



An apex carnivore's life history mediates a predator cascade

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Abstract

Apex predators can shape communities via cascading top–down effects, but the degree to which such effects depend on predator life history traits is largely unknown. Within carnivore guilds, complex hierarchies of dominance facilitate coexistence, whereby subordinate species avoid dominant counterparts by partitioning space, time, or both. We investigated whether a major life history trait (hibernation) in an apex carnivore (black bears *Ursus americanus*) mediated its top–down effects on the spatio-temporal dynamics of three sympatric mesocarnivore species (coyotes *Canis latrans*, bobcats *Lynx rufus*, and gray foxes *Urocyon cinereoargenteus*) across a 15,000 km² landscape in the western USA. We compared top–down, bottom–up, and environmental effects on these mesocarnivores using an integrated modeling approach. Black bears exerted top–down effects that varied as a function of hibernation and were stronger than bottom–up or environmental impacts. High black bear activity in summer and fall appeared to buffer the most subordinate mesocarnivore (gray foxes) from competition with dominant mesocarnivores (coyotes and bobcats), which were in turn released by black bear hibernation in winter and early spring. The mesocarnivore responses occurred in space (i.e., altered occupancy and site visitation intensity) rather than time (i.e., diel activity patterns unaffected). These results suggest that the spatio-temporal dynamics of mesocarnivores in this system were principally shaped by a spatial predator cascade of interference competition mediated by black bear hibernation. Thus, certain life history traits of apex predators might facilitate coexistence among competing species over broad time scales, with complex implications for lower trophic levels.

Keywords Carnivore guild · Coexistence · Hibernation · Interference competition · Sympatry

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Introduction

Apex predators can influence ecosystems via top–down effects that can cascade among and across biotic communities (Ritchie and Johnson 2009; Ripple et al. 2014; Prugh and Sivy 2020). Early work on such effects was guided by theory that focused on the lethal removal of prey by predators (cf. Hairston et al. 1960). More contemporary research has revealed that apex predators also exert top–down effects along nonlethal pathways by inducing behavioral antipredator responses (Heithaus et al. 2008; Ferretti et al. 2010). Such behavioral responses not only occur in prey species, but also in subordinate predators that compete with their apex counterparts for space and resources (Schoener 1983; Holt and Polis 1997; Ritchie and Johnson 2009). These dynamics are broadly encapsulated in the Mesopredator Release Hypothesis, which predicts that the decline or disappearance of apex predators will alter the distribution, behavior, or abundance of subordinate mesopredators, with

potentially cascading effects on lower trophic levels (Soulé et al. 1988; Elmhagen and Rushton 2007; Elmhagen et al. 2010; Ritchie et al. 2012). This hypothesis has received broad support across diverse ecosystems globally (Prugh et al. 2009; Ritchie and Johnson 2009; Ripple et al. 2014) although the degree to which top–down effects influence mesopredators vary across and within systems (Jachowski et al. 2020).

While it is clear that apex predators affect subordinate predators, the role that life history traits play in mediating these effects is largely unstudied (Polis et al. 1996; Linnell and Strand 2000; Ritchie and Johnson 2009; Ferretti et al. 2010). Indeed, most research considering life history theory in relation to predators has focused on how predation risk shapes prey life history [e.g., in birds (Martin 1995), fish (Reznick and Endler 1982), and mammals (Promislow and Harvey 1990)]. In contrast, we know little about how predators' life history traits modulate their top–down effects. Nonetheless, given that life history traits influence predator activity and behavior (e.g., variation in hunting behavior by sex and reproductive class; Young and McCabe 1997), there is reason to suspect that such traits can mediate top–down effects. In particular, life history strategies involving periods of prolonged inactivity, such as hibernation, could play a key role in the presence and nature of top–down effects because such effects would strongly vary across periods of predator activity and inactivity.

Communities of terrestrial predators within the order Carnivora (hereafter *carnivores*) are often organized around dominance hierarchies in which subordinate species typically avoid ecologically similar, but larger-bodied and proximately dominant species (Levi and Wilmers 2012; Vanak et al. 2013). Such avoidance is often aimed at reducing competition, which takes two general forms. Exploitative competition occurs over shared but limited resources, including food and space, while interference competition includes agonistic interactions and aggression (Birch 1957; Schoener 1983). In wide-ranging carnivores, interference competition is often driven by exploitative competition for limited space (Schoener 1983). Subordinate carnivores frequently mitigate this competition by avoiding dominant counterparts in space (Moll et al. 2018), time (Hayward and Slotow 2009), or both (Vanak et al. 2013). Such avoidance can result in cascading effects in communities with ≥ 3 species. For example, an apex carnivore might suppress a subordinate mesocarnivore, which could lead to a positive association with a third species subordinate to the second (e.g., as seen in gray wolves (*Canis lupus*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*); Levi and Wilmers 2012). Simple patterns of alternating direct and indirect effects, however, are complicated by habitat heterogeneity and prey availability (Vanak et al. 2013; Sivy et al. 2017). Ecosystem productivity and seasonality also play important roles in mediating cascading

interference interactions among carnivores. For example, harsh conditions and less productive environmental contexts can intensify bottom–up effects and dampen mesopredator release dynamics (Elmhagen and Rushton 2007; Stoessel et al. 2019). Indeed, understanding the seasonality and intensity of cascading effects of apex carnivores on mesocarnivore communities inhabiting heterogeneous environments remains a key challenge in carnivore community ecology (Linnell and Strand 2000; Ritchie et al. 2012).

Black bears (*Ursus americanus*) are the most abundant apex carnivore in the world and one of the only large carnivore species with an expanding range and increasing population trajectory (Ripple et al. 2014; Elbroch and Kusler 2018). Yet, few studies have investigated the effects black bears have on sympatric mesocarnivores (Litvaitis 1992; Ripple et al. 2014; Gompper et al. 2016). Importantly, black bears employ a life history strategy that entails hibernating in winter and early spring. Therefore, the top–down effects of this apex carnivore should vary across an annual scale, thereby resulting in potentially complex patterns of mesocarnivore response across time periods. There is particularly strong potential for black bears to affect coyotes, another species that has expanded in number and distribution over the past half-century (Hody and Kays 2018). Black bears and coyotes share the traits of habitat and diet generalism, and thus likely compete over both resources and space for territories (Litvaitis 1992). In turn, coyotes are dominant over other mesocarnivores [i.e., bobcats (*Lynx rufus*), and red and gray foxes (*Urocyon cinereoargenteus*)] and can suppress their populations via interference competition and interspecific killing (Henke and Bryant 1999; Fedriani et al. 2000). Such effects are expected to be most intense between canid species due to niche and taxonomic similarity (Birch 1957; Carothers and Jaksić 1984; Prugh and Sivy 2020). Thus, black bears might shape mesocarnivore community dynamics via effects on coyotes that cascade to other subordinate species, especially foxes.

