CARNIVORE COMMUNITY STRUCTURE IN A CHANGING WORLD

By

Mauriel Rodriguez Curras

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The dissertation is approved by the following members of the Final Oral Committee:

Jonathan N. Pauli, Professor, Forest and Wildlife Ecology

Benjamin Zuckerberg, Professor, Forest and Wildlife Ecology

Bill Karasov, Professor Emeritus, Forest and Wildlife Ecology

John Orrock, Professor, Integrative Biology

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Dissertation Abstract

Carnivores are ecologically important members of communities and ecosystems because a relatively low number of individuals can cause both strong direct (consumptive) and indirect (non-consumptive) effects that structure the habitat use, distribution, and abundance of subordinate guild members, and ultimately shape the interactions of entire food webs. Understanding how species interactions cascade throughout carnivore guilds is important for predicting community-wide responses to the ongoing repatriation of the largest carnivores– either naturally or through human assistance – especially in the face of global change. Accordingly, a wholistic framework that integrates the negative effects from suppression (i.e., intraguild aggression) and the positive effects from facilitation (i.e., resource subsidies) will improve our understanding of community dynamics. The overarching goal of my dissertation is (i) to provide greater insights how suppression and facilitation structure carnivore communities across resource gradients, (ii) disentangle the mechanisms underlying meso- and small carnivore resource use, and (iii) develop novel testable and predictive models of carnivore community interactions following the repatriation of large carnivores to human landscapes.

Each chapter of this dissertation is written and formatted for publication as a manuscript in a peer-reviewed journal. **Chapter 1** (Rodriguez Curras et al. 2021, *Behavioral Ecology*) explicitly tests the behavioral mechanisms that drive carnivore community interactions. We used a combination of giving up density experiments and a novel modeling approach to test the impacts of habitat structure, behavior, and space use. We found that there was a dominance hierarchy from the apex carnivore through the meso-carnivore to the subordinate small carnivore, which was reflected in space. Although both meso- and small carnivores exhibited similar predator avoidance behavioral responses to apex carnivores, the habitat associations of

apex carnivores only altered meso-carnivore space use. Our results broadly suggest that the bias in risk management we observed for meso-carnivores likely translates into a stable co-existence of this community of competing carnivores. In **Chapter 2** (Rodriguez Curras et al. 2024, *Frontiers in Ecology and the Environment*), we took advantage of the wolf (*Canis lupus*) reintroduction to Isle Royale in 2018 to test the drivers of community structure. In a before-after study, we quantified the spatial, behavioral, trophic, and demographic effects that a large carnivore (wolves) reintroduction to Isle Royale National Park had on meso- (foxes; *Vulpes vulpes*) and small carnivores (martens; *Martes americana*). The reintroduction of wolves produced a phase-dependent pulse perturbation; wolves constrained the distribution of foxes benefiting martens, yet foxes altered their behavior, notably using human campsites and food more frequently, which buffered demographic consequences. Once wolf packs coalesced, all observed changes subsided, and competitive interactions returned to their pre-wolf values. Our results show that some predicted – and often desired – consequences of large carnivore reintroductions may not be permanent due to the transitory dynamics of social carnivores and the presence of humans, even within a “pristine wilderness”. **Chapter 3** (Rodriguez Curras et al. 2024, in Review at *Oikos*) explores the drivers of Eltonian niche conservatism in carnivore communities. Specifically, we found that trophic facilitation by wolves and resource subsidies from humans altered the foraging strategies of individual subordinate carnivores, resulting in disparate foraging strategies for foxes. Our results highlight that Eltonian niche conservatism in carnivore communities is driven by resource subsidies, both from the provisioning of carrion by large carnivores to meso-carnivores and from human foods subsidizing small carnivores. More broadly, our work suggests that large carnivore repatriation can restore some species interactions, while human resource subsidies can strongly decouple competitive interactions. Finally,

Chapter 4 (Rodriguez Curras and Pauli, prepared for *Conservation Letters* or *Biology Letters*) explores a similar theme to Chapter 3 though in a seasonal context. Not surprisingly, seasonality strongly influenced meso-carnivore diet and we found strong support for yearly periodicity in their diet. Broadly, our results suggest that trophic facilitation from wolves and resource subsidies from humans are complementary and operate asynchronously throughout the year. The results from this chapter suggest that asynchronous dual subsidies from restored large carnivores during winter and human recreation during summer can lead to an increase to the overall nutritional landscape for plastic meso-carnivores, which can ultimately destabilize meso-carnivore populations and provides alternative means for 'the rise of the meso-predator'.

My dissertation provides important insights into ecological and conservation issues of local and global importance – the impacts of humans to carnivore community interactions. Broadly, my research supports the expected consequences of restoring community interactions through the repatriation of large carnivores though highlights an underappreciated force in these community interactions: humans and human resource subsidies strongly mediating carnivore community interactions.

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Perceived risk structures the space use of competing carnivores

Mauriel Rodriguez Curras[1*], Emiliano Donadio[2±], Arthur D. Middleton[3], and Jonathan N. Pauli[1]

[1] University of Wisconsin-Madison, Forest and Wildlife Ecology, 1630 Linden Dr., Madison, Wisconsin 53706.

[2] INIBIOMA, CONICET-Universidad Nacional Comahue, 8400 Bariloche, Argentina

[3] University of California-Berkeley, Department of Environmental Science, Policy, and Management, 130 Mulford Hall, Berkeley, California 94720.

[*] Corresponding Author: Mauriel Rodriguez Curras. E-mail: mrodriguezcu@wisc.edu

[±] Current Affiliation: Rewilding Argentina, Estancia La Ascensión, Los Antiguos, Santa Cruz 9041, Argentina.

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Abstract

Competition structures ecological communities. In carnivorans, competitive interactions are disproportionately costly to subordinate carnivores who must account for risk of interspecific killing when foraging. Accordingly, missed opportunity costs for meso-carnivores imposed by risk can benefit the smallest-bodied competitors. However, the extent to which the risk perpetuates into spatial partitioning in hierarchically structured communities remains unknown. To determine how risk-avoidance behaviors shape the space-use of carnivore communities, we studied a simple community of carnivores in northern Patagonia, Argentina: pumas (*Puma concolor*; an apex carnivore), culpeo foxes (*Lycalopex culpaeus*; a meso-carnivore), and chilla foxes (*Lycalopex griseus*; a small carnivore). We used multi-species occupancy models to quantify the space use within the carnivore community and giving-up densities to understand the behaviors that structure space use. Notably, we applied an analytical framework that tests whether actual or perceived risk of predation most strongly influences the space use of subordinate carnivores while accounting for their foraging and vigilance behaviors. We found that there was a dominance hierarchy from the apex carnivore through the meso-carnivore to the subordinate small carnivore, which was reflected in space. Although both meso- and small carnivores exhibited similar predator avoidance behavioral responses to apex carnivores, the habitat associations of apex carnivores only altered meso-carnivore space use. The biases in risk management we observed for meso-carnivores likely translates into stable co-existence of this community of competing carnivores. We believe our analytical framework can be extended to other communities to quantify the spatial-behavioral tradeoffs of risk.

Introduction

The exploitation of a limited resource by two or more species can strongly structure ecological communities (Gause, 1934; Hardin, 1960; Holt, 1977). Within the carnivore guild, competition is especially apparent because carnivores have evolved to become highly effective killers (Gittleman, 1989). For carnivores, interspecific competition is often manifested as interference, whereby dominant guild members display aggression or even kill subordinate species (Case and Gilpin, 1974; Holt and Polis, 1997). These interactions are disproportionately costly to smaller bodied species (Palomares and Caro, 1999; Donadio and Buskirk, 2006; de Oliveira and Pereira, 2014), though subordinate species can benefit from large carnivore provisioning (i.e., facultative scavenging; Prugh *et al.*, 2009; Elbroch and Wittmer, 2012). Consequently, subordinate carnivores must navigate risky landscapes to avoid interspecific killing while maximizing foraging opportunities (Suraci *et al.*, 2016).

Much of what we know about risk perception and avoidance comes from predator-prey interactions (Lima and Dill, 1990). Prey simultaneously balance energetic demands and anti-predator behaviors, though the quality of prey information about predation risk and the costs and benefits of refuge use predominantly influence behavioral adaptations (Sih, 1992). Intuitively, prey are expected to overestimate risk and be more cautious – despite ambiguity in the signal – because the fitness cost of underestimating risk (i.e., death) is higher than missed opportunity costs (Abrams, 1994; Brown *et al.*, 1999). Direct cues of risk, like smelling, hearing, or seeing a predator, relate immediate information and can be informative for escaping predation when being targeted (Lima and Dill, 1990). Such direct cues are often extrapolated beyond the given encounter by tying them to indirect cues like habitat type or horizontal cover, which can reveal generally risky areas to be avoided (Preisser *et al.*, 2005; Preisser *et al.*, 2007). These indirect cues of predation risk culminate in the “landscape of fear” (Laundre *et al.*, 2010) and often influence space-use more broadly (Janssen *et al.*, 2007; Laundre *et al.*, 2010). Predators that exhibit a narrow habitat domain, with a preference for specific habitat characteristics, have been found to influence space-use more strongly (Schmitz, 2008), causing prey to spatially or temporally avoid those areas (Schmitz *et al.*, 2017; Smith *et al.*, 2019). Because indirect cues of risk provide less accurate information on the identity and state of potential risk, the costs of false-positive (missed opportunity costs) and false-negative errors (potential death) will generally lead species to become more wary (i.e., cause species to perceive a higher level of risk than is actually present; Sih, 1992; Lima and Bednekoff, 1999). The way species cope with predation risk is an important component of community structure because the fear of death has at least as strong of an effect on prey distribution and abundances as direct predation (Preisser *et al.*, 2005; Preisser *et al.*, 2007; Guiden *et al.*, 2019).

Much like prey, subordinate carnivores navigate potentially deadly encounters with dominant carnivores (Berger *et al.*, 2008) and so our understanding of risk avoidance interactions are largely transferable between predator-prey and predator-predator systems (Mukherjee *et al.*, 2009); indeed, predator-prey interactions shape how we think about carnivore intraguild interactions and competition (Polis *et al.*, 1989; Holt and Polis, 1997). Carnivore communities, however, are further structured by facilitation (i.e., resource provisioning); these two opposing forces (suppression and facilitation) create a “fatal attraction” for meso- and small carnivores (Sivy *et al.*, 2017). The lower resource availability found at higher trophic levels, compounded by difficulty in acquiring or subduing profitable prey, tends to aggregate carnivores over shared and limited resources like carrion (Sivy *et al.*, 2017). Consequently, risk avoidance in carnivore communities is an especially important driver of community structure (Ritchie and Johnson, 2009), particularly since prey can more easily move to different resource patches to avoid predation (Smith *et al.*, 2019). In multi-carnivore communities featuring a hierarchy of three or more levels (*sensu* Prugh and Sivy, 2020), the missed opportunity costs of being overly cautious has the added cost that these tradeoffs for safety can be beneficial for smaller bodied competitors.

