centres where fishers were removed (2010–2011; Figure 3, Table 1). Regions of Klamath located closer to the sites of fisher removals had a larger decrease in density from 2009 to 2010 (Table 1). Grid cells located near female removals had a smaller change in density than did grid cells located near male removals, and the interaction between distance and sex was significant (Table 1, Appendix S2). The removal of older animals also led to a larger decrease in localized density (Table 1). Female fishers had a lower probability of detection than male fishers (median [lower 95% CI, upper 95% CI] on the logit scale: $\alpha_0 = -1.69$

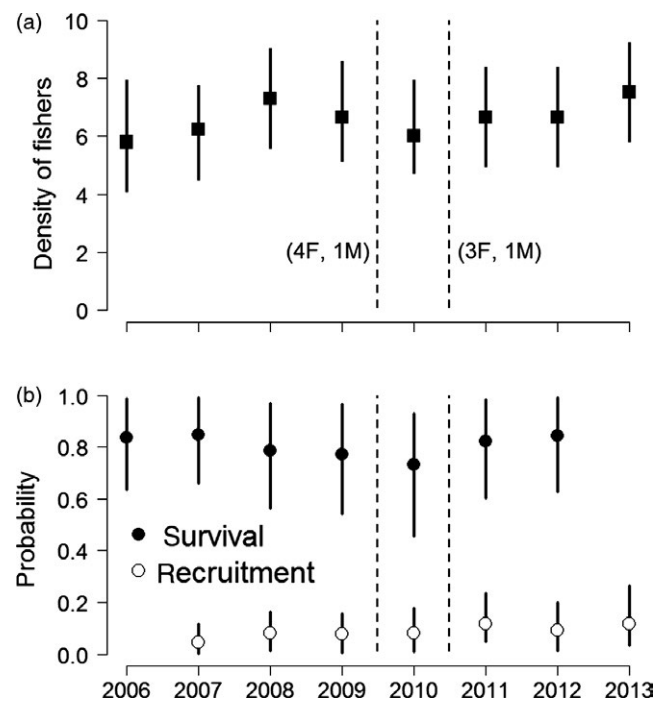


FIGURE 2 The modelled median and 95% credible intervals of (a) fisher density, and (b) apparent survival and recruitment in Klamath, estimated by a spatial Jolly-Seber open population model. Density is reported as the number of fishers per 100 km² within the convex hull encompassing our sampling sites. Apparent survival indicates the probability of an individual surviving to the following year and apparent recruitment indicates the probability of an individual being recruited into the population in that year. The dashed lines indicate the timing of removals along with the quantity and sexes of fishers removed. Density, survival and recruitment estimates were not significantly different among years (95% credible intervals overlapped)