Here, we investigated the degree to which black bears can shape the spatio-temporal dynamics of three mesocarnivore species (coyotes, bobcats, and gray foxes) via cascading interspecific competition. If black bears were driving mesocarnivore dynamics via interference competition, we would expect strong top–down effects on these mesocarnivores that varied across periods of black bear activity and hibernation (Fedriani et al. 2000). For example, if mesocarnivore species were responding to black bears by shifting temporal activity patterns, we would expect species' temporal activity overlap to change as a function of bear hibernation. Conversely, if exploitative competition over prey was most important, we would expect strong associations between mesocarnivore dynamics and prey availability across periods, with the dominant mesocarnivore species (coyotes) most strongly associated with prey availability. Finally, if

neither kinds of interspecific competition were present, we would expect mesocarnivore dynamics to respond primarily to environmental variables (e.g., snow or habitat; Gompper et al. 2016). To assess these possibilities, we implemented a field design in the western USA that combined data collected from a broad camera trapping grid with black bear GPS locations and analyzed these data using an integrated modeling approach. We acknowledge that this study is correlational in nature, and that the seasonal presence and absence of black bears is potentially confounded with other factors that vary seasonally. We have sought to control for the most important of these potentially confounding factors and interpret our findings in light of the correlational patterns observed and alternative mechanisms that might underlie our results. Overall, the unique apex predator life history trait of seasonal hibernation facilitates an opportunity to study carnivore community dynamics and the results presented here suggest potential mechanisms that should be tested by more resource-intensive experimental approaches in the future (Estes 1995; Ritchie et al. 2012).

Methods

Study system and focal species

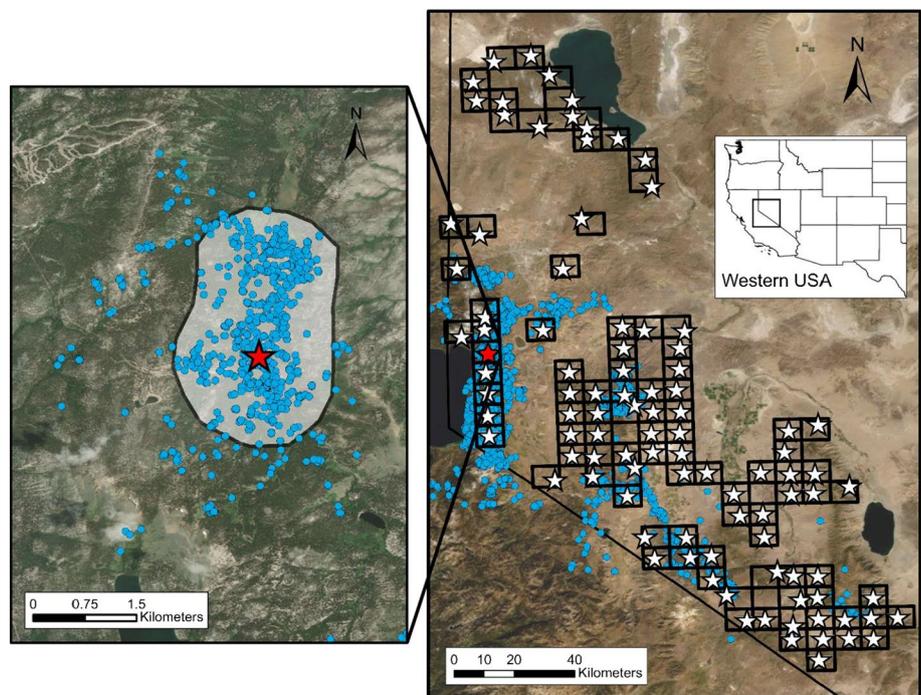
We conducted research from May 2016 to April 2019 across a 15,000 km² study area in Nevada, USA (Fig. 1). This area lies in the Great Basin of the western USA, which is an arid region with connected endorheic watersheds and several

mountain ranges. The western portion of the study area included the Carson Range of the Sierra Nevada mountains, where the vegetation community is primarily composed of mixed conifer forest. The remaining portions of the study area consist of mixed desert shrub-scrublands with interspersed agricultural and rangelands, as well as mixed conifer and pinyon-juniper woodlands (dominated by *Pinus monophylla* and *Juniperus osteosperma*) that are more prominent within mountain ranges.

We delineated two study periods, a *bears active* period in summer and early fall (May 22 to October 15), and a *bears hibernating* period in winter and early spring (December 4 to April 1). This delineation was based upon previous research on black bear activity in the study area (Beckmann and Berger 2003) and was supported by our camera trap data, which featured 111 black bear detections across all sites during the *bears active* period compared to a single detection during the *bears hibernating* period. We omitted the mid-fall period (October 16 to December 3) because black bear activity during that time varies by factors not captured in our study design (e.g., individual bear characteristics; Beckmann and Berger 2003). Snow was common during the *bears hibernating* period in mountainous portions of the study area, while the *bears active* period was generally dry and hot (the mean temperature was 20.9 °C; National Climatic Data Center, <https://www.ncdc.noaa.gov/cdo-web/>).

Black bear populations have become re-established in the western and southeastern portions of the study area following regional extirpation in the 1930s (Lackey et al. 2013;

Fig. 1 A map of the study area. The right panel depicts May–October locations of GPS-collared black bears (*Ursus americanus*; $N = 22$; blue circles) and camera traps ($N = 100$; white stars near the centroid of black 49 km² grid squares) deployed in 2018 in western Nevada, USA. The left inset depicts an example of a core area (white polygon) enveloping a camera trap site (red star). Note that only a representative subset of the ~17,000 black bear GPS locations are depicted for clarity. Basemap source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community



Malaney et al. 2018). Lackey et al. (2013) estimated a total adult black bear population of 262 (± 31) in western Nevada and recent work has suggested continued population growth (Nevada Department of Wildlife unpublished data). In addition to mesocarnivores (coyotes, bobcats, and gray foxes), this ecosystem also supports cougars (*Puma concolor*). The densities of black bears and cougars vary across the study area and current research is ongoing to produce population-level estimates. We focused on the effects of black bears on mesocarnivores rather than those of cougars because the latter species was present at much lower densities in the study area (P. Jackson, pers. comm.).

Field methods

Camera trapping

We established camera trap sites (hereafter synonymous with *sites*; $N=100$) using a grid design (Tobler and Powell 2013). We established 49 km² grid cells across the current estimated range of black bears in the study area (Beckmann 2002; Lackey 2004; Malaney et al. 2018; Beckmann and Lackey 2018). This grid cell size was smaller than the lower bound of home ranges of black bears inhabiting the study area (Beckmann 2002). We placed a camera trap in the centroid of each cell, with adjustments to accommodate site access (see Fig. 1 and Appendix A). Across sites, elevation ranged from 1219 to 2555 m (mean = 1761 m; sd = 322 m). The proportion of conifer and pinyon-juniper forest in 5000 m buffers around sites also varied, ranging from 0 to 0.74 (mean = 0.11; sd = 0.19) and 0 to 0.75 (mean = 0.17; sd = 0.19), respectively.

At each site, we affixed a Bushnell Trophy Cam HD Aggressor to a tree or metal post ~50 cm off the ground. We used camera trap settings that optimized wildlife detectability while minimizing bias in occupancy modeling (Lepard et al. 2019; Moll et al. 2018; Appendix A). We programmed cameras to capture three images whenever the passive infrared sensor was triggered and set the delay period after each trigger to 10 min (Lepard et al. 2019). We set the sensitivity of the passive infrared sensor to “Auto” and set the LED, which controls the infrared light used during nighttime triggers, to “high” (see Appendix D for full details regarding camera settings and placement). Camera traps ran from May 2018 to April 2019 and we visited sites every 7–10 days from June to August 2018 to download data and apply attractant, which was a mixture of raspberry extract (Mother Murphy’s Laboratories, Inc., Greensboro, NC), fish oil, anise extract (Minnesota Snareline Products, Pennock, MN), and Ultimate Bear Lure (Wildlife Research Center, Ramsey, MN). We used this attractant, which was implemented to attract black bears of both sexes, during a portion of the *bears active* period (i.e., June to August) as

part of a concurrent black bear population estimation project. We accounted for the potential effect of attractant in our modeling approach (see below). We also visited sites in December 2018 and May 2019 to download data.