To minimize the risk of fatal interactions, the best strategy for subordinate carnivores is to partition space (Fedriani *et al.*, 2000), especially in environments where resources are limited (Robinson *et al.*, 2014) and where species exhibit constrained diel patterns (Balme *et al.*, 2017). Understanding the ecological consequences of behaviorally mediated space-use provides insight into the structure of communities (Schmitz *et al.*, 1997). Indeed, the "landscape of fear" for meso-predators may be especially steep, with little safety offered (Ritchie and Johnson, 2009). Much of the focus on risk avoidance in carnivores has come from dyadic interactions attempting to untangle how predation risk affects foraging (Hunter and Caro, 2008; Leo *et al.*, 2015) or from systems where multiple dominant carnivores affect a single subordinate species (Durant, 2000; Creel *et al.*, 2001). The combination of behavioral interactions and interspecific killing have been shown to cause continental scale trophic cascades (i.e., meso-predator release; Soule *et al.*, 1988; Crooks and Soule, 1999) from dominant apex carnivores through small, subordinate species (Newsome and Ripple, 2014). However, the extent to which the risk of predation perpetuates into spatial partitioning in a multi-level, hierarchical community of carnivores remains unknown and a framework for understanding these effects has not been established.

To assess how risk avoidance shapes the space-use of carnivore communities, we studied a simple community of carnivores in northern Patagonia, Argentina. Pumas (*Puma concolor*) are dominant, apex carnivores that select areas to maximize hunting success (Smith *et al.*, 2019), kill large ungulates that provision smaller carnivores (Elbroch and Wittmer, 2013), and potentially mediate the structure of carnivore communities (Novaro *et al.*, 2005). Culpeo foxes (*Lycalopex culpaeus*) exhibit dietary and temporal niche overlap with pumas (Rodriguez Curras et al. *in Review*) and are also killed by pumas (Donadio and Buskirk, 2006). The smaller chilla foxes (*Lycalopex griseus*) overlap somewhat in niche space with pumas and culpeo foxes (Rodriguez Curras et al. *in Review*) and are occasionally killed by both (see de Oliveira and Pereira, 2014). We hypothesized that the fear of interspecific conflict with dominant carnivores would alter the behavior of subordinate species. Specifically, we predicted that culpeo and chilla foxes would exhibit heightened levels of anti-predator behaviors (i.e., vigilance and exploratory behavior) in areas of high puma occupancy, and, therefore, will trade food consumption for safety. Furthermore, we predicted that culpeo foxes would alter their space-use in response to indirect cues of predation risk from pumas (i.e., habitat characteristics) to a higher degree than chilla foxes. To test our predictions, we used multi-species occupancy models to address the space-use within the carnivore community and giving-up densities (GUDs) at foraging stations to understand the behaviors that structures space-use. We then integrated these two approaches into an analytical framework to disentangle how subordinate species spatially respond to perceived and actual risk.

Methods

Fieldwork was conducted in and around Laguna Blanca National Park (LBNP; -39.05 W, -70.03 S; Figure 2), located in the Patagonian steppe of northern Patagonia (Figure 1. B). The southeast portion of the park is dominated by the Mellizo Sur Volcano, with sharp volcanic rocks scattered throughout its foothills. Cerro Laguna Volcano shapes the central landscape of the park, providing sharp slag gulches to the west of the peak. The northern portion of the park is a basaltic plateau that surrounds the Laguna Blanca wetlands and meadows. The lake is fed by two ephemeral streams, the Llano Blanco and the Pichi-Ñireco that have carved gorges in the plateaus in the northwestern extent of the park. The climate is arid (150–200 mm precipitation annually) with precipitation mostly in the winter and spring. The average maximum temperature during summer is 23ºC, and the average low temperature during winter is 0°C.

LBNP and the surrounding area is home to a community of six native carnivores: Pumas, Geoffroy's cat (*Leopardus geoffroyi*), pampas cats (*Leopardus colocolo*), and three facultative scavengers, culpeo foxes, chilla foxes, hog-nosed skunks (*Conepatus chinga).* Although designated a national park, ranching of goats, sheep, cows, and horses is prominent in the park and surrounding area, and due to these practices, there are two exotic carnivores within our study site: dogs (*Canis lupus familiaris*) and domestic cats (*Felis catus*). All native carnivores are strictly nocturnal and exhibit high diel overlap (≥75% overlap; Rodriguez Curras et al., *in Review*). Pumas in our study area predominantly consumed livestock, which was found in the diets of both culpeo and chilla foxes (Rodriguez Curras et al., *in Review*).

Field Sampling

To study the space use of chilla foxes, culpeo foxes, and pumas, we deployed 46 camera traps (Bushnell Trophy Cam HD, Bushnell Outdoor Products, Overland Park, KS, USA) within and around LBNP in a random design but buffered 300 m from dirt roads, highways, and peaks, and 500 m from ranchers' houses (Figure 1A). Camera traps were spaced an average of 2.00 km (±0.17) apart, staked 0.75 m above the ground, and angled toward a 0.5 m reference stake ~3 m from the camera. Cameras were programmed to collect a set of three pictures for every trigger, with 0 s delay between triggers. We maintained a relatively brief sampling period, including a two-week burn in period, was during winter (i.e., July 10 – October 10), to help ensure closure for our occupancy modeling. We checked camera traps two or three times a month. Photos were processed and tagged (Adobe Bridge, Adobe Systems, San Jose, CA), and metadata created using the R package *camtrapR* (Niedballa et al. 2016).

To study how pumas influence the space use of chilla and culpeo foxes, we experimentally manipulated foraging stations across a gradient of puma occupancy. We set a total of twenty-five GUD stations (see below) stations within LBNP at least 1 km apart. Within 50 m of these locations, we selected a small patch of open, sandy habitat ≥ 300 m from roads (Figure 1A). GUD stations were set up independently of the camera stations used for our occupancy models (Figure 1) and all baited stations were set up after our camera trap study ended (October 15 – December 10). Each station comprised of a natural, excavated foraging area (30 cm^3) filled with 15 chicken necks cut to equal sizes (~60 g of food offered in total mixed in with excavated dirt to produce diminishing returns) and a single camera trap (Bushnell Trophy Cam HD) supported by a wooden stake 0.75 m above the ground (Figure 1B). Cameras were set to take a video recording for 60 s every trigger, with 0 s between triggers. GUD stations were activated in the late afternoon (between 1600 and 2100) and alternated which stations were set up first daily. GUD stations were checked in the morning (between 0700 and 1100) and, again, alternated which stations were checked first. We alternated which GUD stations were active at any one time so that the minimum distance between active GUD stations was 2 km. Each GUD station was operational for a maximum of five days, until the station was used by avian scavengers, or until a fox used the station, at which point the station was not reactivated. A GUD station was considered used when a fox searched within the GUD station. Following a use event, GUD data was collected from each station and videos were scored to quantify behavior at the feeding stations.

At each camera trap site and GUD station, we measured habitat characteristics at four sampling plots; these plots were established by generating one random angle within each compass quadrant and a random distance between 5–25 m from the camera location. For the GUD stations only, we chose the central location for sampling as 25 m from the GUD station itself because of our selection of open patches for our GUD locations. To test the effects of the horizontal cover and visibility on the occupancy and behavior of foxes, we measured horizontal cover by photographing a 1x1 m plain white sheet and estimating the percent obscured by vegetation and rocks (e.g., low horizontal cover values are sites with less obstructions and clearer sightlines; Collins and Becker, 2001). We took the average horizontal cover of the four measurements to represent the site level cover. We also estimated the minimum distance to lakes and streams for each camera trap and quantified the proportion of cliffs and landscape heterogeneity within a 500 m buffer using a digital elevation model and Landsat 8 satellite imagery data. For cliffs, we created a roughness layer (i.e., the difference in slope between adjacent cells) from our digital elevation model and used the upper 90% values (i.e., the values of the greatest difference between adjoined cells) buffered by 50 m. For landscape heterogeneity, we created a 500 m buffer around each camera trap and GUD station and used the standard deviation of the visual spectral band of the Landsat imagery data within each buffered area. These covariates capture a variety of habitat features that pumas, culpeo foxes, and chilla foxes may partition (Johnson and Franklin, 1994a; Jiménez *et al.*, 1996; Laundré and Hernández, 2003; Novaro *et al.*, 2004), furthermore, they capture the heterogeneity of habitat within LBNP and can they can also mediate the behavioral interactions between these carnivores.

Occupancy Models

We used multi-species occupancy to estimate the probability of occupancy of subordinate carnivores conditional on the probability of occupancy of the dominant member of the guild. As many as twenty-one combined occupancy and detection parameters could be estimated in a single model and lead to unfeasibly large number of models. Consequently, we used three sequential stages of model fitting in the R package *unmarked* (Fiske and Chandler, 2011) to simplify the structure of nuisance parameters (detection) and reduce the final, inferential model set to a reasonable number (Richmond *et al.*, 2010; Doherty *et al.*, 2012; Robinson *et al.*, 2014): (1) single-species detection, (2) single-species occupancy, and (3) multi-species occupancy. For each step, we used the same site- and survey-specific covariates for chilla foxes, culpeo foxes, and pumas. The top detection and occupancy model from each sequential step were carried forward to the multi-species occupancy model. For the single-species models, we identified the covariates to be used in the multi-species model via Akaike Information Criterion (AICc; Burnham and Anderson, 2002), and the likelihood function (Richmond *et al.*, 2010; Rota *et al.*, 2016). We tested for multi-collinearity within the predictor variables and standardized our covariates prior to model fitting.

We split camera trap surveys into ten 10-day intervals. If a species was photographed at a site on one or more days in an interval, we considered it a single detection. Survey periods were used to generate site-specific detection histories for each species (MacKenzie *et al.*, 2002). We assumed sites were closed to changes in occupancy state over the entire period. Because individuals did not have to be continually present at a site for it to be classified as occupied, occupancy in our study can be interpreted as use (MacKenzie *et al.*, 2006). To determine survey specific heterogeneity in detection probability we used survey period, snow cover, moon phase, horizontal cover, and their additive effects as possible covariates.

In our single-species single-season occupancy model (MacKenzie *et al.*, 2002), we identified the best survey specific model covariates for each species. We held occupancy constant ($\psi(\cdot)$) and fit 23 models to explore the influence of the survey period, moon phase, snow cover, horizontal cover, and their additive combinations on the probability of detecting each species. Only for estimating detection probability did we consider additive effects of covariates. We then carried best detection covariates forward into a set of single-species single-season models, from which we determined the important occupancy covariates for each species. We developed six single-covariate models of occupancy, considering the distance to streams and lakes, cliff habitat, landscape heterogeneity, horizontal cover, and $\psi(\cdot)$. Finally, we created a set of conditional three-species occupancy models from which inferences regarding carnivore co-occurrence were drawn. We used the best detection and occupancy covariates (SM Table 1) from the single-species models to compose the individual species components in the multi-species model. For each species pair (chilla:culpeo, chilla:puma, and culpeo:puma), and the co-occurrence of all three species (chilla:culpeo:puma), we used the top performing model of each species and $\psi(\cdot)$ as possible covariates for the co-occurrence of each group of species. Our final multi-species model suite included a total of 144 models from the different combinations of each covariate for the co-occurrence of each species (chilla:puma, chilla:culpeo, culpeo:puma, and chilla:culpeo:puma). We limited all multi-species occupancy models to a single covariate because of the increased complexity of modeling multi-species interactions. All our results and inference are from the top performing multi-species occupancy model as measured by the AICc.