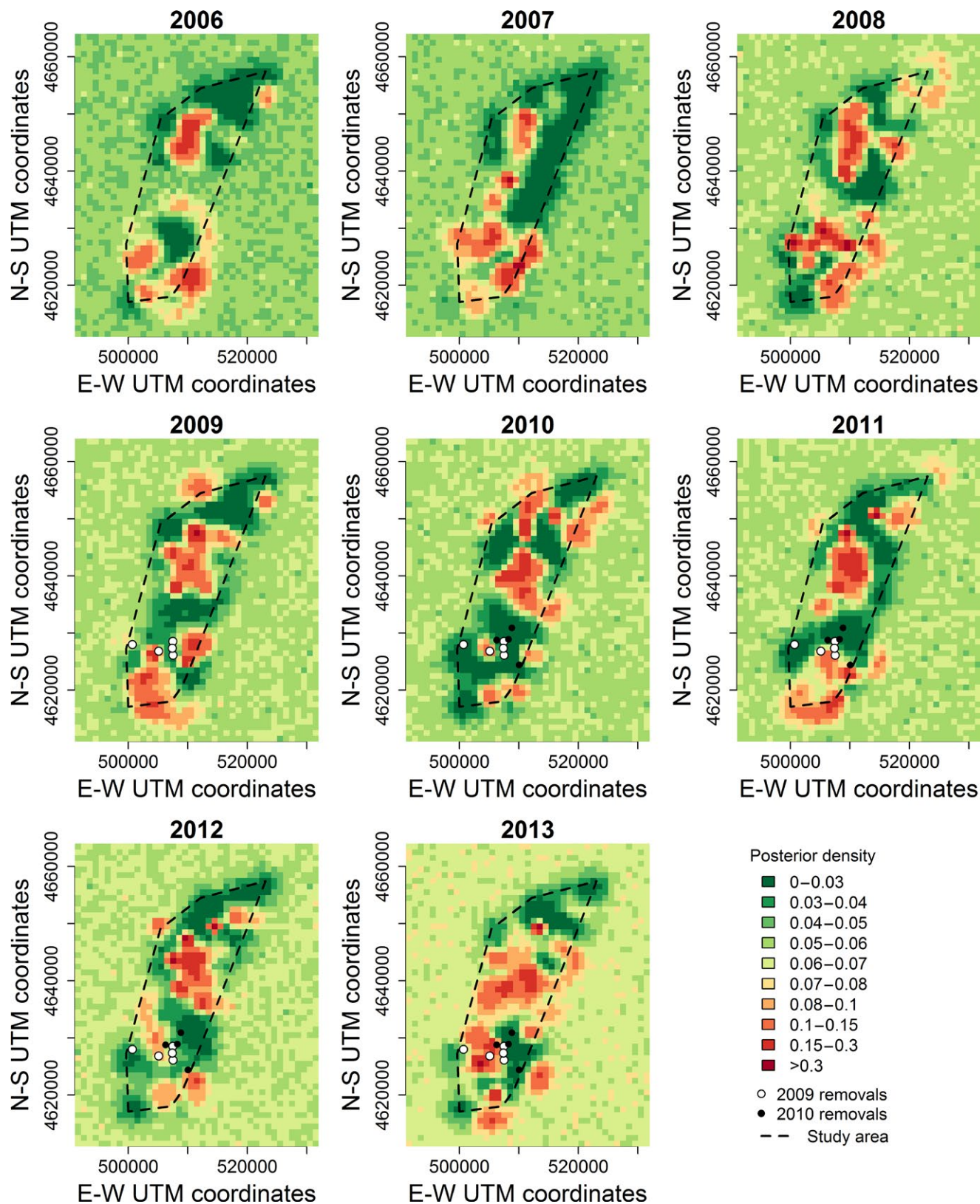


FIGURE 3 Modelled locations of estimated activity centres of fishers in Klamath between 2006 and 2013, as determined with a spatial Jolly-Seber open population model. Warmer colours indicate a larger quantity of fisher activity centres in the 1 × 1-km² grid cell in that year. The locations of live-capture sites used to remove fishers in the winters of 2009 and 2010 are noted with circles, colour coded by year of removal. The convex hull encompassing our sampling sites is indicated with a dashed line [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Results from the analysis investigating the relationship between the change in fisher density following removals for translocation in 2009. All parameters had a statistically significant effect on the change in fisher density from 2009 to 2010 (95% Credible intervals did not overlap 0)

Parameter	M	SD	Credible interval		
			2.5	50	97.5
Intercept	-0.035	0.006	-0.047	-0.035	-0.023
Distance	0.031	0.005	0.02	0.031	0.042
Age	-0.01	0.003	-0.015	-0.010	-0.004
Sex (F)	0.032	0.007	0.019	0.032	0.045
Distance × Sex (F)	-0.023	0.006	-0.035	-0.023	-0.011

$[-2.05, -1.35]$, $\alpha_1 = -1.02 [-1.5, -0.56]$). Detection of fishers increased significantly after an initial detection ($\alpha_2 = 2.35 [1.97, 2.74]$), but did not increase throughout the season ($\alpha_3 = -0.02 [-0.07, 0.02]$). Estimates of σ for male and female fishers did not significantly differ (1.85 km [1.69, 2.04] and 1.64 km [1.35, 2.04], respectively). The sex ratio of fishers in Klamath was estimated to be female biased ($\Psi_{\text{sex}} = 0.61 [0.52, 0.69]$). Full model results can be found in Appendix S3.

Occupancy of fishers, foxes and ringtails varied over the course of this study (Figure 4). The proportion of sites estimated occupied by fishers significantly decreased following the first year of removals in 2009 and remained lower than the estimated occupancy prior to the removals through the end of the current study. The proportion of sites occupied by foxes significantly increased during the 3 years following the initial removal of fishers in 2009 (95% credible intervals did not overlap), and remained elevated through 2012 (Figure 4). The proportion of sites occupied by ringtails showed no direct relationship to the timing of the removals of fishers. Fisher occupancy had a significant negative effect on the

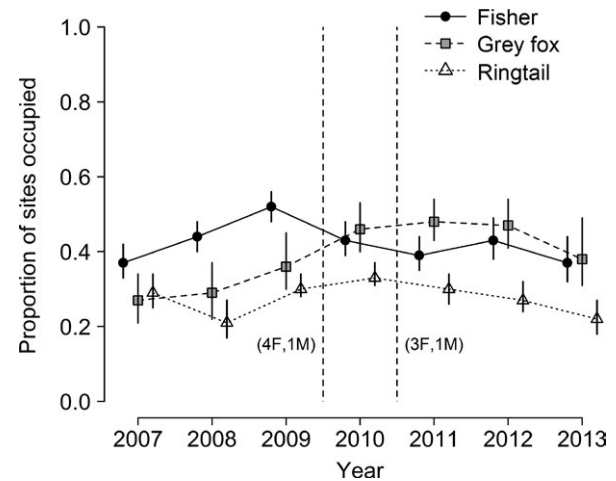


FIGURE 4 The modelled median and 95% credible interval of the proportion of sites occupied by fishers, grey foxes and ringtails from 2007 through 2013 in Klamath. The dashed, vertical lines indicate the timing of removals along with the quantity and sexes of fishers removed

persistence of site occupancy by foxes (β_1 on the logit scale = $-2.58 [-8.4, -0.48]$), but a significant positive effect on their colonization ($\delta_1 = 1.02 [0.14, 2.17]$). Fox occupancy had a significant positive effect on the colonization of sites by ringtails ($\delta_2 = 1.96 [0.72, 4.03]$). No other interspecific interactions were significant (Table 2). Detection of fishers differed by week but detection of the other species did not (Figure 5, Table 2). Full occupancy results can be found in Appendix S4.