Black bear GPS-tracking

Between 2016 and 2018, we captured 26 adult black bears using methods described in Beckmann and Berger (2003). We performed all captures and handling according to Nevada Division of Wildlife protocols and American Society of Mammalogists guidelines (Sikes 2016). We fitted individuals with either Globalstar or Iridium Vertex Plus GPS collars that attempted a locational fix every 3.5 h (Vectorics Aerospace GmbH, Berlin, Germany). We restricted analysis to locations from May to October and omitted data from four bears because these individuals had less than one month of data (Seaman et al. 1999). We used location data from the 22 remaining black bears (11 males, 11 females) in subsequent analyses.

Analysis

Overview

We analyzed mesocarnivores’ spatial activity (i.e., occupancy and site visit frequency) via an integrated multi-species occupancy model (hereafter *integrated model*) and temporal activity via nonparametric kernel analysis. The integrated model included: (i) a model of black bear occupancy across camera trap sites, (ii) a model of black bear core home ranges (hereafter *core areas*, see below) that refined occupancy estimates at those sites, and (iii) a mesocarnivore model that evaluated the effects of black bears, prey, and environmental covariates.

Black bear occupancy

We modeled black bear occupancy as

$$Z_{\text{bear},i} \sim \text{Bernoulli}(\Psi_{\text{bear},i}),$$

where site i was occupied (i.e., used in a given period) by a black bear when $Z_{\text{bear},i}$ equaled one and was unoccupied otherwise (MacKenzie et al. 2002). We modeled covariate effects on black bear occupancy probability ($\Psi_{\text{bear},i}$) using a logit link function. These covariates included the proportion of conifer and pinyon-juniper forest around sites, as well as terrain ruggedness. We created these covariates, and all habitat covariates described below, using 30 m resolution data from the USDA/USDOJ LANDFIRE 2014 database (<https://www.landfire.gov/evt.php>). We used a preliminary analysis to determine the spatial scale at which to represent

habitat covariates (see Appendix B). We modeled weekly detection–non-detection data from camera traps as

$$y_{\text{bear},i,j} | Z_{\text{bear},i} \sim \text{Bernoulli}(Z_{\text{bear},i} \times p_{\text{bear},i,j}),$$

where $y_{\text{bear},i,j}$ was black bear detection–non-detection at site i in week j and p was the probability of black bear detection, given occupancy. We modeled covariate effects on detection probability using a logit link. These covariates included the presence or absence of attractant and a covariate indicating whether or not a black bear was previously detected at a site, which accounted for the tendency of bears to repeatedly visit sites within their home range (Long et al. 2011).

Black bear core areas

Next, we modeled whether a site was within a black bear's core area, given occupancy. To identify black bear core areas, we created utilization distributions (UDs) for each black bear in each year using a fixed kernel and reference bandwidth smoothing parameter that assumed bivariate normality (Worton 1989; Kernohan et al. 2001). Using these UD, we calculated isopleths in increments of five, and assumed that the 95% isopleth represented the extent of the black bear's home range (Vander Wal and Rodgers 2012). We then plotted the percent of home range area at each isopleth against its cumulative UD volume and fit a non-linear exponential model to these data. Finally, we delineated core areas by identifying the isopleth at which the slope of this exponential model equaled one. This isopleth indicated the point at which a black bear's time spent inside its core area was maximized compared to time spent outside of it (Vander Wal and Rodgers 2012). We then categorized each black bear location as either falling inside or outside its core area and used these binary data as a response variable in a mixed effects logistic regression model. This model's covariates were based upon a previously validated model for black bear resource selection in this region (see Johnson et al. 2015). Covariates included aspect (in nine classes, following Johnson et al. 2015), elevation (modeled as a quadratic effect), terrain ruggedness, proportion conifer forest, proportion shrub, and distance to nearest highway. We calculated the proportion-based covariates (conifer and shrub) using a nine-pixel window (i.e., 90×90 m) around each location. The model included a random intercept for each black bear in each year to account for repeated measurements of individuals. Thus, the final model took the form

$$y_{\text{bear_core},k} \sim \text{Bernoulli}(\Omega_k),$$

where $y_{\text{bear_core},k}$ was the binary core–non-core data at each location k and Ω_k was the probability that the k th location fell within a core area. We modeled covariate effects on Ω_k using a logit link. Finally, we multiplied black bear

occupancy ($Z_{\text{bear},i}$) by another latent variable, $CORE_i$, which was generated from this black bear core area model (see model code in Appendix C). $CORE_i$ equaled one if site i was predicted to fall inside a core area and zero otherwise. We propagated uncertainty regarding $CORE_i$ predictions by embedding the model's parameter estimates and their uncertainty within the integrated model (Kéry and Royle 2015).

Mesocarnivore occupancy and site visit frequency

The mesocarnivore model had the same form as the black bear occupancy model, except we used weekly counts of detections (hereafter *site visit frequency*) instead of binary detection–non-detections. This approach still accounts for imperfect detection by estimating site occupancy probability even when zero site visits are recorded (see Moll et al. 2018). We modeled site visit frequency using a mixed Poisson–Gamma distribution that was flexible to overdispersion (i.e., variance larger than the mean; Greene 2008). This portion of the model took the form

$$y_{i,j,m} | Z_{i,j} \sim \text{Poisson}(Z_{i,j} \times \lambda_{i,j,m} \times \rho_{i,j,m}),$$

where $y_{i,j,m}$ was the number of visits made to site i during week j by species m , λ was the expected number of visits, and ρ was a random variable with a one parameter gamma distribution. We modeled covariate effects on mesocarnivore occupancy using a logit link and on site visit frequency using a log link. For both the occupancy and site visit frequency submodels, we included the black bear core area covariate described above. We also included prey and environmental covariates (habitat, attractant, and snow). Inclusion of these covariates was essential for evaluating the strength of black bear effects relative to other factors. The prey covariate quantified prey species detections at a given site divided by the number of days the camera trap at that site was operational. This covariate included prey species previously shown to be associated with mesocarnivore space use (Neale and Sacks 2001), including black-tailed jackrabbit (*Lepus californicus*), desert cottontail (*Sylvilagus audubonii*), and all squirrels and chipmunks, which were impossible to consistently identify to species in camera trap images. Habitat covariates included the proportion of pinyon-juniper forest and terrain ruggedness around sites. As with the black bear occupancy model, we determined covariate spatial scales in a preliminary modeling step (Appendix B). For site visit frequency, we included covariates for attractant and snow. We created the snow covariate by calculating the mean weekly snow depth at each site using data from the National Snow and Ice Data Center (NOHRSC 2004).