The effects of spatial autocorrelation for species pairs has been thoroughly investigated (Rota *et al.*, 2016), but fewer studies have described the effects for more species. Accordingly, we attempted to limit spatial autocorrelation with our trap placement. However, the larger carnivores in our study have home ranges that covered the extent of several camera traps ($HR_{Puma} \approx 10{,}000$ ha, $HR_{Culpeo\ Fox} \approx 1{,}250$ ha, $HR_{Chilla\ Fox} \approx 150$ ha), which could potentially lead to pseudo-replication. However, because we are interpreting our model results as use, rather than occupancy *per se*, we contend this is not an issue for our analysis. We nevertheless tested for spatial autocorrelation between the detections of each species and the distance between cameras using a correlogram, variogram, and spline-correlogram.

To draw inference about the spatial association of the carnivore community, and how the occupancy of a dominant guild member affects a subordinate (in a species pair), we used the conditional occupancy probabilities of chilla and culpeo foxes, given the presence or absence of their intra-guild predators (i.e., ψ(chilla fox | culpeo fox and puma), and ψ(culpeo fox | puma)). Furthermore, we used our top model estimates of occupancy to calculate the species interaction factor (SIF) between chilla foxes, culpeo foxes, and pumas (Richmond *et al.*, 2010). The SIF represents a likelihood ratio of co-occurrence for each pairwise comparison. Since we used a three species model, for each species pair we considered the co-occurrence between species across the occupancy state (i.e., present or absent) of the third species (see Supplementary Material). A SIF value of 1 indicates that the two species occur independently; a value >1 suggests that the two species are more likely to co-occur than would be expected by chance, whereas a value <1 indicates spatial avoidance. For a group of three species, the probability of occurrence for species 1 is conditional on the presence or absence of species 2 and 3 (i.e., four possible outcomes $\psi_{1|11}$, $\psi_{1|10}$, $\psi_{1|01}$, and $\psi_{1|00}$). We used our top multi-species occupancy model estimates of occupancy to calculate the SIF between chilla foxes, culpeos, and pumas (Richmond *et al.*, 2010).

Foraging Behaviors and Giving-Up Density (GUD)

We quantified GUDs as the number of offered chicken pieces remaining in the staged foraging area after foraging. From the recorded videos of foxes at the GUD stations, we constructed an ethogram of six simplified behaviors (Table 1) based on previous literature of fox behavioral studies (Leo *et al.*, 2015). Behaviors were represented as the total proportion of time in sight devoted to each behavior. We used a non-parametric Mann-Whitney-Wilcoxon Test to compare GUDs and behavior between culpeo and chilla foxes. Furthermore, we tested the effect of vigilance on GUD (Figure 3B) with a simple linear model and if there was a difference in vigilance between species using an ANOVA.

We tested an *a priori* set of habitat drivers to explain the GUD of chilla and culpeo foxes. Specifically, we constructed generalized linear models (GLMs; with a binomial error distribution) for each species testing the individual and additive effects of distance to streams and lakes, cliff habitat, landscape heterogeneity, horizontal cover, puma space-use, and a null model; for chilla foxes, we also included the occupancy of culpeo foxes as a potential effect on foraging and vigilance behaviors. At each GUD station, we derived puma and culpeo space-use from our multi-species occupancy model by predicting the occupancy of each species using the measured habitat covariates; we used the expected occupancy at each GUD site. Any variables with a correlation ≥0.70 were not included in candidate models. To assess the relationship between habitat covariates and GUDs, we tested a series of 40 models for chilla foxes and 20 models for culpeo foxes (top candidate models are shown in SM Table 4). We used AICc for model comparison within each species.

Testing Perceived vs. Actual Risk

To test how culpeo and chilla foxes spatially responded to predation risk on the landscape, we used a partial regression framework (i.e., a path analysis) using the observed covariance between puma habitat and space-use with culpeo and chilla fox risk-avoidance behavior and space-use. Using this framework, we explored the relative effects of risk perception from habitat characteristics and the actual risk of predation on subordinate carnivore space-use. To test the effect of perceived predation risk from pumas on the occupancy of culpeo and chilla foxes, we used the covariate that was most influential for puma space-use, based on the single- and multi-species occupancy model (i.e., cliff habitat). The association between pumas and rugged terrain (like cliffs) offers an honest signal for species making decision of habitat use (Laundré and Hernández, 2003; Smith *et al.*, 2019). Indeed, prey, in similar systems have been found to avoid more rugged terrain (i.e., what we classified as cliff habitat) because they are less likely to detect and escape from pumas in these areas (Donadio and Buskirk, 2016). We used the predicted occupancy of pumas at GUD sites as a measure of actual predation risk because occupancy probabilities capture the variation in the encounter rate between species (Trainor and Schmitz 2014). We formulated the following to calculate the perceived and actual risk effects separately:

$$\gamma_{x_1-y_2} = \frac{cov_{x_1-y_2} \times \left(cov_{x_1-y_1} \times cov_{y_1-y_2}\right)}{1 - cov_{x_1-y_1}^2};\ Eqn. 1$$

where, γ is the effect of x_1 on y_2 while accounting for the shared covariance with y_1, *cov* is the standardized covariance shared between the variables in the sub-script, x_1 is either the preferred habitat or the estimated occupancy probability ($\hat{\psi}$) of Species 1 (the dominant species), y_1 is the anti-predator behavior (GUDs) measured of Species 2 (the subordinate species; and y_2 is the $\hat{\psi}$(Species 2). The resulting coefficient (γ) quantifies how the subordinate species spatially responds to (1) the habitat associations of their dominant competitor (which we interpreted as perceived risk) or (2) the risk of encounter with their dominant competitor (which we interpreted as actual risk). This value is standardized by the behavioral response (i.e., GUD) of the subordinate species. Throughout the modeling process, we used standardized values (i.e., how a change in one standard deviation of the predictor variable affects the standard deviation of the response) to compare the effects across species.

To test whether the effect of habitat or the occupancy probability of pumas was more influential to the space use of chilla and culpeo foxes, we defined the perceived risk coefficient (i.e., effect of habitat relative to $\hat{\psi}$[Species 1]) as:

$$Perceived\ Risk\ Coefficient\ (PRC) = \frac{\gamma_{Habitat-\psi(Spp.2)}}{\gamma_{\psi(Spp.1)-\psi(Spp.2)}};\ Eqn. 2$$

The perceived risk coefficient provides an estimate of the spatial response to perceived risk (the effect of habitat standardized by the behavioral response to habitat) relative to the spatial response to actual risk (the effect of puma occupancy standardized by the behavioral response to puma occupancy). A value of 1.0 indicates that the occupancy of the subordinate species is equally influenced by the perception of risk and the actual risk of predation, based on the space use of the dominant species. A value <1.0 indicates that the perception of risk is less influential than actual risk, while a value >1.0 indicates that the perception of risk is more influential than actual risk. We used a bootstrapping routine (N = 10,000) to generate a robust estimate of the spatial responses to perceived and actual risk, and the PRC by incorporating the sampling error of each term in the equation from the partial regression (Eqn. 1). For each modeled parameter, we tested the differences in responses between species using a bootstrapped Z-Test.

Results

We conducted a total of 3,116 total camera trap nights from July 10 – Oct 10, 2018. Chilla foxes were the most detected carnivore throughout the study area, being detected in 0.61 of our camera traps, followed by culpeo foxes (0.27) and pumas (0.20). We did not detect spatial autocorrelation between the residuals of our models for any of the species, though we detected autocorrelation between the predicted occupancy probabilities of chilla foxes between camera traps (SM Figure 1). This was likely because chilla foxes occurred at relatively high abundances within our study area.

Multi-Species Occupancy Model

In our single species analysis of chilla foxes, we found that their detection (0.28±0.02; ±1 SE) was relatively low and decreased throughout the survey period ($\beta = –0.18\pm0.05$, $p > 0.01$) and with lunar luminosity ($\beta = –0.33\pm0.14$, $p = 0.02$). For culpeo foxes, we choose the simpler detection model including only horizontal cover for subsequent modelling because of near-equal support and the minimal effect on the likelihood of the top model which included horizontal cover and survey period. Culpeo fox detection probability (0.23±0.01) was intermediate between the species and increased with horizontal cover ($\beta = 0.07\pm0.03$, $p = 0.06$). Lastly, puma detection probability (0.13±0.01) was lowest and increased throughout the survey period ($\beta = 0.27\pm0.13$, $p = 0.03$; for single-species detection models see SM Table 1).

In our top single-species occupancy model, chilla foxes were the most widespread carnivore species (occupying 0.65±0.04 of the study area) and their predicted occupancy increased further from streams ($\beta = 0.51\pm0.23$). Pumas (0.43±06) were estimated to be more widespread than culpeo foxes (0.28±0.3; Figure 2A). Puma predicted occupancy decreased further from cliff habitat (β = –2.41±1.31) while culpeo fox predicted occupancy decreased further from lakes (β = –0.69±0.33; for the top single-species occupancy models SM Table 2 and SM Figure 2).

In our top multi-species occupancy model, chilla and culpeo foxes exhibited a constant relationship in space-use, while the co-occurrence of chilla foxes and pumas was highest closer to lakes (β = 1.94±1.05) and the co-occurrence of culpeos and pumas was lowest closer to lakes (β = –6.37±4.00; for the top multi-species occupancy models see SM Table 3). Compared to the single-species occupancy estimates, chilla fox predicted occupancy probability decreased by an average of 31% in the presence of culpeo foxes and in the absence of pumas (0.45±0.03). Meanwhile, in the presence of pumas and in the absence of culpeo foxes, chilla occupancy decreased by an average of 19% (0.52±0.06). As expected, in the absence of both potential competitors, chilla occupancy increased by an average of 16% (0.74±0.02; Figure 2B). Likewise, the occupancy probability of culpeo foxes, compared to the single-species occupancy estimates, decreased by an average of 43% (0.16±0.04) in the presence of pumas, and increased to by an average of 42% (0.40±0.03) in their absence (Figure 2C).

The probability of co-occurrence of culpeo foxes and pumas was lowest (0.05±0.02), followed by chilla foxes and culpeo foxes (0.15±0.03), and finally chilla foxes and pumas (0.22±0.06; Table 2). These results were also corroborated from the SIFs of each pairwise species comparison. The SIF of pumas and culpeo foxes was also the lowest (0.21±0.05), followed by culpeo and chilla foxes (0.73±0.03) and then pumas and chilla foxes (0.76±0.04; Table 2).

Foraging Behaviors and GUD

There was no difference between the GUD of chilla (7.0±2.0 g) and culpeo (8.0±3.0g) foxes (z = –0.37, p = 0.71). The consumption of food at the GUD stations by foxes of both species ranged from the entire consumption of food to foxes being present but only investigating the station. The proportion of time that chilla foxes were vigilant (0.18±0.02) was not significantly higher than that of culpeo foxes (0.12±0.04; z = 1.14, p = 0.26). Alternatively, culpeo foxes spent >2x more time exploring the area surrounding the foraging stations compared to chilla foxes (0.51±0.08 and 0.19±0.05, respectively; z = -2.72, p < 0.001, Figure 3A). Chilla foxes spent more time moving in the area surrounding the foraging station compared to culpeo foxes (0.14±0.05 and 0.05±0.02, respectively; z = 2.32, p = 0.02, Figure 3A). Interestingly, both species spent similar times foraging and searching within the foraging station (Figure 3A). There was no difference in the amount of time chilla and culpeo foxes spent searching for food (z = 1.18, p = 0.24) or consuming food (z = 1.47, p = 0.14; Figure 3A).