4 | DISCUSSION

Our results indicate how dominant small carnivores may elicit spatial turnover in other members within the small-carnivore guild. In the

TABLE 2 Results on the logit scale from the dynamic multi-species occupancy model fit with interspecific interactions. Interspecific interactions were modelled as the effect of a species' site occupancy on the persistence or colonization of another species' occupancy at the same site in the following year. Values for the interspecific interactions are displayed as the effect of the species in the left panel on those in the top panel. All estimates are presented as medians and [95% credible intervals] on the logit scale. Significant parameter effects (95% CI did not overlap zero), not including intercepts, are indicated in bold

	Fisher	Fox	Ringtail
Observation process			
α_0	-1.08 [-1.39, -0.78]	-0.86 [-1.24, -0.48]	-0.86 [-1.27, -0.46]
α_1 (week)	0.11 [0.07, 0.15]	-0.01 [-0.07, 0.05]	0.05 [0, 0.11]
Persistence			
β_0	0.82 [0.33, 1.41]	2.39 [1.28, 9.1]	0.9 [0.09, 1.87]
β_1 - Fisher	-	-1.85 [-8.4, -0.48]	-0.03 [-1, 0.96]
β_2 - Fox	-0.47 [-1.31, 0.34]	-	-0.22 [-1.35, 0.8]
Colonization			
δ_0	-1.08 [-1.47, -0.7]	-2.16 [-3.21, -1.57]	-2.86 [-4.83, -2.08]
δ_1 - Fisher	-	0.97 [0.14, 2.17]	-0.2 [-1.1, 0.66]
δ_2 - Fox	0.1 [-0.57, 0.77]	-	1.83 [0.72, 4.03]

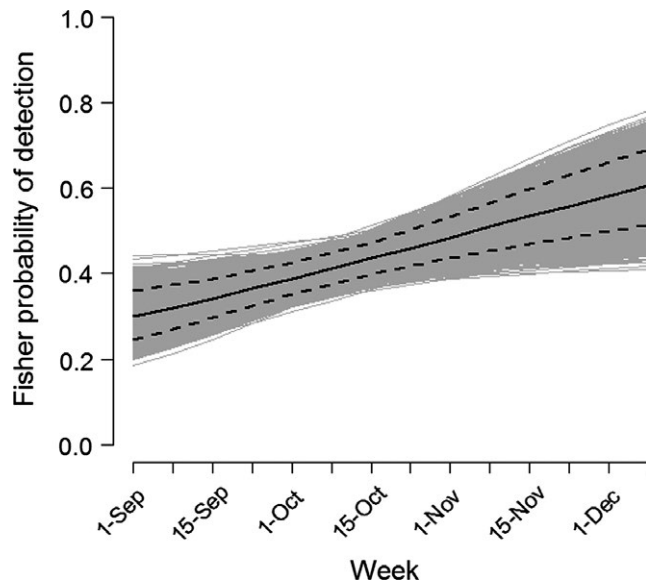


FIGURE 5 The significant effect of sampling week on the probability of detection for fishers, estimated using dynamic occupancy modelling (95% credible interval did not overlap zero). Grey lines indicate the estimated trend from a single MCMC iteration, the solid black line is the median posterior parameter effect, and the dashed lines are the 95% credible interval around this effect

current research, fishers were the dominant predator in the small-predator guild that we monitored, and their presence or absence effected changes in the distribution of grey foxes. Sympatric small carnivores may reduce ecological overlaps through spatial, temporal and niche partitioning (de Satgé et al., 2017). Our findings add to these by showing that subordinate small carnivores may also expand to locations where the numbers of their dominant competitors decline.

Removing nine fishers over 2 years for translocation elsewhere, an approximate 20% of the estimated population in each of the 2 years, had no noticeable effect on the overall density of fishers in Klamath up to 3 years post-removal. These removals did, however, appear to have had an effect on the distribution of the small-carnivore guild. Fishers occupied fewer, and foxes occupied more, sites following the removals. Furthermore, the presence of fishers had a negative effect on sites remaining occupied by foxes but a positive effect on fox site colonization. Thus, the presence of fishers appears to increase turnover in the areas used by foxes, and supports our hypothesis that a hierarchy exists within small-carnivore guilds that affects their distribution on the landscape. A negative relationship between the presence of fishers and the presence of grey foxes in another region of the Pacific States has previously been identified (Campbell, 2004). Our research indicates that this spatial partitioning may also be a function of interspecific competition between fishers and grey foxes.

While we only removed a small percentage of the total fisher population in Klamath, these removals were likely in addition to the natural declines of fishers in Klamath due to death and emigration. Nearly 40% of the fishers we genetically identified each year had not been genotyped previously, and this percentage remained unchanged over time. The relatively stable fisher density over time compared to the

change in occupancy over time, however, is interesting and should be further investigated.