Model analysis, selection, and assessment

We analyzed models in a Bayesian framework via Markov Chain Monte Carlo (MCMC) simulation using R version 3.5.2 in RStudio version 1.1.463 (RStudio Team 2015) and the JAGS language (Plummer 2003) using the package `R2jags` (Su and Yajima 2012). We ran three MCMC chains of 20,000 iterations each following a burn-in of 5000 and used non-informative priors for all parameters. We assessed model convergence by inspecting posterior traceplots and ensuring R-hat statistics were < 1.1 (Gelman and Hill 2007). In the integrated models, we used Bayesian indicator variables for model selection (Kuo and Mallick 1998). Indicator variables were Bernoulli-distributed with a prior probability of 0.5, and their posterior indicated the probability that a given covariate was included in the best model out of all possible combinations (Royle and Dorazio 2008). We model-averaged covariates by calculating the posterior of each parameter when its associated indicator variable was equal to one in the MCMC history (Royle and Dorazio 2008). For model assessment, we calculated Bayesian p values using posterior predictive checks (Gelman et al. 2004). Finally, we checked for spatial autocorrelation in model residuals by inspecting spline correlograms using the package `ncf` (Bjørnstad 2008).

Activity patterns

We also analyzed mesocarnivores' temporal activity to investigate the possibility that patterns of mesocarnivore temporal activity would differ as a function of black bear core areas during the *bear's active* period but not during the *bear's hibernating* period.

We used nonparametric univariate kernel density estimates to quantify mesocarnivore temporal activity based upon the time of day recorded in camera trap detections. We first used the R package `activity` to adjust time of day data to reflect "solar time" (relative to sunset and sunrise) rather than "clock time" (time of day), given that wildlife typically respond to solar cycles (Nouvellet et al. 2012; Rowcliffe 2019). We enforced a 30-min independence window between successive detections of the same species at a given site to avoid pseudoreplication (Moll et al. 2018). We then categorized sites as falling inside or outside black bear core areas by applying a k-means algorithm to the posterior mean of the core area covariate described in the integrated model above (Hartigan and Wong 1979). This algorithm delineated 20 sites as falling inside core areas and 80 falling outside them, and this categorization explained 97.3% of the variance. Using these categories, we quantified the degree to which each mesocarnivores species' temporal activity patterns inside and outside core areas overlapped by calculating a coefficient for the paired density estimates

that ranged from 0 (pattern inside core areas completely different than those outside) to 1 (patterns inside and outside core areas identical) for each period. We used bootstrapping to estimate uncertainty in these overlap coefficients (Ridout and Linkie 2009).

Results

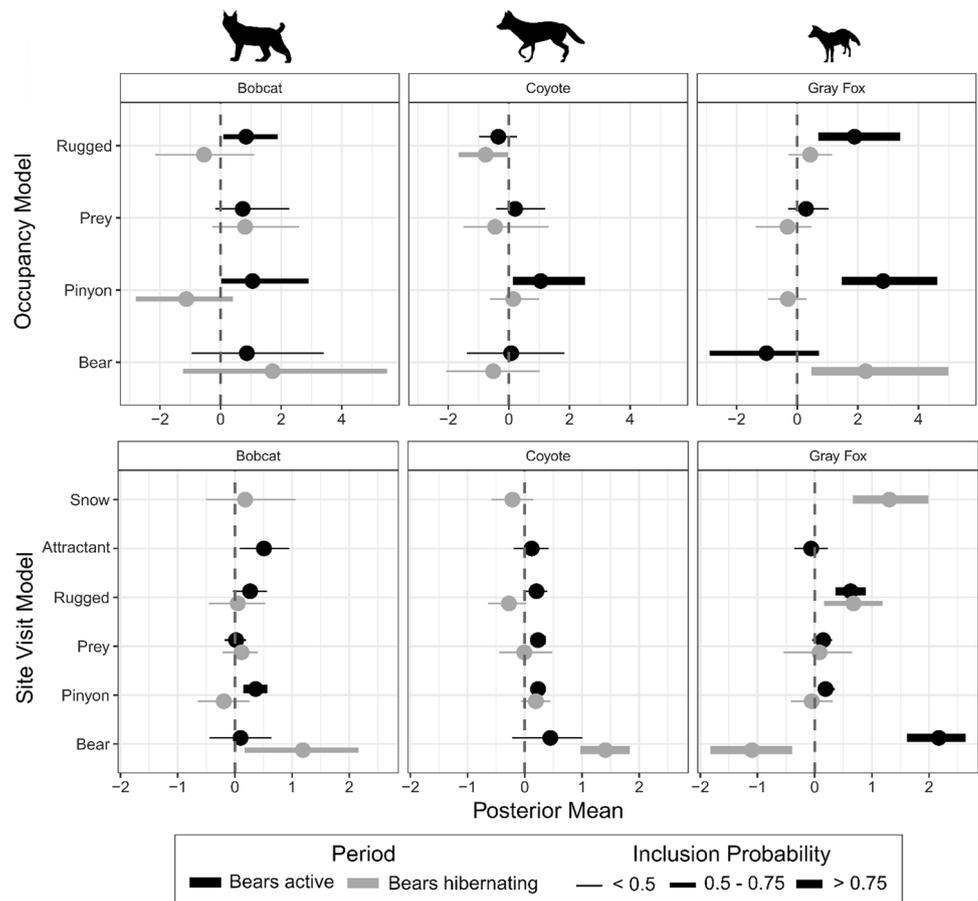
Between 2016 and 2018, we recorded 16,679 locations from 22 black bears (mean = 538.0 locations/bear/year; $sd = 334.1$). Of these, 12,638 (75.8%) fell inside black bear core areas. These core areas comprised the area within the 54.6% to 69.0% isopleths of the black bears' home ranges (median = 58.8%, mean = 59.3%). These core areas exhibited a right-skewed distribution (median = 14.5 km², mean = 132.0 km², range = 1.1–999.1 km²). During 22,386 camera trap nights, we recorded 1107 detections of our focal carnivores ($N_{blackbear} = 112$, $N_{bobcat} = 140$, $N_{coyote} = 469$, and $N_{grayfox} = 386$), and 10,479 detections of prey ($N_{jackrabbit} = 7811$, $N_{cottontail} = 1198$, $N_{squirrel/chipmunk} = 1470$).

Bayesian p values for integrated models indicated good fit for all species (range 0.49–0.84; Appendix D). Spline correlograms likewise indicated little to no spatial autocorrelation in model residuals (Appendix D). Out of 100 sites, the model estimated that black bears occupied 29.9 ($sd = 3.4$), bobcats occupied 54.6 ($sd = 5.9$), coyotes occupied 75.7 ($sd = 3.5$), and gray foxes occupied 32.6 ($sd = 2.2$) during the *bears active* period. The model estimated that bobcats occupied 67.0 sites ($sd = 14.6$), coyotes occupied 73.0 ($sd = 4.7$), and gray foxes occupied 29.1 ($sd = 3.6$) during the *bears hibernating* period.

Black bear occupancy was positively associated with conifer forest (posterior mean = 3.63) and pinyon-juniper forest (posterior mean = 0.40), and unassociated with terrain ruggedness (Appendix D). Black bear detection probability increased when attractant was present and when bears had been previously detected at a site (Appendix D). Black bear core areas were associated with less rugged sites at moderate elevations located far from roads and surrounded by lower proportions of shrub habitat (Appendix D).