The GUD for both species of foxes was positively and strongly related to the amount of time foxes remained vigilant (Figure 3B), and the response of each species was similar (β_{Chilla} = 0.74[±0.22] and β_{Culpeo} = 0.89[±0.26]). For both foxes, the most best model of GUDs was the predicted occupancy of pumas (Figure 3C); similarly, the response of each species was similar (β_{Chilla} = 0.89±0.15 and β_{Culpeo} = 0.95±0.13). Interestingly, the predicted occupancy of pumas influenced the vigilance of both culpeo and chilla foxes, but it only influenced exploratory behavior in culpeo foxes (Figure 3 D and E). The predicted occupancy of culpeo foxes influenced the GUD of chilla foxes in the absence of pumas but not in their presence (GUD_{Chilla} = 0.73(□□Culpeo|Pumas Absent); SM Figure 3).

Perceived and Actual Risk

We combined the occupancy probabilities of pumas, culpeos, and chillas from our multi-species occupancy models with the spatial associations of pumas and the GUDs of meso- and small carnivores to determine how culpeo and chilla foxes responded to puma risk. We found that the perception of risk (i.e., the habitat features most closely associated with pumas) had a lesser effect on the space use of chilla foxes than that of culpeo foxes ($z = 15.98$, $p < 0.01$). Indeed, chilla fox occupancy decreased by 0.44±0.01 and culpeo fox occupancy decreased by 0.91±0.02 with increasing cliff habitat. Meanwhile, the effect of puma occupancy (actual risk) was higher for chilla foxes and lower for culpeo foxes ($z = –5.35$, $p < 0.01$); chilla fox space-use decreased by 0.83±0.01 and culpeo space-use decreased by 0.69±0.04 as puma occupancy increased. Together, this translated into a perceived risk coefficient for chilla foxes which was lower than that of culpeo foxes, 0.53±0.02 and 1.38±0.06, respectively ($z = 8.13$, $p < 0.01$; Figure 4).

Discussion

Our results indicate that the dominance hierarchy from pumas through culpeo foxes to chilla foxes was reflected in space. Although both meso- and small-carnivores responded similarly to the predicted space-use of apex carnivores, the indirect cues associated with risk led to a heightened spatial response for meso-carnivores, but not small-carnivores. This resulted in pumas altering the space-use of culpeo foxes to the benefit of chilla foxes. Our results suggest that the landscape of fear for meso-carnivores can create a ‘landscape of opportunity’ for subordinate, small carnivores. Our research aligns with meso-predator suppression found at continental scales (Newsome and Ripple, 2014) but highlights the underlying behavioral mechanisms that likely drive these relationships at local scales.

Behavior, especially in the context of risk avoidance, operates across multiple niche axes. Indeed, carnivores can modify their space use (Fedriani *et al.*, 2000; Berger and Gese, 2007), diel activity (Hayward and Slotow, 2009; Di Bitetti *et al.*, 2010), and resource use (Crooks and Van Vuren, 1995; Karanth and Sunquist, 1995; Bolnick *et al.*, 2003) in response to competition. Although temporal partitioning has been proposed as a mechanism promoting carnivore coexistence in southern South America (Johnson and Franklin, 1994b; Di Bitetti *et al.*, 2010), pumas, culpeos, and chilla foxes in our study area were strictly nocturnal and exhibited high diel overlap (Rodriguez Curras *et al., in Review*). Additionally, while culpeo and chilla foxes in our study system exhibit some resource partitioning, they both likely scavenged from puma kills (Rodriguez Curras *et al., in Review*). Space, then, appears to be the singular most important niche axis that these carnivores partition to avoid risk. However, we did not have the data to explicitly test the importance of spatio-temporal partitioning (Amarasekare, 2008; Vanak *et al.*, 2013). Future research should focus on the interaction between behavior and spatio-temporal partitioning, which can be an important mechanism for facilitating sympatry among carnivores (Ullas Karanth *et al.*, 2017).

The observed differences in habitat use between competing carnivores might be attributed to hunting strategies (Broekhuis *et al.*, 2013) or resource availability (Rosenheim, 2004). However, subordinate carnivores can minimize negative encounters by avoiding the habitat features associated with their predators (Heithaus, 2001; Schmitz, 2008), especially if the predators have a narrow habitat domain (Schmitz *et al.*, 2017). Although culpeo and chilla fox co-occurrence was mediated by open habitat, pumas strongly influenced the space-use of both species. Importantly, culpeo and chilla foxes mitigated risk as part of their habitat selection, and although both species avoided the habitat associated with pumas (i.e., cliffs), culpeo foxes more strongly avoided these areas. This fear of puma presence had a greater effect on culpeo fox space-use and was expected given the body size difference and degree of niche overlap between these species (Donadio and Buskirk, 2006; Rodriguez Curras *et al. in Review*). Ultimately, the stronger avoidance of pumas by culpeo foxes created a refuge for chilla foxes near cliff habitat; indeed, culpeo foxes had a greater effect on the space use of chilla foxes. This relationship, too, was predicted by the more similar body size, hunting strategy, and taxonomic relationship between culpeo and chilla foxes, which theoretically have a higher likelihood of competition and aggressive interactions (Donadio and Buskirk, 2006; de Oliveira and Pereira, 2014). These findings expand the previous literature on the cascading effects of a hierarchally structured community of carnivores in which risk aversion of meso-carnivores benefits the total space available for subordinate small carnivores.

Research on the non-consumptive effects of predation risk may incorrectly estimate risk effects by measuring only one risk-avoidance behavior (Geraldi and Macreadie, 2013). Indeed, subordinate carnivores in our study used multiple strategies to mitigate risk. Vigilance can be useful for perceiving direct cues of predation risk and escaping predation once targeted (Lima and Dill, 1990). Other strategies, such as olfactory cues (i.e., exploratory behavior) can be more influential in perceiving indirect cues of predation risk (Bytheway *et al.*, 2013; Leo *et al.*, 2015). Although both species were more vigilant at foraging stations associated with greater puma presence, culpeo foxes explored the staged foraging area roughly two-times more than chilla foxes. Furthermore, we detected a strong correlation between puma space-use and exploratory behaviors for culpeo foxes, but not chilla foxes. GUDs are the culmination of direct and indirect cues of risk because they capture predator avoidance strategies (i.e., vigilance and exploring) relative to resource acquisition (i.e., searching and eating; Brown *et al.*, 1999; Gaynor *et al.*, 2019). Although we found a strong relationship between vigilance and GUDs for both culpeo and chilla foxes, exploratory behavior only influenced the GUD of culpeo foxes. Interestingly, although we found no difference in the average GUD or the GUD response to predation risk between culpeo and chilla foxes, risk avoidance behaviors strongly mediated space-use but the underlying driver was different for each species.

Direct and indirect cues of predation risk are often subtle and difficult to detect by prey (Guiden *et al.*, 2019). Indirect cues like habitat type are particularly important if they offer an honest signal of space use, which is the case for species with a narrow habitat domain (Schmitz *et al.*, 2017). However, the coupling between perceived and actual risk can break down due to the large fitness cost of predation, leading to some species showing a tendency to perceive a higher probability of predation than is actually present, and to 'play it safe' (Abrams, 1994). For species avoiding predation or interspecific killing, perceived risk does not necessarily match the actual risk of predation. While accounting for the behavioral responses of meso- and small-carnivores to the actual (i.e., encounter probability) and perceived (i.e., risky habitat) risk of predation, meso-carnivores responded more strongly to the perception of risk and subordinate small carnivores responded more strongly to actual risk on the landscape. The higher perception of risk by meso-carnivores aligned with the higher proportion of time exploring, indicating that meso-carnivores used indirect cues of predation risk to assess their foraging decisions, and ultimately their space-use. Alternatively, small carnivores were more vigilant relative to the proportion of time they spent exploring, indicating they look for direct cues of predation risk to avoid potentially aggressive interactions.

The push-pull of suppression and facilitation has recently been highlighted as a key hypothesis of carnivore community structure (Sivy *et al.*, 2017; Prugh and Sivy, 2020). Behavior certainly mediates suppression and facilitation between mammalian carnivores because these interactions take place between cognitive species (Clinchy *et al.*, 2011). Using our described Perceived-Actual Risk framework, we found that meso-carnivores more strongly avoided the habitat features associated with apex carnivores (perceived risk), while small carnivores avoided conflict with apex carnivores by avoiding their actual space use (actual risk). The differences we observed in meso- and small carnivore strategies to avoid risk translated into community level effects that structured the space-use of the carnivore community, and can lead to the co-existence of competing carnivores. We believe that this analytical approach is applicable to other systems, including predator-prey, where dominant carnivores (or predators) have strong habitat associations and influence the space use of subordinate carnivores (or prey). The data needs include (1) risk avoidance behaviors (e.g., as GUDs, vigilance or feeding rates, flight initiation distances) that captures missed opportunity costs between risk and foraging; (2) space use of the dominant carnivore (or predator) and subordinate carnivore (or prey); and (3) site level habitat characteristics associated with the dominant carnivore (or predator). We encourage future research to combine behavioral and spatial utilizing this analytical framework across risk gradients to better understand the drivers of risk avoidance for species.

Patterns of species distributions or occurrence often lack the nuanced behavioral understanding needed to explain the mechanisms that drive space-use (Paine, 2010). Unifying the space-use of dominant species with the fear responses of subordinates is important for understanding how carnivore communities are structured. Overall, carnivores can be flexible in their risk avoidance strategies, reacting to direct cues of predation risk or avoiding the habitat associations of their competitors. Understanding the strategies that carnivores use to avoid aggressive interactions and gain access to resources can advance our understanding of carnivore community structure and better predict how these interactions will change in the future.

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Analyses reported in this article can be reproduced using the data provided by the authors (Rodriguez Curras *et al.*, 2021).

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Tables

Table 1. Ethogram of the behaviors that we quantified from fox videos.

Behavior	Definition
Vigilance	Head up above body level, ears pricked, sniffing/looking/listening, not doing anything else.
Exploration	Smelling the ground, shrubs, air, or anything outside of the staged foraging area.
Searching	Actively digging or sniffing within the staged foraging area.
Eating	Chewing, tearing, or otherwise consuming the bait.
Moving	Moving on all four legs (regardless of speed).
Other	Jumps backwards, startled. Dig around or near tray but not inside tray. Laying down or sitting, but not foraging or vigilant.

Table 2. Estimates (95% CI) of the probability of co-occurrence and the Species Interaction Factor (SIF) of each pairwise group of carnivores using the output of our top performing multi-species occupancy model.

Species Pair	P(Co-Occurrence)	SIF
Puma–Culpeo Fox	0.05 (0.02–0.08)	0.21 (0.11–0.30)
Puma–Chilla Fox	0.28 (0.15–0.41)	0.76 (0.68–0.84)
Culpeo Fox–Chilla Fox	0.14 (0.09–0.20)	0.73 (0.66–0.79)

Table 3. Top five GLM for chilla and culpeo foxes of standardized values, including the R^2, log-Likelihood (logLik), and the ΔAICc. For chilla foxes, the null model is included for reference.