Linden et al. (2017) reported a strong relationship between density and occupancy over broad spatial scales for fisher but our study, similar to that of Matthews, Higley, Yaeger, and Fuller (2011), provides evidence that this may not always be the case when looking at changes over time or at finer spatial scales. We hypothesize that this discrepancy in the current study is because the removals decreased intraspecific competition among fishers. The stable fisher density over time but a change in occupancy could have then resulted from increases in female reproduction and juvenile survival, lack of juvenile dispersal, or increases in the number of fishers immigrating into Klamath; none of these predictions are mutually exclusive. Our results support an increase in female reproduction, an increase in juvenile survival or decreased dispersal based on the locations of estimated activity centres of fishers. If the fisher density in Klamath was unchanged due to an increase in colonizing individuals moving into territories vacated by the removals, then we would predict the spatially explicit densities in Klamath to be static following the removals. There are noticeable gaps in the distribution of fisher activity centres around the locations where animals were removed, especially in 2010 (Figure 3), and our analysis indicated that areas closer to the removals exhibited a greater change in fisher density than areas further away. Both male and female fishers exhibit intrasexual territoriality (Powell, 1993, 1994), making it unlikely that new fishers dispersing into Klamath would colonize regions where fishers were already present. Thus, we surmise the consistent annual densities of fishers we observed was either due to the removals positively affecting reproduction, or that offspring born in Klamath experienced an increase in survival or a decrease in dispersal. The lack of precision with our spatial Jolly-Seber open population model (Figure 2b) prevented us from elucidating the predictions of these hypotheses, but the variation in both apparent survival and recruitment did increase following the initial year of fisher removals (Figure 2b).

The estimated occupancy of ringtails over time appeared to be unaffected by the removals of fishers, but the occupancy of foxes did have a positive effect on the colonization of sites by ringtails. This result, combined with the negative effect of fishers on fox persistence, indicates a possible indirect negative effect of fishers on ringtails. Although ringtails are listed as a sensitive species in Oregon (Oregon Biodiversity Information Center, 2016) and fully protected in California (California Department of Fish and Wildlife, Natural Diversity Database, 2017), very limited, if any, long-term monitoring of ringtail populations has been undertaken. No research to date has identified any interspecific interactions that may affect their distribution or population dynamics. Our results indicate that the turnover fishers elicit on sites occupied by foxes may ultimately have a negative effect on ringtails.

The links between decreasing apex carnivore numbers and subsequent increases in the numbers of mesopredators are well documented (e.g. Johnson et al., 2007; Ritchie & Johnson, 2009), but very limited research has investigated how sympatric mesopredator populations respond to changing numbers of other mesopredators. Our

research indicates that the documented world-wide increases in the number of mesopredators (Prugh et al., 2009) may not only be explained by mesopredator releases but that changing populations of competing mesopredators should also be included in competing hypotheses. For example, declines in the number of fishers, regardless of changing numbers of apex carnivores, may be a source for increased numbers or distribution of grey foxes.

Understanding what currently limits fisher recolonization and expansion into historically occupied habitats is a priority for long-term conservation of fishers in the Pacific States (Naney et al., 2012). Predation by sympatric, larger carnivores (e.g. bobcats, mountain lions) has been identified as one of the greatest natural sources of mortality for fishers (Gabriel et al., 2015; Wengert et al., 2014). Our results suggest that interspecific interactions within the mesopredator guild is a previously unexplored hypothesis that requires attention. Historical and contemporary distributions of fishers and grey foxes overlap in the Pacific States (Figure 1) and individuals of both species are generalist carnivores. While fishers appear limited by habitat (Lofroth et al., 2010), foxes occupy a wide diversity of habitats (Cypher, 2003). We posit that densities of grey foxes are high in places historically, but not presently, occupied by fishers due to the wide distribution of acceptable habitats and lack of fishers. Recolonization of these areas by fishers now, after 100 years of absence, could be hampered by interspecific competition with foxes or predation by larger carnivores (LaPoint, Belant, & Kays, 2015).

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AUTHORS' CONTRIBUTIONS

J.Y., R.C., S.F., M.S., and R.P. conceived the sampling design and field methods; R.S., J.Y., S.F., R.C., and D.G. collected data; D.G. and S.M. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.qb8m4> (Green et al., 2018).