During the *bears active* period, only gray foxes were influenced by black bears (Figs. 2, 3). During that period, gray fox occupancy probability was lower inside core areas (0.15; 95% CI 0.02, 0.42) than outside them (0.29; 95% CI 0.13, 0.50; Fig. 3). In contrast, gray fox visit frequency during the *bears active* period was more than five times higher inside core areas (0.46 visits/week; 95% CI 0.36, 0.55) than outside them (0.09 visits/week; 95% CI 0.06, 0.13; Fig. 3). During the *bears hibernating* period, bobcat and gray fox occupancy probabilities were higher inside black bear core areas (0.85 and 0.65, respectively) than outside them (0.61 and 0.19, respectively; Fig. 3). Bobcat site visit frequency

Fig. 2 Posterior means (circles) and 95% credible intervals (lines) of parameters from an occupancy and site visit frequency model fit to data collected from 100 camera traps deployed in 2018–2019 in western Nevada, USA. The color depicts period (*bears active*: May–October; *bears hibernating*: December–April) and the line width indicates the value of inclusion parameters, which quantify the probability that a given covariate is in the best model. The *bear* covariate indicates the effect of being within a black bear core area, while the *prey* covariate quantifies the effect of prey (rodent and lagomorph) availability



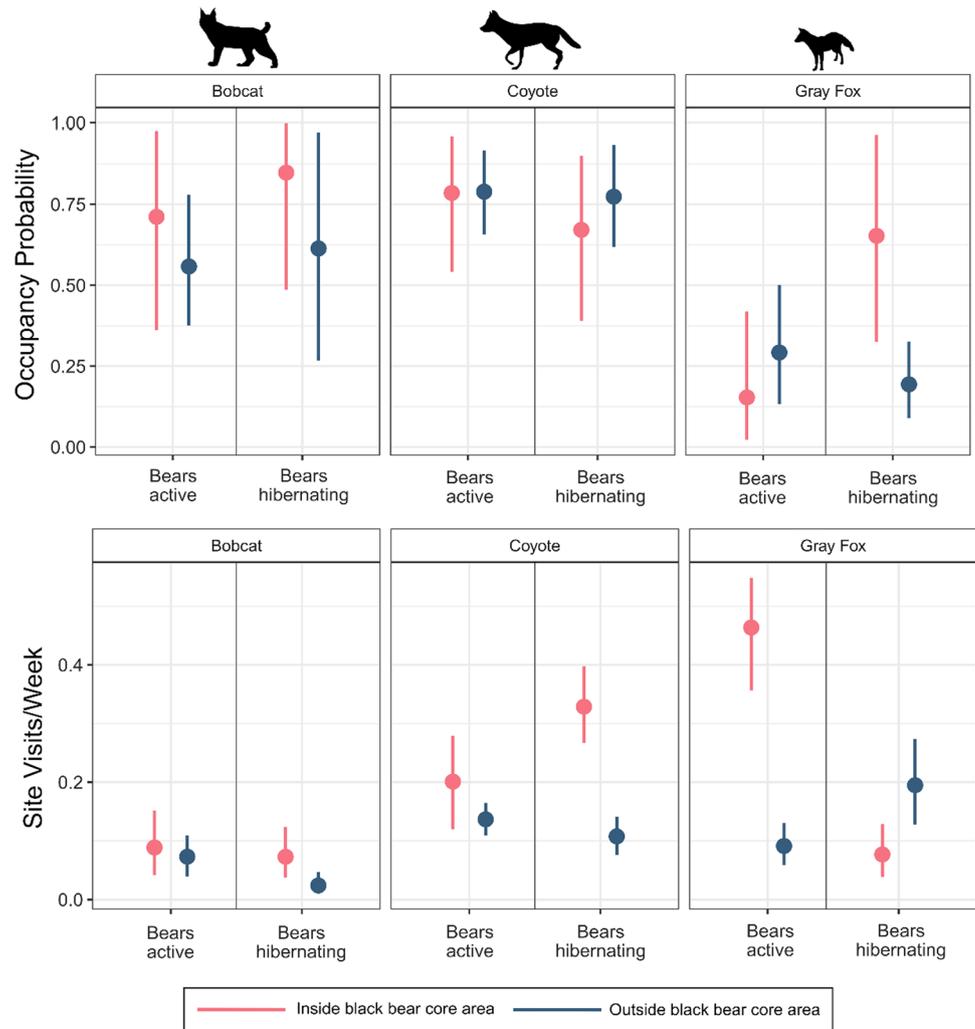
during this period was over three times higher in black bear core areas (0.07 visits/week; 95% CI 0.04, 0.12) than outside them (0.02 visits/week; 95% CI 0.01, 0.05; Fig. 3). Similarly, during the *bears hibernating* period, coyote site visit frequency was three times higher inside black bear core areas (0.33 visits/week; 95% CI 0.27, 0.40) than outside them (0.11 visits/week; 95% CI 0.08, 0.14; Fig. 3). Conversely, during this period, gray fox visit frequency inside core areas (0.08 visits/week; 95% CI 0.04, 0.13) was half that outside them (0.19 visits/week; 95% CI 0.13, 0.27; Fig. 3).

In contrast, all prey and most environmental covariates had weak associations with mesocarnivore occupancy and site visit frequency, as indicated by inclusion probabilities of < 0.5 and 95% credible intervals (CIs) that overlapped zero (Fig. 2; Appendix D). Exceptions included pinyon-juniper forest, which had a strong positive association with mesocarnivore occupancy for all species during the *bears active* period (Fig. 3, Appendix D). This association was absent for coyotes and gray foxes and reversed its sign for bobcats during the *bears hibernating* period (Fig. 2, Appendix D). Terrain ruggedness also had a positive association with bobcat and gray fox occupancy during the *bears active* period and a negative association with coyote occupancy during the *bears hibernating* period (Fig. 2, Appendix D). Site visit frequency was

positively associated with pinyon-juniper forest for bobcats during the *bears active* period and with terrain ruggedness for gray foxes in both periods (Fig. 2; Appendix D). Snow depth had a positive association with gray fox site visit frequency (Appendix D).

Gray foxes were highly nocturnal across periods (Fig. 4). Black bears, bobcats, and coyotes exhibited crepuscular peaks in temporal activity during the *bears active* period (Fig. 4). This pattern persisted for coyotes during the *bears hibernating* period while bobcats became more nocturnal (Fig. 4). During the *bears active* period, temporal activity patterns of all mesocarnivores were similar inside and outside black bear core areas, with overlap ranging from 0.85 to 0.88 (Fig. 4). During the *bears hibernating* period, overlap values inside and outside core areas for these mesocarnivores mirrored those during the *bears active* period, ranging from 0.82 to 0.90 while exhibiting uncertainty that was comparable to the *bears active* estimates (Fig. 4).

Fig. 3 Predicted mesocarnivore occurrence probability and site visit frequency at locations inside (red) and outside (blue) black bear (*Ursus americanus*) core areas. Circles are mean predictions and lines are 95% credible intervals from a model fit to data collected from 100 camera traps deployed from May 2018 to April 2019 in western Nevada, USA. The color depicts period (*bears active*: May–October; *bears hibernating*: December–April)



Discussion

Recent research has demonstrated that apex predators can strongly affect mesopredators, with cascading implications for ecosystem structure and function (Ritchie and Johnson 2009; Ferretti et al. 2010; Ritchie et al. 2012; Ripple et al. 2014). Nonetheless, little is known about the role that life history traits such as hibernation play in mediating these effects (cf. Polis et al. 1996) and studies examining changes across summer and winter are especially needed to clarify seasonal community dynamics (Stoessel et al. 2019). These factors make understanding the complex dynamics of top–down effects in space and time, and how they compare to bottom–up and environmental factors, a considerable challenge (Linnell and Strand 2000; Stoessel et al. 2019). We found that spatio-temporal mesocarnivore dynamics were influenced by an apex carnivore, the black bear, and varied according to this species' life history strategy of hibernating in winter and early spring. Further, these top–down effects were stronger than those associated with bottom–up factors

or environmental variables (Fig. 2; Appendix D). Although correlative in nature, our results suggest mesocarnivores responded to variation in interference competition with black bears by altering spatial activity over seasonal time scales rather than temporal activity over daily time scales (Figs. 2, 4). Such interference competition appeared to be a stronger proximal driving force than exploitative competition for prey (given prey availability's lack of effect on all species; Fig. 2). These results are consistent with a mechanism of cascading interference competition among black bears, coyotes, and gray foxes that was mediated by black bear hibernation.