Chilla GUD Functions	R^2	logLik	ΔAICc	AICwt
$\beta_{Puma} = 0.89\ (\pm 0.15)$	0.79	-6.61	0.00	0.69
$\beta_{Cliff} = 0.82(\pm 0.19)$	0.67	-8.98	4.75	0.06
$\beta_{Puma} = 0.84(\pm 0.19)$ + $\beta_{Stream} = -0.10(\pm 0.19)$	0.79	-6.43	4.87	0.06
$\beta_{Puma} = 0.89(\pm 0.16)$ + $\beta_{Lake} = 0.07(\pm 0.16)$	0.79	-6.49	4.99	0.06
$\beta_{Puma} = 0.89(\pm 0.20)$ + $\beta_{Culpeo} = 0.01(\pm 0.19)$	0.79	-6.61	5.24	0.05
…	…	…	…	
Average GUD = 7.09 (±1.86)	0.00	-15.08	13.02	0.00
…	…	…	…	

Culpeo GUD Formulas	R^2	logLik	ΔAICc	AICwt
$\beta_{Puma} = 0.95(\pm 0.13)$	0.91	-0.95	0.00	0.78
$\beta_{Cliff} = 0.93(\pm 0.17)$	0.86	-2.45	3.00	0.17
$\beta_{Cover} = 0.89(\pm 0.21)$	0.77	-4.23	6.56	0.03
Average GUD = 7.57 (±2.78)	0.00	-9.39	9.88	0.01
$\beta_{Land} = 0.70(\pm 0.31)$	0.49	-7.04	12.17	0.00
…	…	…	…	

Figures

Figure 1. (a) Map of our study area at Laguna Blanca National Park, Neuquen, Argentina, and the surrounding area including the locations of camera traps and giving-up density (GUD) stations. The insert shows our study site (black dot) in relation to Argentina (green). (b) An image of our simplified GUD stations, showing a camera trap pointing at the staged foraging area which blends with the surrounding area.

Figure 2. (a) The estimated occupancy probability (circles) of South American chilla foxes (Lycalopex griseus), culpeo foxes (Lycalopex culpaeus), and pumas (Puma concolor), based on the top performing single-species, single-season occupancy model of each species at Laguna Blanca National Park, Argentina, 2018. B and C. The conditional occupancy probability (circles) of South American chilla foxes (b) and culpeo foxes (c) given the presence or absence of their dominant interspecific competitors. The black bars around the circles represent the 95% confidence intervals of the estimated occupancy probability, the solid lines are the single species models, and the dashed lines are the 95% confidence intervals of the estimated occupancy probability of the single-species model.

Figure 3. (a) The average proportion (±SE) of time spent engaged in Exploration, Vigilance, Searching, Eating, and Moving behaviors for chilla (Lycalopex griseus) and culpeo foxes (Lycalopex culpaeus; see Table 1 for our detailed Ethogram). Bars with a star (*) represent a significant difference between species ($P \leq 0.05$). (b) The response of GUDs to the amount of time chilla (gray, r2 = 0.55, F1,9 = 10.88, $P < 0.01$) and culpeo foxes (red, r2 = 0.67, F1,5 = 10.2,

P = 0.02) remained vigilant, and (c) the response of GUDs to the expected occupancy of pumas (Ψ(Puma)) at each GUD station (chilla: r2 = 0.76, F1,9 = 33.02, P < 0.01 and culpeo: r2 = 0.89, F1,5 = 50.75, P < 0.01). (d) The response of Vigilance to the expected occupancy of pumas (Ψ(Puma)) at each GUD station (chilla: r2 = 0.50, F1,9 = 10.88, P < 0.01 and culpeo: r2 = 0.67, F1,5 = 10.20, P = 0.02). (e) The response of Exploring to the expected occupancy of pumas (Ψ(Puma)) at each GUD station (chilla: r2 = 0.08, F1,9 = 0.80, P = 0.39 and culpeo: r2 = 0.69, F1,5 = 11.29, P = 0.02).

Figure 4. The spatial responses to perceived (brown shading) versus actual (blue shading) risk model for chilla foxes (Lycalopex griseus; left) and culpeo foxes (L. culpaeus; right) using the effect of cliff habitat (i.e., because pumas [Puma concolor] were strongly associated with cliff habitat). The coefficients in the boxes show the values (±SE) of the shared covariance of the two variables linked by the arrows. “Perceived Risk” (brown shading) is the estimate (95% CI) of Equation 1 using cliff habitat, “Actual Risk” (blue shading) is the estimate (95% CI) of Equation 1 using (Puma), and the Perceived Risk Coefficient (PRC) is Perceived/Actual Risk (Equation 2).

Figure 1.

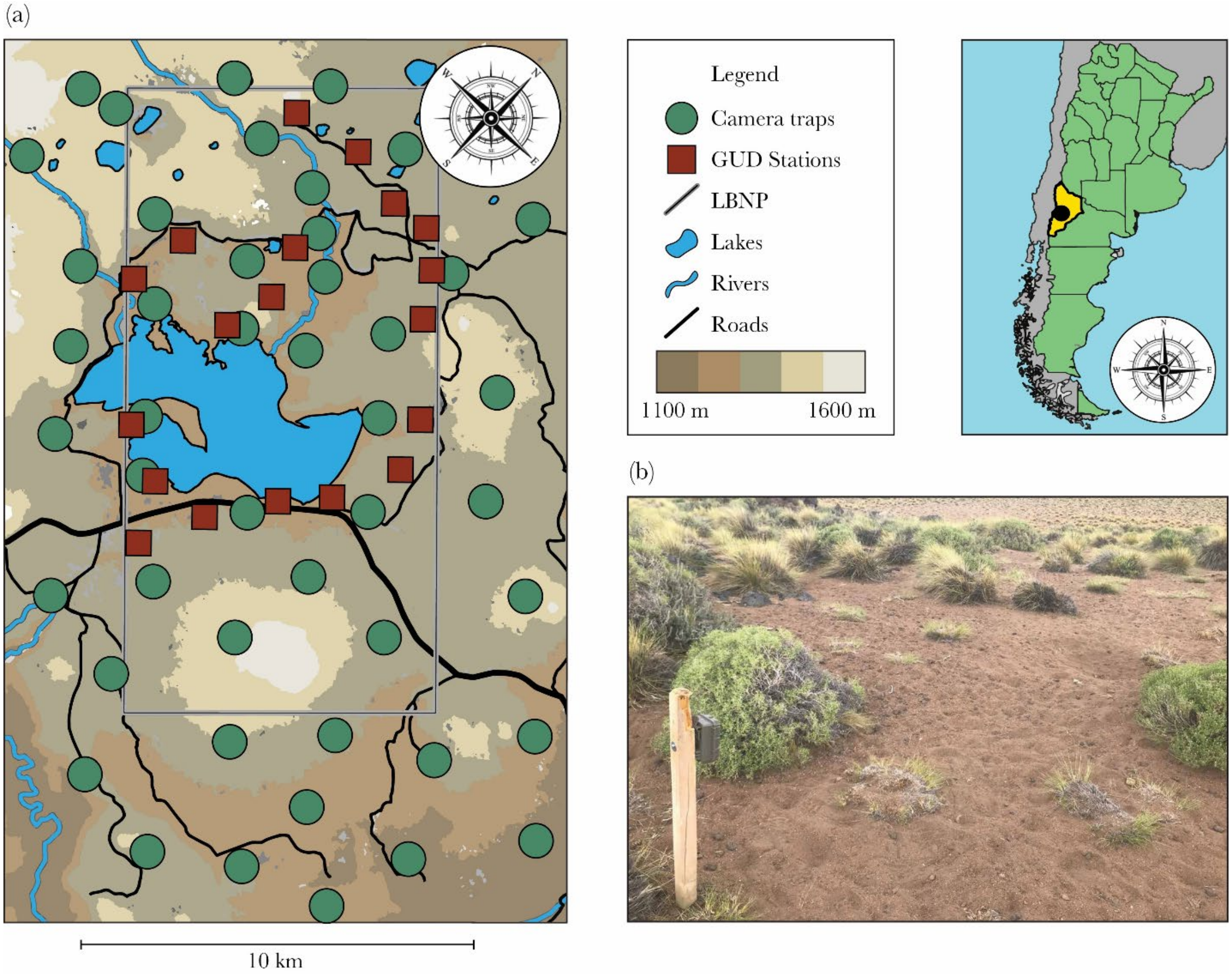

(a)
Legend
Camera traps
GUD Stations
LBNP
Lakes
Rivers
Roads
1100 m
1600 m
N
E
S
W
10 km
(b)

Figure 2.

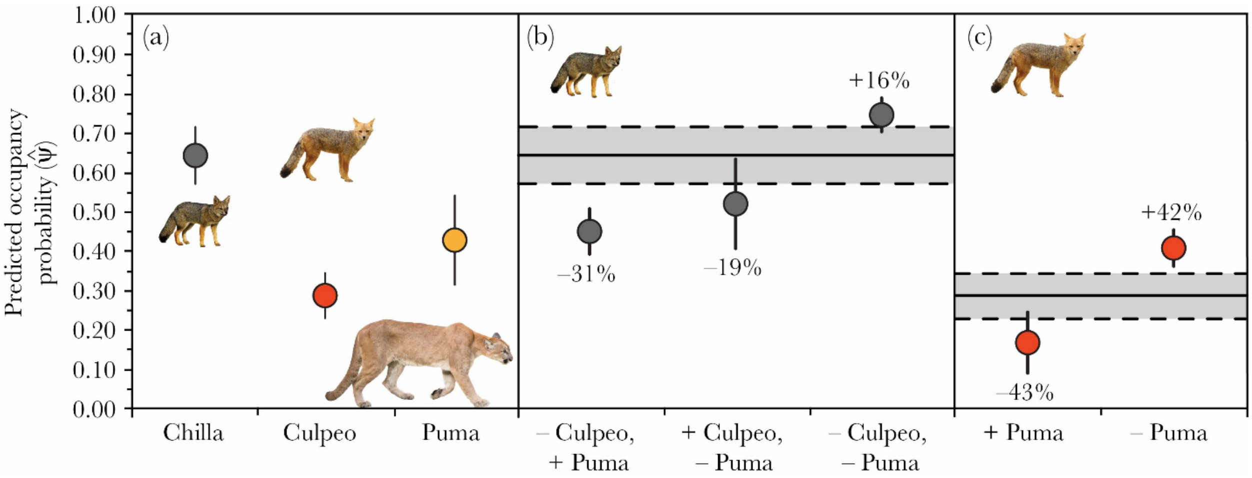

Predicted occupancy probability (ψ̂)
1.00
0.90
0.80
0.70
0.60
0.50
0.40
0.30
0.20
0.10
0.00
(a)
Chilla
Culpeo
Puma
(b)
+16%
–31%
–19%
– Culpeo, + Puma
+ Culpeo, – Puma
– Culpeo, – Puma
(c)
+42%
–43%
+ Puma
– Puma

Figure 3.