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REFERENCES

- Arthur, S. M., Paragi, T. F., & Krohn, W. B. (1993). Dispersal of juvenile fishers in Maine. *The Journal of Wildlife Management*, 57, 868–874. <https://doi.org/10.2307/3809091>
- Aubry, K. B., & Lewis, J. C. (2003). Extirpation and reintroduction of fishers (*Martes pennanti*) in Oregon: Implications for their conservation in the Pacific states. *Biological Conservation*, 114, 79–90. [https://doi.org/10.1016/S0006-3207\(03\)00003-X](https://doi.org/10.1016/S0006-3207(03)00003-X)
- Belant, J. L. (2003). Comparison of 3 tracking mediums for detecting forest carnivores. *Wildlife Society Bulletin*, 31, 744–747.
- Bischof, R., Ali, H., Kabir, M., Hameed, S., & Nawaz, M. A. (2014). Being the underdog: An elusive small carnivore uses space with prey and time without enemies. *Journal of Zoology*, 293, 40–48. <https://doi.org/10.1111/jzo.12100>
- California Department of Fish and Wildlife, Natural Diversity Database. (2017). *Special animals list*, Periodic publication, 65 pp.
- Campbell, L. A. (2004). *Distribution and habitat associations of mammalian carnivores* (PhD dissertation). University of California, Davis.
- Creel, S. (2001). Four factors modifying the effect of competition on carnivore population dynamics as illustrated by African wild dogs. *Conservation Biology*, 15, 271–274. <https://doi.org/10.1111/j.1523-1739.2001.99534.x>
- Crooks, K. R., & Soulé, M. E. (1999). Mesopredator release and avifaunal extinctions in a fragmented system. *Nature*, 400, 563–566. <https://doi.org/10.1038/23028>
- Cusack, J. J., Dickman, A. J., Kalyahe, M., Rowcliffe, J. M., Carbone, C., MacDonald, D. W., & Coulson, T. (2017). Revealing kleptoparasitic and predatory tendencies in an African mammal community using camera traps: A comparison of spatiotemporal approaches. *Oikos*, 126, 812–822. <https://doi.org/10.1111/oik.03403>
- Cypher, B. L. (2003). Foxes: *Vulpes* species, *Urocyon* species, and *Alopex lagopus*. In G. A. Feldhammer, B. C. Thompson & J. A. Chapman (Eds.), *Wild mammals of North America: Biology, management, and conservation* (pp. 511–546). Baltimore, MD: Johns Hopkins University Press.
- de Sātge, J., Teichman, K., & Cristescu, B. (2017). Competition and coexistence in a small carnivore guild. *Oecologia*, 184, 873–884. <https://doi.org/10.1007/s00442-017-3916-2>
- Dröge, E., Creel, S., Becker, M. S., & M'soka, J. (2017). Spatial and temporal avoidance of risk within a large carnivore guild. *Ecology and Evolution*, 7, 189–199. <https://doi.org/10.1002/ece3.2616>
- Efford, M. (2004). Density estimation in live-trapping studies. *Oikos*, 106, 598–610. <https://doi.org/10.1111/j.0030-1299.2004.13043.x>
- Ergon, T., & Gardner, B. (2014). Separating mortality and emigration: Modelling space use, dispersal and survival with robust-design spatial capture–recapture data. *Methods in Ecology and Evolution*, 5, 1327–1336. <https://doi.org/10.1111/2041-210X.12133>
- Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., ... Wardle, D. A. (2011). Trophic downgrading of planet Earth. *Science*, 333, 301–306. <https://doi.org/10.1126/science.1205106>
- Facka, A. N., Lewis, J. C., Happe, P., Jenkins, K., Callas, R., & Powell, R. A. (2016). Timing of translocation influences birth rate and population dynamics in a forest carnivore. *Ecosphere*, 7, e01223. <https://doi.org/10.1002/ecs2.1223>
- Gabriel, M. W., Woods, L. W., Wengert, G. M., Stephenson, N., Higley, J. M., Thompson, C., ... Sacks, B. N. (2015). Patterns of natural and human-caused mortality factors of a rare forest carnivore, the fisher (*Pekania pennanti*) in California. *PLoS ONE*, 10, e0140640. <https://doi.org/10.1371/journal.pone.0140640>
- Gardner, B., Reppucci, J., Lucherini, M., & Royle, J. A. (2010). Spatially explicit inference for open populations: Estimating demographic parameters from camera-trap studies. *Ecology*, 91, 3376–3383. <https://doi.org/10.1890/09-0804.1>
- Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A., & Rubin, D. B. (2014). *Bayesian data analysis*, 3rd ed. Boca Raton, FL: CRC Press.
- Gelman, A., & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. New York, NY: Cambridge University Press.