Competition between black bears and coyotes is potentially widespread due shared characteristics, including habitat generalism, broad dietary niches, and overlapping ranges (Birch 1957; Litvaitis 1992; Ripple et al. 2014; Hody and Kays 2018). Nonetheless, studies of interactions between these species are rare (cf. Gompper et al. 2016; Litvaitis 1992). We found a lack of black bear effects on coyotes when bears were active (Fig. 2). This finding is similar to that reported in the eastern USA (Gompper et al. 2016).

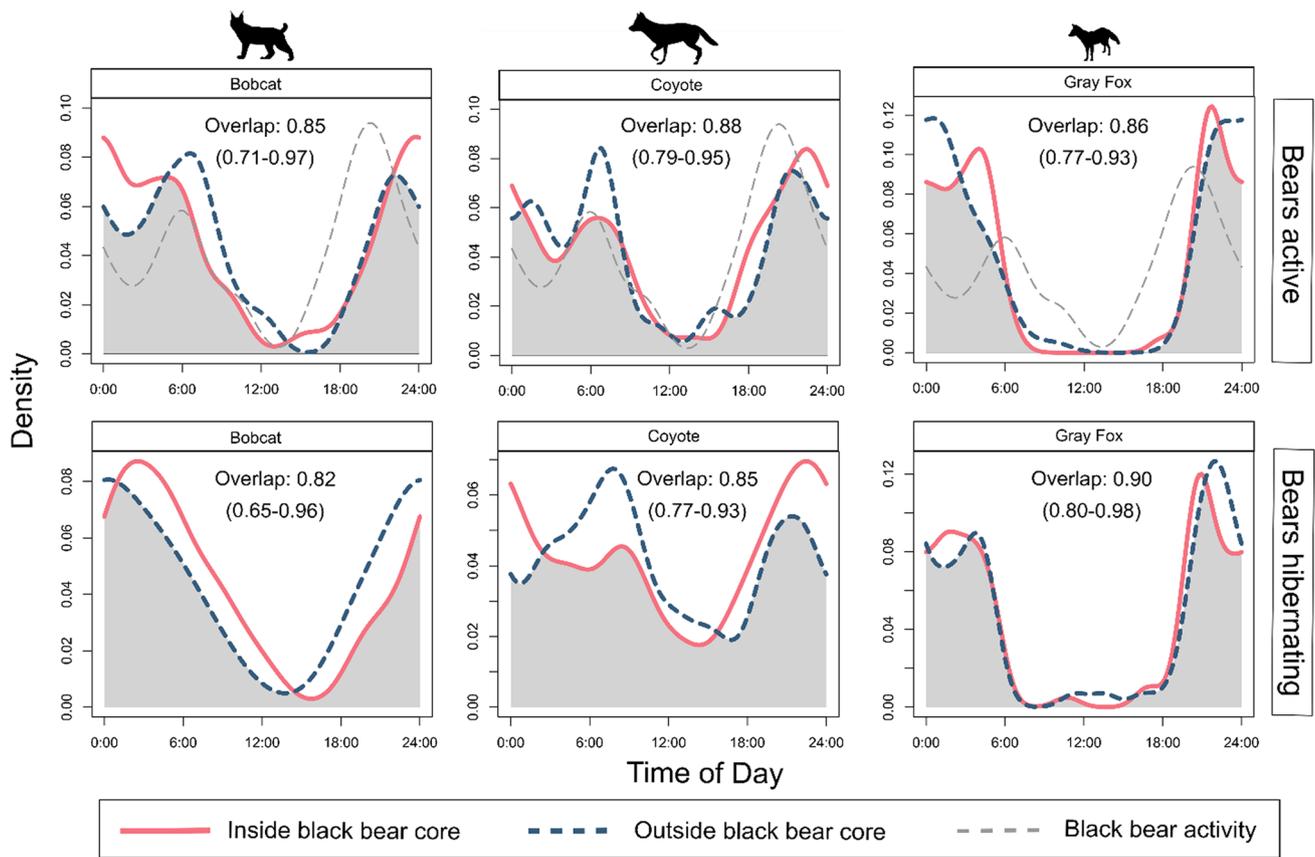


Fig. 4 Temporal activity patterns of mesocarnivores captured on camera traps inside (red; $N=20$ sites) and outside (blue; $N=80$ sites) black bear (*Ursus americanus*) core areas during periods where bears were active (May–October 2018) or hibernating (December 2018–

April 2019) in western Nevada, USA. Values indicate the proportion of activity overlap inside vs. outside black bear core areas for each mesocarnivore species (gray shaded regions), with 95% bootstrapped confidence intervals in parentheses

However, when black bears were hibernating, coyote site visits to black bear core areas were three times higher than those outside such areas (Figs. 2; 3; Appendix D). Given that numerous factors vary across seasons, it is possible that other, non-bear related factors could explain such a pattern. In our system, the most important of these factors are prey availability, habitat, and snow depth, but all of these were controlled for in the model. Thus, our results are consistent with the hypothesis that seasonal interference competition with black bears was an important driver of carnivore community dynamics in this system, while acknowledging the limitations of our correlative study design (Blanchet et al. 2020). Black bears had a concomitant, opposing effect on gray fox site visit frequency, with a strong positive association in the *bears active* period inverting to become strongly negative during the *bears hibernating* period, during which coyotes visited black bear core areas frequently (Figs. 2, 3; Appendix D). Taken in context with other studies showing spatial partitioning between coyotes and gray foxes (e.g., Atwood et al. 2011), this pattern suggests a seasonally contingent predator cascade where black bear hibernation

released coyotes to use areas that were previously risk-prohibitive, while gray foxes reduced visit frequencies in such areas to avoid coyotes (cf. Levi and Wilmers 2012; Sivy et al. 2017). Gray foxes’ increased visitation of black bear core areas in summer could plausibly be related to increased scavenging opportunities of black bear kills. This, coupled with a reduced tolerance of black bears for coyote scavenging, could partially explain the pattern of gray fox and coyote summer visitation rates to black bear core areas. A positive spatial attraction of mesocarnivores to apex predators due to increased scavenging opportunity has been recently observed in another North American system (Sivy et al. 2017), thus this plausible but speculative explanation deserves future research effort. Bobcats were less responsive to black bears, and, like coyotes, increased site visit frequency in black bear core areas during the *bears hibernating* period (Fig. 3). Coyotes can suppress bobcats (Henke and Bryant 1999), thus a lack of this effect in our system suggests reduced competition between the species due to bobcats’ dietary specialization or lower abundance (bobcats were detected ~3 times less than coyotes; Fig. 3). A potential explanation for

increased coyote and bobcat visitation to black bear core areas in winter is that these areas, which tended to be located in coniferous forest (Table D2), might have afforded greater cover from harsh winter conditions.