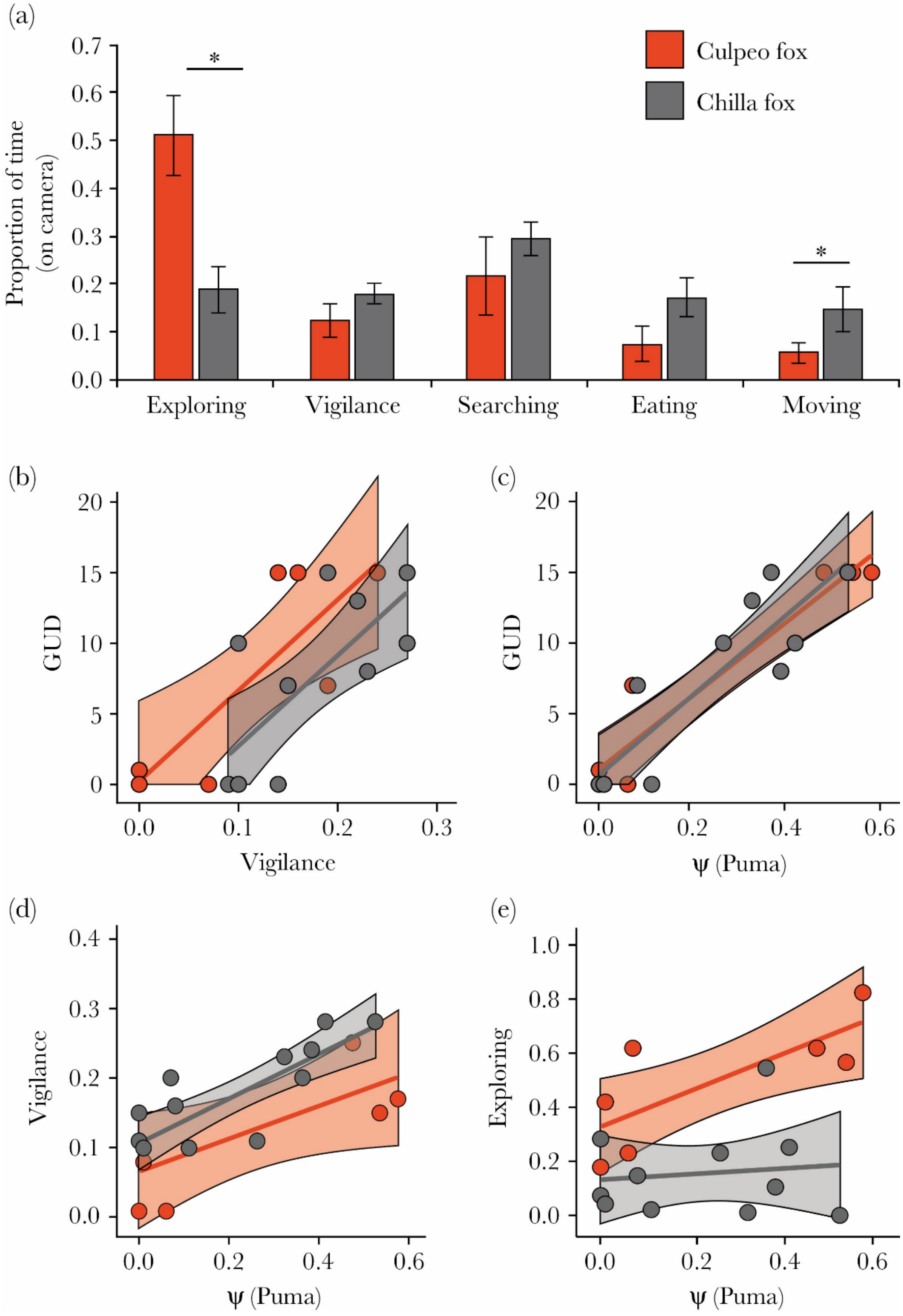
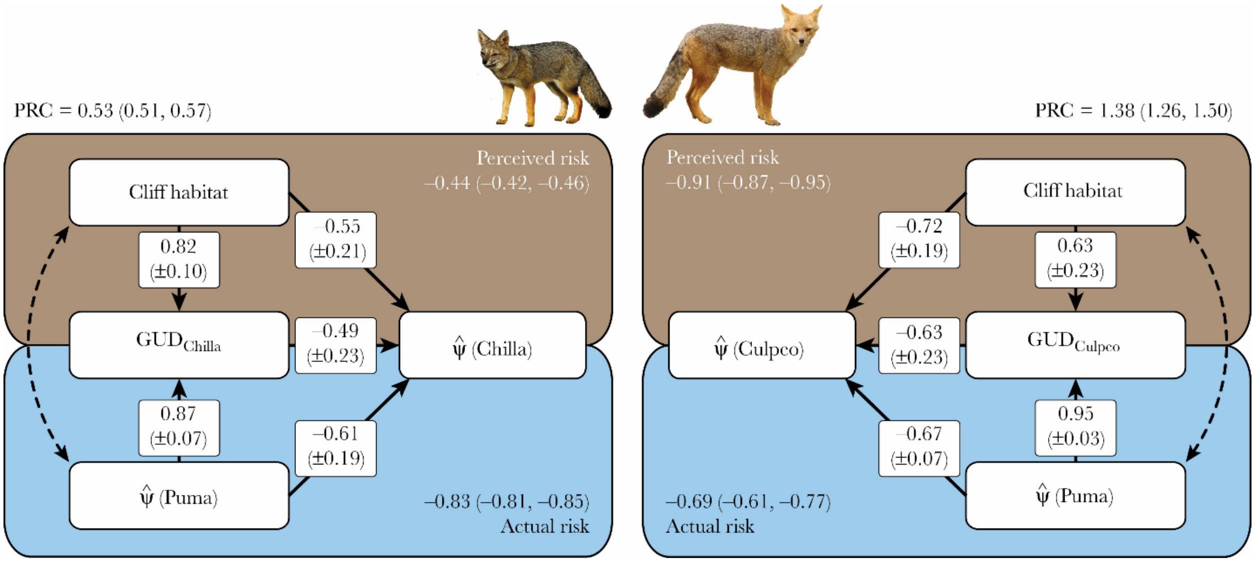

(a)
Culpeo fox
Chilla fox
Proportion of time (on camera)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
*
*
Exploring
Vigilance
Searching
Eating
Moving
(b)
GUD
0
5
10
15
20
0.0
0.1
0.2
0.3
Vigilance
(c)
GUD
0
5
10
15
20
0.0
0.2
0.4
0.6
ψ (Puma)
(d)
Vigilance
0.0
0.1
0.2
0.3
0.4
0.0
0.2
0.4
0.6
ψ (Puma)
(e)
Exploring
0.0
0.2
0.4
0.6
0.8
1.0
0.0
0.2
0.4
0.6
ψ (Puma)

Figure 4.


PRC = 0.53 (0.51, 0.57)
Perceived risk
–0.44 (–0.42, –0.46)
Cliff habitat
0.82
(±0.10)
–0.55
(±0.21)
GUD$_{Chilla}$
–0.49
(±0.23)
$\hat{\psi}$ (Chilla)
0.87
(±0.07)
–0.61
(±0.19)
$\hat{\psi}$ (Puma)
–0.83 (–0.81, –0.85)
Actual risk
PRC = 1.38 (1.26, 1.50)
Perceived risk
–0.91 (–0.87, –0.95)
Cliff habitat
–0.72
(±0.19)
0.63
(±0.23)
$\hat{\psi}$ (Culpeo)
–0.63
(±0.23)
GUD$_{Culpeo}$
0.95
(±0.03)
–0.67
(±0.07)
$\hat{\psi}$ (Puma)
–0.69 (–0.61, –0.77)
Actual risk

Supplementary Material: Perceived risk structures the space use of competing carnivores

Perceived-Actual Risk Framework

Understanding the behavioral drivers behind community assembly is critically important. Indeed, there is broad interest in testing how carnivores (Broekhuis *et al.*, 2013; Leo *et al.*, 2015; Dröge *et al.*, 2017; Prugh and Sivy, 2020; Davies *et al.*, 2021) and prey (Clinchy *et al.*, 2004; Schmitz *et al.*, 2017; Creel, 2018; and many others) respond to predation risk. Further, there is particular interest to how they perceive risk on the landscape and make tradeoffs between space and safety (Laundre *et al.*, 2010; Schmitz *et al.*, 2017; Gaynor *et al.*, 2019). Risk-avoidance behaviors operate across multiple niche axes; species can (1) avoid the times that their predators are active (Cozzi *et al.*, 2012) or (2) avoid the areas where their predators are present (either by avoiding the habitat features of their predators [Schmitz *et al.*, 1997; Preisser *et al.*, 2007] or selecting resources that do not overlap with the preferred prey of their predators [Broekhuis *et al.*, 2013; Swanson *et al.*, 2014]). These relationships have been previously described in the 'landscape of fear' framework – the spatial variation in the perception of predation risk (Gaynor *et al.*, 2019) – however, an analytical approach that parses out the importance of perceived and actual risk on the space use of a subordinate carnivore (*or a prey species*) has not been presented.

Predators with a narrow habitat domain (i.e., strongly associated with specific habitat features) use habitat which is expected to provide subordinate carnivores (*or prey*) an honest signal of their general space use which they can use to avoid predation (Schmitz *et al.*, 2017). Herein, we developed the Perceived-Actual Risk Management framework to explicitly parse out whether the perception of risky places ('perceived risk') or the space use of a predator ('actual risk') was more influential in determining the space use of subordinate carnivores. This framework can be applied to any sit-and-wait predators – from pumas to snakes, monkfish to spiders (see *Discussion*) – because of their strong associations with the physical landscape (Schmitz, 2008).

The perception of risk, risk of predation, and spatial responses of species often fail to map closely onto one another (Gaynor *et al.*, 2019). 'Perceived risk' is generally derived from risk-avoidance behaviors in association to physical characteristics of the landscape – using our data, the relationship between the habitat features associated with pumas and the vigilance/feeding rate/GUDs of culpeo or chilla foxes. Ultimately, we were interested in whether a habitat feature associated with a predator or the predicted space use of that predator was more important in determining the space use of subordinate carnivores (or prey). Indeed, our main interest was not just to make the association of the perception of risk with certain habitat features of predators, but the spatial outcome of that perception for subordinate carnivores. This could be done with a simple standardized regression framework taking the difference of the relationship between subordinate carnivore space use and the habitat feature associated with the predator over the relationship between subordinate carnivore space use and the predicted space use of the predator (i.e., using our data $\frac{\psi(Subordinate\ Carnivore)|Habitat\ Feature_{Predator}}{\psi(Subordinate\ Carnivore)|\psi(Predator)}$). However, because risk avoidance behaviors strongly influence the space use of subordinate carnivores (or prey), we expanded this simple formulation to account for how habitat features associated with predators and predator space use affect the behavior of the species and ultimately the space use (*Methods: Eqn. 1*). In our formulation of the Perceived-Actual Risk Management framework, we defined 'perceived risk' following general nomenclature – risk avoidance behaviors that reflect the perception of predation risk – but our main interest was the spatial outcome of a subordinate carnivore avoiding a habitat feature associated with their predator; particularly a habitat feature that is perceived by the subordinate species (or prey) to provide information about a predator's whereabouts, though it may not be fully accurate (Willems and Hill, 2009; Kauffman *et al.*, 2010; Gaynor *et al.*, 2019). Subsequently, we used the spatial response to 'actual risk' of predation as the outcome (in space) of a subordinate carnivore avoiding the space use of the predator. To compare the influence of perceived and actual risk, we used a partial regression statistical framework (see *Methods*) because this method accounts for the influence of mediating variables that affect the underlying process of interest (Grace, 2006) – in our case, the space that species give up for safety. We considered perceived risk as the influence of the habitat features associated with predators on the space use of subordinate species, while accounting for the behavioral responses of subordinate carnivores to those habitat features. Similarly, we considered actual risk as the influence of the space use of predators on the space use of subordinate species, while accounting for the behavioral responses of subordinates to the space use of their predator. In this way, our formulation of the spatial influence of perceived and actual risk account for the behavioral responses of species to the physical landscape (i.e., the relationship between the physical landscape and the predator avoidance behaviors) and the space use of the predator (i.e., the expected occupancy probabilities of the predator on the landscape) and derived the total effect on the space use of subordinate carnivore space use.