- Gompper, M. E., Lesmeister, D. B., Ray, J. C., Malcolm, J. R., & Kays, R. (2016). Differential habitat use or intraguild interactions: What structures a carnivore community? *PLoS ONE*, 11, e0146055. <https://doi.org/10.1371/journal.pone.0146055>
- Green, D. S., Matthews, S. M., Swiers, R. C., Callas, R. L., Yaeger, J. S., Farber, S., ... Powell, R. A. (2018). Data from: Dynamic occupancy modeling reveals a hierarchy of competition among fishers, grey foxes, and ringtails. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.qb8m4>
- Helgen, K., & Reid, F. (2016). *Martes pennanti*. The IUCN Red List of Threatened Species 2016: eT41651A101161196. <https://doi.org/10.2305/iucn.uk.2016-2.rlts.t41651a101161196.en>
- Johnson, C. N., Isaac, J. L., & Fisher, D. O. (2007). Rarity of a top predator triggers continent-wide collapse of mammal prey: Dingoes and marsupials in Australia. *Proceedings of the Royal Society of London B: Biological Sciences*, 274, 341–346. <https://doi.org/10.1098/rspb.2006.3711>
- Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika*, 52, 225–248. <https://doi.org/10.1093/biomet/52.1-2.225>
- Kamler, J. F., Ballard, W. B., Gilliland, R. L., Lemons, P. R., & Mote, K. (2003). Impacts of coyotes on swift foxes in northwestern Texas. *The Journal of Wildlife Management*, 67, 317–323. <https://doi.org/10.2307/3802773>
- Kellner, K. (2016). *jagsUI: A wrapper around 'rjags' to streamline 'JAGS' analyses*. R package version 1.4.4. Retrieved from <https://CRAN.R-project.org/package=jagsUI>
- Krohn, W. B. (2012). Distribution changes of American martens and fishers in eastern North America, 1699–2001. In K. B. Aubry, W. J. Zielinski, M. G. Raphael, G. Proulx & S. W. Buskirk (Eds.), *Biology and conservation of martens, sables and fishers* (pp. 58–73). Ithaca, NY: Cornell University Press.
- LaPoint, S. D., Belant, J. L., & Kays, R. W. (2015). Mesopredator release facilitates range expansion in fisher. *Animal Conservation*, 18, 50–61. <https://doi.org/10.1111/acv.12138>
- Laundré, J. W., Hernández, L., & Ripple, W. J. (2010). The landscape of fear: Ecological implications of being afraid. *Open Ecology Journal*, 3, 1–7. <https://doi.org/10.2174/1874213001003030001>
- Lesmeister, D. B., Nielsen, C. K., Schaubert, E. M., & Hellgren, E. C. (2015). Spatial and temporal structure of a mesocarnivore guild in midwestern North America. *Wildlife Monographs*, 191, 1–61. <https://doi.org/10.1002/wmon.1015>
- Levi, T., Kilpatrick, A. M., Mangel, M., & Wilmsers, C. C. (2012). Deer, predators, and the emergence of Lyme disease. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 10942–10947. <https://doi.org/10.1073/pnas.1204536109>
- Lewis, J. C., Powell, R. A., & Zielinski, W. J. (2012). Carnivore translocations and conservation: Insights from population models and field data for fishers (*Martes pennanti*). *PLoS ONE*, 7, e32726. <https://doi.org/10.1371/journal.pone.0032726>
- Linden, D. W., Fuller, A. K., Royle, J. A., & Hare, M. P. (2017). Examining the occupancy-density relationship for a low-density carnivore. *Journal of Applied Ecology*, 53, 2043–2052. <https://doi.org/10.1111/1365-2664.12883>
- Lofroth, E. C., Raley, C. M., Higley, J. M., Truex, R. L., Yaeger, J. S., Lewis, J. C., ... Brown, R. N. (2010). *Conservation of fishers (Martes pennanti) in South-Central British Columbia, Western Washington, Western Oregon, and California-Volume 1: Conservation assessment*. Denver, CO: USDI Bureau of Land Management.
- MacKenzie, D. I., Bailey, L. L., & Nichols, J. D. (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*, 73, 546–555. <https://doi.org/10.1111/j.0021-8790.2004.00828.x>
- MacKenzie, D. I., Nichols, J. D., Hines, J. E., Knutson, M. G., & Franklin, A. B. (2003). Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology*, 84, 2200–2207. <https://doi.org/10.1890/02-3090>
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83, 2248–2255. [https://doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)