Nuance is required in interpreting occupancy and site visit frequency. Occupancy indicates that a site was used at least once in a period, while site visit frequency measures the intensity of visits at occupied sites. The overall effects of black bears on mesocarnivores were more evident in site visit frequency than occupancy (Fig. 2; Appendix D). Indeed, spatial patterns of occupancy might represent an overly coarse metric for inferring species interactions (Blanchet et al. 2020). Interestingly, gray fox occupancy was higher in black bear core areas when bears were hibernating than outside them, whereas site visit frequencies exhibited an opposing pattern (Fig. 3). This implies that gray foxes did not vacate black bear core areas altogether during hibernation, but rather appeared to “spread out” among such areas by visiting them infrequently. Further, gray foxes’ site visit frequency during the *bears hibernating* period increased in more rugged areas with deeper snowfall (Fig. 2). Such areas would have reduced rodent prey availability (Halpin and Bissonette 1988) and might have been more energetically costly to inhabit (e.g., due to difficulty moving through snow or on steep slopes). Hence, risk of interference with coyotes might lead gray foxes to use suboptimal areas in much the same way that predation risk from large carnivores drives ungulates into safer but less productive habitat (Caro 2005). Ideally, future studies would combine camera trapping and GPS data with small rodent trapping to examine these alternative hypotheses.

The time during which species are active is an important niche axis that can facilitate spatial coexistence when partitioned among competitors (MacArthur and Levins 1967; Carothers and Jaksic 1984). Such temporal partitioning has been found in competing carnivores (Fedriani et al. 2000; Hayward and Slotow 2009) but was absent here (Fig. 4). This result could have been partly due to the nocturnal nature of the prey species hunted by the mesocarnivores in our system (i.e., lagomorphs and rodents; Neale and Sacks 2001). Notably, coyote and black bear activity peaked at sunrise and sunset and were similar when both species were active, even within black bear core areas (Fig. 4). This similarity further emphasizes that the dynamics of these species tended to be characterized by variation in spatial activity over annual scales rather than temporal activity over daily scales (Figs. 3, 4). More broadly, temporal niche partitioning in terrestrial mammals is an area of active research, and there remains a critical need for additional studies that address how biotic and abiotic factors shape such partitioning (Frey et al. 2017).

As apex carnivore populations have declined over the last century, mesocarnivores have been released in many

areas, which has led to a variety of cascading outcomes on ecosystems (Ritchie and Johnson 2009; Ripple et al. 2014). However, some apex carnivores are being reintroduced or are naturally recolonizing areas from which they were extirpated. Here, we showed how one such species, the black bear, might shape sympatric mesocarnivore space use across a broad region of recolonization (Malaney et al. 2018), with potentially strong but unknown implications for lower trophic levels (e.g., rodent population dynamics; Levi et al. 2012) and ecosystem function (e.g., seed dispersal; Enders and Vander Wall 2012). Black bears’ life history strategy of hibernation implies that this long-lived species likely moderates coexistence of sympatric mesocarnivore communities via activity that varies across the annual scale. Thus, changes in black bear hibernation triggered by climate change and urbanization (e.g., reduced hibernation durations; Beckmann and Berger 2003) have the potential to disrupt community dynamics via alteration of top–down regulation of interference competition. More broadly, this study highlights how a rarely considered factor—the life history traits of apex predators—can play an important role in mediating top–down effects. While some studies have examined how apex predator hunting behavior changes according to life history traits (e.g., Young and McCabe 1997), our results highlight a research need regarding the role such traits play in nonlethal top–down effects. Finally, several multi-year and long-term studies in northern Europe have found that the top–down effects of apex predators intensify with increasing productivity, while bottom–up factors become more limiting in less productive environments and during winter (Elmhagen and Rushton 2007; Elmhagen et al. 2010; Stoessel et al. 2019). In our study system, black bears primarily occupied higher elevation areas with greater vegetative productivity than the more arid, shrub-scrub areas at lower elevations. Thus, our results are consistent with the general prediction that top–down effects become more limiting as productivity increases, even if we were not able to test this hypothesis fully due to the relative paucity of black bear activity in desert lowlands.

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Author contribution statement RAM and RJM conceived the ideas and designed methodology. RJM analyzed the data and led the writing

of the manuscript. All authors contributed to drafts and gave approval for publication.