Because habitat features do not fully capture the space use of a predator (i.e., they can be only be used as a 'rule of thumb'; Lima and Dill, 1990) it is critically important, from a behavioral perspective, to understand what types of cues different species are using to shape their space use. If the space use of subordinate carnivore (or prey) is more strongly influenced by the perception of risk on the landscape, these species could be over-responding to habitat features and giving up space they could potentially occupy, which could have community level consequences. The discrepancy between the spatial associations to perceived and actual risk (*Perceived Risk Coefficient (PRC); Eqn. 2*) informs (1) the non-linear process between the perception of risk on the landscape and the actual risk of predation and (2) the importance of cues that subordinate carnivores (or prey) utilize to inform their space use in relation to predation risk.

Data Needs

Although our interest is the spatial relationships between predators and subordinate carnivores (or prey), risk avoidance behavioral data is the foundation of the Perceived-Actual Risk framework. These data could be collected from observation, giving-up density experiments, flight initiation distances, sequence of return, time in cover, or any other observational or experimental studies on the behavioral responses of species to predation risk. Additionally, the expected (or observed) space use of the predator and the species in question, and a measured habitat feature that is associated with the predator is necessary; these data can come from relocation data (GPS), camera traps, scat surveys along transects, visual observation, etc.

Supplementary Tables

SM Table 1. The top seven single-species detection models for pumas (*Puma concolor*), culpeo foxes (*Lycalopex culpaeus*), and chilla foxes (*Lycalopex griseus*), using ψ(·), fit for each species in Laguna Blanca National Park, Argentina during winter 2018. We fit models using a null model, survey period, low horizontal cover (LHC), snow cover, and moon phase and their additive combinations (total 15 models) for each species. The top performing detection model was carried forward for the rest of the modelling procedure (bold) except for culpeo foxes where the simpler model was chosen to be carried forward.

PUMAS (*PUMA CONCOLOR*)	**K**	**AIC**	**ΔAIC**	**AIC WT**	**BETAS**
$\boldsymbol{p(Survey), \psi(\cdot)}$	**3**	**66.61**	**0.00**	**0.23**	**-3.69+0.28(Survey)**
$\boldsymbol{p(Survey + Snow), \psi(\cdot)}$	**4**	67.18	0.57	0.18	-4.02+0.29(Survey)+0.83(Snow)
$\boldsymbol{p(Survey + LHC), \psi(\cdot)}$	4	67.87	1.26	0.12	-2.39+0.29(Survey)-0.03(LHC)
$\boldsymbol{p(Survey + Snow + LHC), \psi(\cdot)}$	5	68.49	1.88	0.09	-2.69+0.27(Survey)+0.81(Snow)-0.03(LHC)
$\boldsymbol{p(Survey + Moon), \psi(\cdot)}$	4	68.59	1.99	0.09	-3.61+0.28(Survey)-0.03(Moon)
$\boldsymbol{p(\cdot), \psi(\cdot)}$	2	69.77	3.16	0.05	-1.92

$\boldsymbol{p(Survey + LHC + Moon)}, \psi(\cdot)$	5	69.86	3.86	0.05	-2.24+0.29(Survey)-0.03(LHC)-0.04(Moon)
…	…	…	…	…	…
CULPEO FOX (*LYCALOPEX CULPAEUS*)	K	AIC	ΔAIC	AIC_{wt}	Betas
$\boldsymbol{p(Survey + LHC)}, \psi(\cdot)$	4	124.16	0.00	0.20	-3.60-0.12(Survey)+0.07(LHC)
$\boldsymbol{p(LHC)}, \boldsymbol{\psi(\cdot)}$	**3**	**124.26**	**0.11**	**0.19**	**-4.11+0.7(LHC)**
$\boldsymbol{p(Survey + Snow + LHC)}, \psi(\cdot)$	5	125.92	1.76	0.08	-3.70-0.12(Survey)+0.24(Snow)+0.07(LHC)
$\boldsymbol{p(Survey + Moon + LHC)}, \psi(\cdot)$	5	125.97	1.81	0.08	-3.36-0.12(Survey)-0.10(Moon)+0.07(LHC)
$\boldsymbol{p(Snow + LHC)}, \psi(\cdot)$	4	126.02	1.86	0.08	-4.20+0.24(Snow)+0.07(LHC)
$\boldsymbol{p(LHC + Moon)}, \psi(\cdot)$	4	126.42	2.00	0.08	-3.95+0.07(LHC)-0.07(Moon)
$\boldsymbol{p(\cdot)}, \psi(\cdot)$	2	126.50	2.27	0.06	-1.22
…	…	…	…	…	…

CHILLA FOX (LYCALOPEX GRISEUS)	K	AIC	ΔAIC	AIC$_{wt}$	Betas
$\boldsymbol{p(Survey + Moon)}, \psi(\cdot)$	**4**	**277.60**	**0.00**	**0.42**	**0.80-0.18(Survey)-0.33(Moon)**
$\boldsymbol{p(Survey + Moon + LHC)}, \psi(\cdot)$	5	279.06	1.46	0.20	0.13-0.18(Survey)-0.33(Moon)+0.01(LHC)
$\boldsymbol{p(Survey + Snow)}, \psi(\cdot)$	4	279.63	2.02	0.15	-0.23-0.17(Survey)+0.55(Snow)
$\boldsymbol{p(Survey)}, \psi(\cdot)$	3	280.80	3.19	0.09	-0.05-0.17(Survey)
$\boldsymbol{p(Survey + LHC + Snow)}, \psi(\cdot)$	5	281.07	3.47	0.07	-0.16-0.17(Survey)+0.56(Snow)
$\boldsymbol{p(Survey + Lhc + Snow)}, \psi(\cdot)$	4	282.26	4.66	0.04	-0.91-0.17(Survey)+0.01(LHC)+0.56(Snow)
$\boldsymbol{p(Survey + LHC)}, \psi(\cdot)$	4	286.58	8.97	0.01	-0.71-0.17(Survey)+0.01(LHC)
…	…	…	…	…	…
$\boldsymbol{p(\cdot)}, \psi(\cdot)$	5	289.21	11.61	0.01	-0.88
…	…	…	…	…	…

SM Table 2. Single-species occupancy models fit for pumas (*Puma concolor*), culpeo foxes (*Lycalopex culpaeus*), and chilla foxes (*Lycalopex griseus*) in Laguna Blanca National Park, Argentina during winter 2018. The top model (bold) was selected as the best fit, and the covariate was carried forward to create the multi-species occupancy model (see Methods).

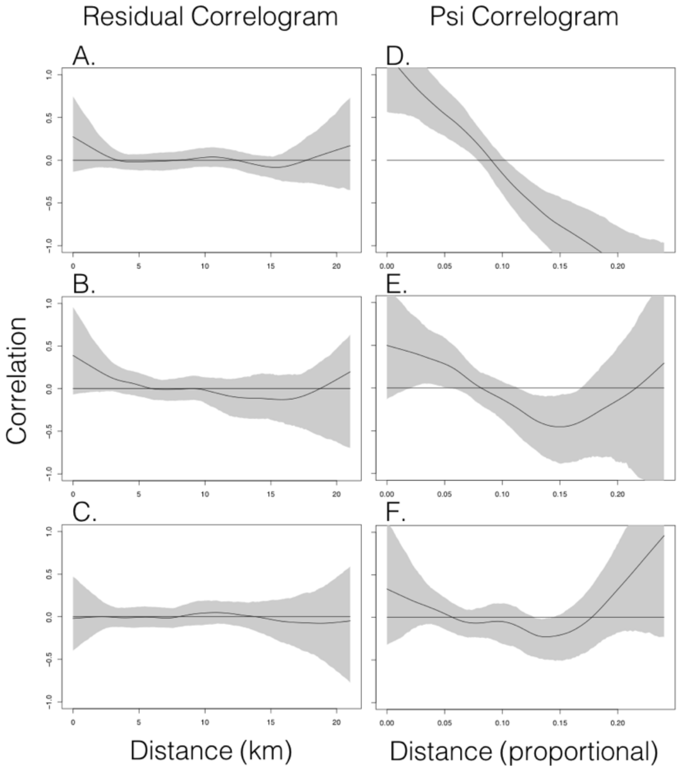
PUMAS (*PUMA CONCOLOR*)	**K**	**AIC$_C$**	**ΔAIC$_C$**	**AIC$_C$ WT**	**BETAS**
$\boldsymbol{p(Survey), \psi(Cliff)}$	**4**	**94.20**	**0.00**	**0.69**	**-2.12 + 2.41(Cliff)**
$\boldsymbol{p(Survey)}, \psi(\boldsymbol{Land})$	4	97.73	3.53	0.12	-8.66 + 0.23(Land)
$\boldsymbol{p(Survey)}, \psi(\boldsymbol{River})$	4	98.50	4.30	0.08	1.08 – 0.55(River)
$\boldsymbol{p(Survey)}, \psi(\boldsymbol{LHC})$	4	99.68	5.48	0.05	5.01 + 0.11(LHC)
$\boldsymbol{p(Survey)}, \psi(\cdot)$	3	99.69	5.49	0.04	-0.56
$\boldsymbol{p(Survey)}, \psi(\boldsymbol{Lake})$	4	101.14	6.94	0.02	0.94 – 0.31(Lake)
CULPEO FOX (*LYCALOPEX CULPAEUS*)	K	AIC$_C$	ΔAIC$_C$	AIC$_C$WT	Betas
$\boldsymbol{p(LHC)}, \psi(\boldsymbol{Lake})$	**4**	**169.05**	**0.00**	**0.52**	**0.36 – 0.69(Lake)**
$\boldsymbol{p(LHC), \psi(LHC)}$	4	170.36	1.31	0.27	5.8 – 0.14(LHC)
$\boldsymbol{p(LHC)}, \psi(\boldsymbol{River})$	4	172.37	3.32	0.10	0.05 – 0.33(River)
$\boldsymbol{p(LHC)}, \psi(\cdot)$	3	173.40	4.34	0.06	-0.81