- Matthews, S. M., Higley, J. M., Rennie, K. M., Green, R. E., Goddard, C. A., Wengert, G. M., ... Fuller, T. K. (2013). Reproduction, recruitment, and dispersal of fishers (*Martes pennanti*) in a managed Douglas-fir forest in California. *Journal of Mammalogy*, 94, 100–108. <https://doi.org/10.1644/11-MAMM-A-386.1>
- Matthews, S. M., Higley, J. M., Yaeger, J. S., & Fuller, T. K. (2011). Density of fishers and the efficacy of relative abundance indices and small-scale occupancy estimation to detect a population decline on the Hoopa Valley Indian Reservation, California. *Wildlife Society Bulletin*, 35, 69–75. <https://doi.org/10.1002/wsb.19>
- McDonald, P. T., Nielsen, C. K., Oyana, T. J., & Sun, W. (2008). Modelling habitat overlap among sympatric mesocarnivores in southern Illinois, USA. *Ecological Modelling*, 215, 276–286. <https://doi.org/10.1016/j.ecolmodel.2008.03.021>
- McKelvey, K. S., & Schwartz, M. K. (2004). Providing reliable and accurate genetic capture-mark-recapture estimates in a cost-effective way. *The Journal of Wildlife Management*, 68, 453–456. [https://doi.org/10.2193/0022-541X\(2004\)068\[0453:PRAAGC\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2004)068[0453:PRAAGC]2.0.CO;2)
- Naney, R. H., Finley, L. L., Lofroth, E. C., Happe, P. J., Krause, A. L., Raley, C. M., ... Yaeger, J. S. (2012). *Conservation of fishers (Martes pennanti) in South-Central British Columbia, Western Washington, Western Oregon, and California-Volume III: Threat assessment*. Denver, CO: USDI Bureau of Land Management.
- Ohmann, J. L., Gregory, M. J., Henderson, E. B., & Roberts, H. M. (2011). Mapping gradients of community composition with nearest-neighbour imputation: Extending plot data for landscape analysis. *Journal of Vegetation Science*, 22, 660–676. <https://doi.org/10.1111/j.1654-1103.2010.01244.x>
- Oregon Biodiversity Information Center. (2016). *Rare, threatened and endangered vertebrate species of Oregon*. Portland, OR: Institute for Natural Resources, Portland State University.
- Palomares, F., & Caro, T. M. (1999). Interspecific killing among mammalian carnivores. *The American Naturalist*, 153, 492–508. <https://doi.org/10.1086/303189>
- Périquet, S., Fritz, H., & Revilla, E. (2015). The Lion King and the Hyaena Queen: Large carnivore interactions and coexistence. *Biological Reviews*, 90, 1197–1214.
- Plummer, M. (2003). *JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling*. Proceedings of the 3rd International Workshop on Distributed Statistical Computing, 2003. Vienna, Austria.
- Polis, G. A., Myers, C. A., & Holt, R. D. (1989). The ecology and evolution of intraguild predation: Potential competitors that eat each other. *Annual Review of Ecology and Systematics*, 20, 297–330. <https://doi.org/10.1146/annurev.es.20.110189.001501>
- Pollock, K. H. (1982). A capture-recapture design robust to unequal probability of capture. *The Journal of Wildlife Management*, 46, 752–757. <https://doi.org/10.2307/3808568>
- Popescu, V. D., de Valpine, P., & Sweitzer, R. A. (2014). Testing the consistency of wildlife data types before combining them: The case of camera traps and telemetry. *Ecology and Evolution*, 4, 933–943. <https://doi.org/10.1002/ece3.997>
- Powell, R. A. (1993). *The fisher: Life history, ecology, and behavior*. Minneapolis, MN: University of Minnesota Press.
- Powell, R. A. (1994). Structure and spacing of Martes populations. In S. W. Buskirk, A. S. Harestad, M. G. Raphael & R. A. Powell (Eds.), *Martens, sables, and fishers: Biology and conservation* (pp. 101–121). Ithaca, NY: Cornell University Press.
- Powell, R. A., Lewis, J. C., Slough, B. G., Brainerd, S. M., Jordan, N. R., Abramov, A. V., ... Murakami, T. (2012). Evaluating translocations of martens, sables, and fishers: Testing model predictions with field data. In K. B. Aubry, W. J. Zielinski, M. G. Raphael, G. Proulx & S. W. Buskirk