References

- Atwood TC, Fry TL, Leland BR (2011) Partitioning of anthropogenic watering sites by desert carnivores. *J Wildl Manag* 75:1609–1615
- Beckmann JP (2002) Changing dynamics of a population of black bears (*Ursus americanus*): causes and consequences. University of Nevada, Reno
- Beckmann JP, Berger J (2003) Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *J Zool* 261:207–212
- Beckmann JP, Lackey CW (2018) Lessons learned from a 20-year collaborative study on American black bears. *Human-Wildlife Interact* 12:396–404
- Birch LC (1957) The meanings of competition. *Am Nat* 91:5–18
- Bjørnstad ON (2008) The ncf package: spatial nonparametric covariance functions
- Blanchet FG, Cazelles K, Gravel D (2020) Co-occurrence is not evidence of ecological interactions. *Ecol Lett* 23:1050–1063
- Caro T (2005) Antipredator defenses in birds and mammals. University of Chicago Press
- Carothers JH, Jaksic FM (1984) Time as niche difference: the role of interference competition. *Oikos* 42:403–406
- Elbroch LM, Kusler A (2018) Are pumas subordinate carnivores, and does it matter? *PeerJ* 6:e4293
- Elmhagen B, Rushton SP (2007) Trophic control of mesopredators in terrestrial ecosystems: top-down or bottom-up? *Ecol Lett* 10:197–206
- Elmhagen B, Ludwig G, Rushton SP et al (2010) Top predators, mesopredators and their prey: Interference ecosystems along bioclimatic productivity gradients. *J Anim Ecol* 79:785–794
- Enders MS, Vander Wall SB (2012) Black bears *Ursus americanus* are effective seed dispersers, with a little help from their friends. *Oikos* 121:589–596
- Estes JA (1995) Top-level carnivores and ecosystem effects: question and approaches. In: Jones C, Lawton JH (eds) *Linking species and ecosystems*. Chapman & Hall, New York, pp 151–158
- Fedriani JM, Fuller TK, Sauvajot RM, York EC (2000) Competition and intraguild predation among three sympatric carnivores. *Oecologia* 125:258–270
- Ferretti F, Worm B, Britten GL et al (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecol Lett* 13:1055–1071
- Frey S, Fisher JT, Burton AC, Volpe JP (2017) Investigating animal activity patterns and temporal niche partitioning using camera-trap data: challenges and opportunities. *Remote Sens Ecol Conserv* 5:272–285
- Gelman A, Hill J (2007) *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press, New York
- Gelman A, Carlin JB, Stern HS, Rubin DB (2004) *Bayesian data analysis*. Chapman & Hall/CRC, London
- Gompper ME, Lesmeister DB, Ray JC et al (2016) Differential habitat use or intraguild interactions: what structures a carnivore community? *PLoS ONE* 11:e0146055
- Greene W (2008) Functional forms for the negative binomial model for count data. *Econ Lett* 99:585–590
- Hairston NG, Smith FE, Slobodkin LB (1960) Community structure, population control, and competition. *Am Nat* 94:421–425
- Halpin MA, Bissonette JA (1988) Influence of snow depth on prey availability and habitat use by red fox. *Can J Zool* 66:587–592
- Hartigan JA, Wong MA (1979) A k-means clustering algorithm. *J R Stat Soc C* 28:100–108
- Hayward MW, Slotow R (2009) Temporal partitioning of activity in large African carnivores: tests of multiple hypotheses. *South Afr J Wildl Res* 39:109–125
- Heithaus MR, Frid A, Wirsing AJ, Worm B (2008) Predicting ecological consequences of marine top predator declines. *Trends Ecol Evol* 23:202–210
- Henke SE, Bryant FC (1999) Effects of coyote removal on the faunal community in western Texas. *J Wildl Manag* 63:1066–1081
- Hody JW, Kays R (2018) Mapping the expansion of coyotes (*Canis latrans*) across North and central America. *Zookeys* 2018:81–97
- Holt RD, Polis GA (1997) A theoretical framework for intraguild predation. *Am Nat* 149:745–764
- Jachowski DS, Butler A, Eng RYY et al (2020) Identifying mesopredator release in multi-predator systems: a review of evidence from North America. *Mamm Rev* 50:367–381
- Johnson HE, Breck SW, Baruch-Mordo S et al (2015) Shifting perceptions of risk and reward: dynamic selection for human development by black bears in the western United States. *Biol Conserv* 187:164–172
- Kernohan BJ, Gitzen RA, Millspaugh JJ (2001) Analysis of animal space use and movements. In: Millspaugh JJ, Marzluff JM (eds) *Radio tracking and animal populations*. Academic Press, San Diego, pp 125–166
- Kéry M, Royle JA (2015) *Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS*, vol 1. Prelude and static models. Elsevier, San Diego
- Kuo L, Mallick B (1998) Variable selection for regression models. *Sankhya Ser B* 60:65–81
- Lackey CW (2004) Nevada's black bear: ecology and conservation of a charismatic carnivore. *Biol Bull Number* 15
- Lackey CW, Beckmann JP, Sedinger J (2013) Bear historical ranges revisited: documenting the increase of a once-extirpated population in Nevada. *J Wildl Manag* 77:812–820
- Lepard CC, Moll RJ, Cepek JD et al (2019) The influence of the delay-period setting on camera-trap data storage, wildlife detections and occupancy models. *Wildl Res* 46:37–53
- Levi T, Wilmers C (2012) Wolves–coyotes–foxes: a cascade among carnivores. *Ecology* 93:921–929. <https://doi.org/10.1890/11-0165.1>
- Levi T, Kilpatrick AM, Mangel M, Wilmers CC (2012) Deer, predators, and the emergence of Lyme disease. *Proc Natl Acad Sci* 109:10942–10947
- Linnell JDC, Strand O (2000) Interference interactions, co-existence and conservation of mammalian carnivores. *Divers Distrib* 6:169–176
- Litvaitis JA (1992) Niche relations between coyotes and sympatric carnivora. In: Boer AH (ed) *Ecology and management of the eastern Coyote*. Wildlife Research Unit, University of New Brunswick, Fredericton
- Long RA, Donovan TM, MacKay P et al (2011) Predicting carnivore occurrence with noninvasive surveys and occupancy modeling. *Landscape Ecol* 26:327–340
- MacArthur R, Levins R (1967) The limiting similarity, convergence, and divergence of coexisting species. *Am Nat* 101:377–385
- MacKenzie DI, Nichols JD, Lachman GB et al (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255
- Malaney JL, Lackey CW, Beckmann JP, Matocq MD (2018) Natural rewilding of the Great Basin: genetic consequences of recolonization by black bears (*Ursus americanus*). *Divers Distrib* 24:168–178

- Martin TE (1995) Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol Monogr* 65:101–127
- Moll RJ, Cepek JD, Lorch PD et al (2018) Humans and urban development mediate the sympatry of competing carnivores. *Urban Ecosyst* 21:765–778
- Neale JCC, Sacks BN (2001) Resource utilization and interspecific relations of sympatric bobcats and coyotes. *Oikos* 94:236–249
- NOHRSC (2004) Snow data assimilation system (SNODAS) data products at NSIDC, Version 1
- Nouvellet P, Rasmussen GSA, MacDonald DW, Courchamp F (2012) Noisy clocks and silent sunrises: measurement methods of daily activity pattern. *J Zool* 286:179–184
- Plummer M (2003) JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Proceedings of the 3rd international workshop on distributed statistical computing, pp 124:1–8
- Polis GA, Holt RD, Menge BA, Winemiller KO (1996) Time, space, and life history: Influences on food webs. In: Polis GA, Winemiller KO (eds) *Food webs: integration of patterns and dynamics*. Springer, Boston, pp 435–460
- Promislow DEL, Harvey PH (1990) Living fast and dying young: a comparative analysis of life-history variation among mammals. *J Zool* 220:417–437
- Prugh LR, Sivy KJ (2020) Enemies with benefits: integrating positive and negative interactions among terrestrial carnivores. *Ecol Lett* 23:902–918
- Prugh LR, Stoner CJ, Epps CW et al (2009) The rise of the mesopredator. *Bioscience* 59:779–791
- Reznick D, Endler JA (1982) The impact of predation on life history evolution in Trinidadian Guppies (*Poeciliareticulata*). *Evolution* (N Y) 36:160–177
- Ridout MS, Linkie M (2009) Estimating overlap of daily activity patterns from camera trap data. *J Agric Biol Environ Stat* 14:322–337
- Ripple WJ, Estes JA, Beschta RL et al (2014) Status and ecological effects of the world's largest carnivores. *Science* 343:1241484
- Ritchie EG, Johnson CN (2009) Predator interactions, mesopredator release and biodiversity conservation. *Ecol Lett* 12:982–998
- Ritchie EG, Elmhagen B, Glen AS et al (2012) Ecosystem restoration with teeth: what role for predators? *Trends Ecol Evol* 27:265–271
- Rowcliffe JM (2019) Package “activity”
- Royle JA, Dorazio RM (2008) *Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities*. Elsevier Academic Press, Oxford
- RStudio Team (2015) *RStudio: integrated development for R*
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Seaman DE, Millsbaugh JJ, Kernohan BJ et al (1999) Effects of sample size on kernel home range estimates. *J Wildl Manag* 63:739–747
- Sikes RS (2016) 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *J Mammal* 97:663–688
- Sivy KJ, Pozzanghera CB, Grace JB, Prugh LR (2017) Fatal attraction? Intraguild facilitation and suppression among predators. *Am Nat* 190:663–679
- Soulé ME, Bolger DT, Alberts AC et al (1988) Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. *Conserv Biol* 2:75–92
- Stoessel M, Elmhagen B, Vinka M et al (2019) The fluctuating world of a tundra predator guild: bottom-up constraints overrule top-down species interactions in winter. *Ecography (Cop)* 42:488–499
- Su YS, Yajima M (2012) R2jags: a package for running jags from R
- Tobler MW, Powell GVN (2013) Estimating jaguar densities with camera traps: problems with current designs and recommendations for future studies. *Biol Conserv* 159:109–118
- Vanak AT, Fortin D, Thaker M et al (2013) Moving to stay in place: behavioral mechanisms for coexistence of African large carnivores. *Ecology* 94:2619–2631
- Vander Wal E, Rodgers AR (2012) An individual-based quantitative approach for delineating core areas of animal space use. *Ecol Model* 224:48–53
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168
- Young DD, McCabe TR (1997) Grizzly bear predation rates on caribou calves in Northeastern Alaska. *J Wildl Manag* 61:1056–1066