- (Eds.), *Biology and conservation of martens, sables, and fishers: A new synthesis* (pp. 93–137). Ithaca, NY: Cornell University Press.
- Prugh, L. R., Stoner, C. J., Epps, C. W., Bean, W. T., Ripple, W. J., Laliberte, A. S., & Brashares, J. S. (2009). The rise of the mesopredator. *BioScience*, 59, 779–791. <https://doi.org/10.1525/bio.2009.59.9.9>
- R Core Team. (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>
- Reid, F., Schipper, J., & Timm, R. (2016). *Bassariscus astutus*. The IUCN Red List of Threatened Species 2016: e.T41680A45215881. <https://doi.org/10.2305/iucn.uk.2016-1.rlts.t41680a45215881.en>
- Remonti, L., Balestrieri, A., Ruiz-González, A., Gómez-Moliner, B. J., Capelli, E., & Prigioni, C. (2012). Intraguild dietary overlap and its possible relationship to the coexistence of mesocarnivores in intensive agricultural habitats. *Population Ecology*, 54, 521–532. <https://doi.org/10.1007/s10144-012-0326-5>
- Richmond, O. M. W., Hines, J. E., & Beissinger, S. R. (2010). Two-species occupancy models: A new parameterization applied to co-occurrence of secretive rails. *Ecological Applications*, 20, 2036–2046. <https://doi.org/10.1890/09-0470.1>
- Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., ... Wirsing, A. J. (2014). Status and ecological effects of the world's largest carnivores. *Science*, 343, 1241484. <https://doi.org/10.1126/science.1241484>
- Ritchie, E. G., & Johnson, C. N. (2009). Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters*, 12, 982–998. <https://doi.org/10.1111/j.1461-0248.2009.01347.x>
- Roemer, G., Cypher, B., & List, R. (2016). *Urocyon cinereoargenteus*. The IUCN Red List of Threatened Species 2016: e.T22780A46178068. <https://doi.org/10.2305/iucn.uk.2016-1.rlts.t22780a46178068.en>
- Rota, C. T., Ferreira, M. A. R., Kays, R. W., Forrester, T. D., Kalies, E. L., McShea, W. J., ... Millsaugh, J. J. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, 7, 1164–1173. <https://doi.org/10.1111/2041-210X.12587>
- Royle, J. A., Chandler, R. B., Sollmann, R., & Gardner, B. (2014). *Spatial capture–recapture* (pp. 577). Waltham, MA: Academic Press.
- Royle, J. A., & Dorazio, R. M. (2008). *Hierarchical modeling and inference in ecology: The analysis of data from populations, metapopulations and communities* (pp. 444). San Diego, CA: Academic Press.
- Royle, J. A., Fuller, A. K., & Sutherland, C. (2016). Spatial capture–recapture models allowing Markovian transience or dispersal. *Population Ecology*, 58, 53–62. <https://doi.org/10.1007/s10144-015-0524-z>
- Royle, J. A., & Kéry, M. (2007). A Bayesian state-space formulation of dynamic occupancy models. *Ecology*, 88, 1813–1823. <https://doi.org/10.1890/06-0669.1>
- Royle, J. A., & Young, K. V. (2008). A hierarchical model for spatial capture–recapture data. *Ecology*, 89, 2281–2289. <https://doi.org/10.1890/07-0601.1>
- Schwartz, M. K., Cushman, S. A., McKelvey, K. S., Hayden, J., & Engkjer, C. (2006). Detecting genotyping errors and describing American black bear movement in northern Idaho. *Ursus*, 17, 138–148. [https://doi.org/10.2192/1537-6176\(2006\)17\[138:DGEADA\]2.0.CO;2](https://doi.org/10.2192/1537-6176(2006)17[138:DGEADA]2.0.CO;2)
- Schwartz, M. K., & Monfort, S. L. (2008). Genetic and endocrine tools for carnivore surveys. In R. A. Long, P. MacKay, W. J. Zielinski & J. C. Ray (Eds.), *Noninvasive survey methods for carnivores* (pp. 238–262). Washington DC: Island Press.
- Seber, G. A. F. (1965). A note on the multiple-recapture census. *Biometrika*, 52, 249–259. <https://doi.org/10.1093/biomet/52.1-2.249>
- Simberloff, D., & Dayan, T. (1991). The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics*, 22, 115–143. <https://doi.org/10.1146/annurev.es.22.110191.000555>
- Swanson, A., Caro, T., Davies-Mostert, H., Mills, M. G. L., Macdonald, D. W., Borner, M., ... Packer, C. (2014). Cheetahs and wild dogs show contrasting patterns of suppression by lions. *Journal of Animal Ecology*, 83, 1418–1427. <https://doi.org/10.1111/1365-2656.12231>
- Sweitzer, R. A., & Furnas, B. J. (2016). Data from camera surveys identifying co-occurrence and occupancy linkages between fishers (*Pekania pennanti*), rodent prey, mesocarnivores, and larger predators in mixed-conifer forests. *Data in Brief*, 6, 783–792. <https://doi.org/10.1016/j.dib.2016.01.032>
- Sweitzer, R. A., Furnas, B. J., Barrett, R. H., Purcell, K. L., & Thompson, C. M. (2016). Landscape fuel reduction, forest fire, and biophysical linkages to local habitat use and local persistence of fishers (*Pekania pennanti*) in Sierra Nevada mixed-conifer forests. *Forest Ecology and Management*, 361, 208–225. <https://doi.org/10.1016/j.foreco.2015.11.026>
- Taylor, R. A., Ryan, S. J., Brashares, J. S., & Johnson, L. R. (2016). Hunting, food subsidies, and mesopredator release: The dynamics of crop-raiding baboons in a managed landscape. *Ecology*, 97, 951–960. <https://doi.org/10.1890/15-0885.1>
- Tucker, J. M., Schwartz, M. K., Truex, R. L., Wisely, S. M., & Allendorf, F. W. (2014). Sampling affects the detection of genetic subdivision and conservation implications for fisher in the Sierra Nevada. *Conservation Genetics*, 15, 123–136. <https://doi.org/10.1007/s10592-013-0525-4>
- Wengert, G. M., Gabriel, M. W., Matthews, S. M., Higley, J. M., Sweitzer, R. A., Thompson, C. M., ... Sacks, B. N. (2014). Using DNA to describe and quantify interspecific killing of fishers in California. *The Journal of Wildlife Management*, 78, 603–611. <https://doi.org/10.1002/jwmg.698>
- Whittington, J., & Sawaya, M. A. (2015). A comparison of grizzly bear demographic parameters estimated from non-spatial and spatial open population capture-recapture models. *PLoS ONE*, 10, e0134446–17. <https://doi.org/10.1371/journal.pone.0134446>
- Zielinski, W. J., Schlexer, F. V., Pilgrim, K. L., & Schwartz, M. K. (2006). The efficacy of wire and glue hair snares in identifying mesocarnivores. *Wildlife Society Bulletin*, 34, 1152–1161. [https://doi.org/10.2193/0091-7648\(2006\)34\[1152:TEOWAG\]2.0.CO;2](https://doi.org/10.2193/0091-7648(2006)34[1152:TEOWAG]2.0.CO;2)
- Zielinski, W. J., & Truex, R. L. (1995). Distinguishing tracks of marten and fisher at track-plate stations. *The Journal of Wildlife Management*, 59, 571–579. <https://doi.org/10.2307/3802465>

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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