$\boldsymbol{p(LHC)}, \psi(\boldsymbol{Cliff})$	4	174.85	5.80	0.03	-1.15 – 0.28(Cliff)
$\boldsymbol{p(LHC)}, \psi(\boldsymbol{Land})$	4	175.04	5.98	0.03	-2.46 + 0.05(Land)
CHILLA FOX (*LYCALOPEX GRISEUS*)	K	AIC$_C$	ΔAIC$_C$	AIC$_{CWT}$	Betas
$\boldsymbol{p(Survey + Moon)}, \psi(\boldsymbol{River})$	**5**	**324.62**	**0.00**	**0.41**	**-0.66 + 0.51(River)**
$\boldsymbol{p(Survey + Moon)}, \psi(\boldsymbol{Lake})$	5	325.13	0.51	0.32	-0.54 + 0.65(Lake)
$\boldsymbol{p(Survey + Moon)}, \psi(\boldsymbol{LHC})$	5	326.23	1.62	0.18	-4.65 + 0.12(LHC)
$\boldsymbol{p(Survey + Moon)}, \psi(\cdot)$	4	329.46	4.84	0.04	0.52
$\boldsymbol{p(Survey + Moon)}, \psi(\boldsymbol{Land})$	5	329.61	4.99	0.03	3.88 - 0.09(Land)
$\boldsymbol{p(Survey + Moon)}, \psi(\boldsymbol{Cliff})$	5	330.05	5.43	0.03	0.06 – 0.44(Cliff)

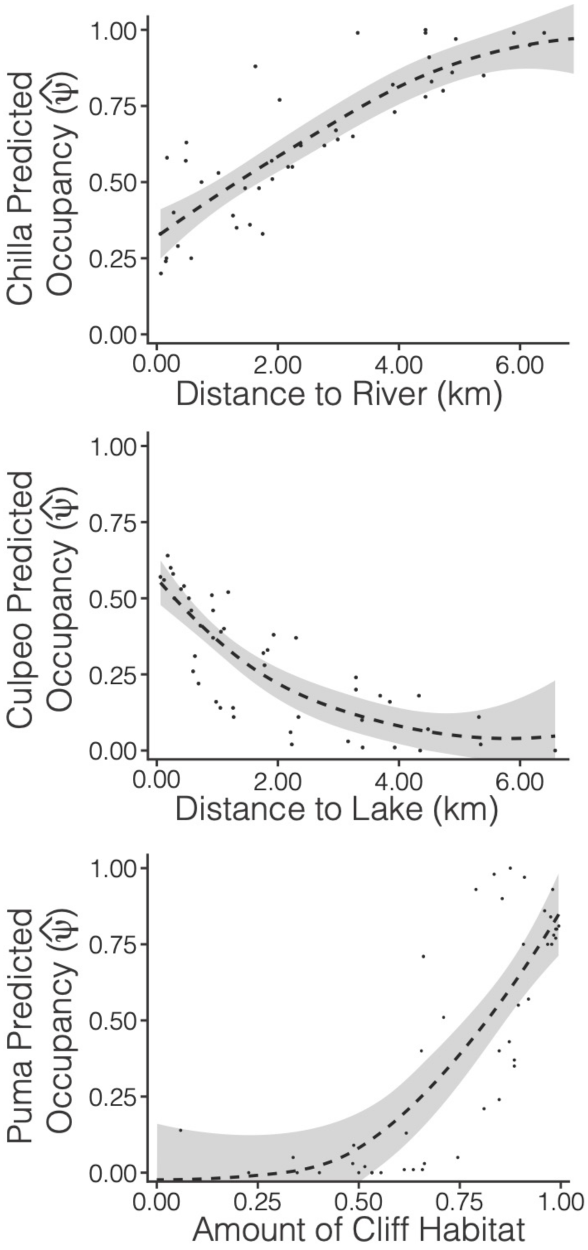
SM Table 3. Multi-Species Occupancy

Multi-Species Parameters and Betas (when applicable)	*K*	*AICc*	*DAICc*
[Chilla:Culpeo] + 1.94[Chilla:Puma](Lake) – 6.37[Culpeo:Puma](Lake) + [Chilla:Culpeo:Puma]	**19**	**586.82**	**0.00**
[Chilla:Culpeo] + 1.75[Chilla:Puma](Lake) – 6.42[Culpeo:Puma](Lake) – 2.03[Chilla:Culpeo:Puma](River)	20	587.19	0.37
0.90[Chilla:Culpeo](River) + 2.16[Chilla:Puma](River) + 6.82[Culpeo:Puma](Cliff) – 5.23[Chilla:Culpeo:Puma](River)	21	588.24	1.42
0.35[Chilla:Culpeo](Lake) + 1.96[Chilla:Puma](Lake) + [Culpeo:Puma] – 6.64[Chilla:Culpeo:Puma](Lake)	20	588.50	1.69
0.35[Chilla:Culpeo](Lake) + 1.96[Chilla:Puma](Lake) – 6.65[Culpeo:Puma](Lake) + [Chilla:Culpeo:Puma]	20	588.50	1.69
[Chilla:Culpeo] + 2.01[Chilla:Puma](Lake) + 0.89[Culpeo:Puma](Cliff) – 6.05[Chilla:Culpeo:Puma](Lake)	20	588.75	1.94
0.01[Chilla:Culpeo](River) + 1.94[Chilla:Puma](Lake) – 6.43[Culpeo:Puma](Lake) + [Chilla:Culpeo:Puma]	20	588.82	2.00
...	…	…	…
[Chilla:Culpeo] + [Chilla:Puma] + [Culpeo:Puma] + [Chilla:Culpeo:Puma]	17	591.15	4.33

Supplementary Figures

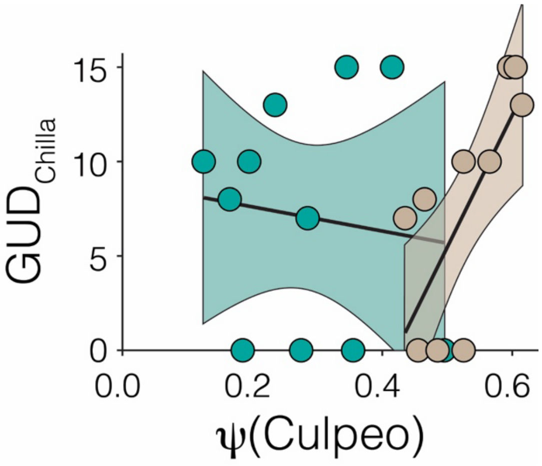


SM Figure 1A and 1B. Correlograms of the residuals (A) and the occupancy probabilities (B) from the single-species occupancy model across the distances between camera traps for chilla foxes (*Lycalopex griseus;* A and D), culpeo foxes (*Lycalopex culpaeus;* B and E), and pumas (*Puma concolor;* C and F) in Laguna Blanca National Park, Argentina during winter 2018.



SM Figure 2. Occupancy probability of pumas chilla foxes (*Lycalopex griseus*; A), culpeos (*Lycalopex culpaeus*; B), and (*Puma concolor*; C) by each species' most supported single-species model covariate (see Methods) in Laguna Blanca National Park, Argentina during winter

2018. For interpretability, we fit a loess function for each relationship (black dotted line) with the corresponding 95% confidence interval (grey cloud).



SM Figure 3. The response of the giving up density of chilla foxes (GUD_{Chilla}) to the expected occupancy of culpeo foxes ($\hat{\psi}$(Culpeo)) given the presence (green) and absence (brown) of pumas at each GUD station chillas were observed (GUD_{Chilla} ~ Culpeo|Puma Present: $r^2 = 0.01$, $F_{1,9} = 0.13$, $p = 0.73$ and GUD_{Chilla} ~ Culpeo|Puma Absent: $r^2 = 0.53$, $F_{1,5} = 10.01$, $p = 0.01$).

The pulsed effects of reintroducing wolves on the carnivore community of Isle Royale

***Running Title*:** Carnivore community interactions on Isle Royale

***Authors and Affiliations*:**

Mauriel Rodriguez Curras[1]*, Mark C. Romanski[2], and Jonathan N. Pauli[1]

[1]University of Wisconsin-Madison, Department of Forest & Wildlife Ecology, Madison, WI, USA.

[2]National Park Service, Isle Royale National Park, Houghton, Michigan, USA.

*Corresponding Author: Mauriel Rodriguez Curras; mrodriguezcu@wisc.edu

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Abstract

Large carnivores are globally reintroduced with the goal of restoring ecological interactions. However, the extent that competitive interactions within communities are restored is often unclear. In a before-after study, we quantified the spatial, behavioral, trophic, and demographic effects that a large carnivore (wolves; *Canis lupus*) reintroduction to Isle Royale National Park had on meso- (foxes; *Vulpes vulpes*) and small carnivores (martens; *Martes americana*). The reintroduction produced a phase-dependent pulse perturbation; wolves constrained the distribution of foxes benefiting martens, yet foxes altered their behavior, notably using human campsites and food more frequently, which buffered demographic consequences. Once wolf packs coalesced, all observed changes subsided, and competitive interactions returned to their pre-wolf values. Our results show that some predicted – and often desired – consequences of large carnivore reintroductions may not be permanent due to the transitory dynamics of social carnivores and the presence of humans, even within a "pristine wilderness".

Introduction

The "extinction of ecological interactions" (Janzen 1974) – exemplified by the widespread functional extirpation of the world's largest terrestrial carnivores (Ripple *et al.* 2014) – is a primary concern for conservation (Valiente-Banuet *et al.* 2015). Due to the disproportionate effects that carnivores have on community- to ecosystem-level processes (Ritchie *et al.* 2012), restoring the functional role of carnivores has been classified as a priority for conservation efforts (Pettorelli *et al.* 2019). Nevertheless, there is considerable debate on whether carnivore reintroductions restore these functional roles (Pauli *et al.* 2018). Much of this dispute is due to the limited experimental evidence on the ecological interactions that large carnivores restore in practice (Pettorelli *et al.* 2019), hindering our ability to predict the efficacy of large carnivore reintroductions to restore the community interactions and ecosystem function that we seek. Reintroductions, then, can serve as valuable quasi-experiments to quantify the impacts of carnivore recovery to communities and ecosystems.

Traditionally, large carnivore reintroductions have been studied in reference to their top-down effects to primary producers (i.e., predator-prey relationships and cascading consequences; Estes *et al.*, 2011). Critically, however, large carnivores structure carnivore communities via a dynamic interplay of interactions ranging from suppression (via competitive exclusion) to facilitation (via resource subsidies; Prugh and Sivy, 2020). Accordingly, reintroductions provide an opportunity to study how large carnivores alter competitive interactions within the carnivore guild (Smith *et al.* 2003) and, further, quantify the stability of competitive interactions. Although large-carnivore impacts are context dependent (Haswell *et al.* 2017), it is unclear whether large carnivore reintroductions represent a short-term disturbance (a pulse perturbation) or long-term forcing (a press perturbation) for competitive interactions, and what this means for community resilience. Indeed, reintroductions (or natural colonization) should feature ecologically relevant phases of restoration: the initial reintroduction of naïve individuals that are adjusting to novel surroundings, establishing social dynamics, and exhibiting transient interactions, which will eventually lead to a functional reintegration featuring more permanent interactions. While these phases of species reintroductions likely have very different implications for restoring community structure and population dynamics (Pringle *et al.* 2019), they have largely been overlooked.

Isle Royale National Park (Michigan; Figure 1A and B) is an isolated, wilderness archipelago in the western reaches of Lake Superior, USA and home to the longest predator-prey (gray wolf [*Canis lupus*]-moose [*Alces alces*]) study on record (Mech *et al.* 2017). The wolf population historically fluctuated but went functionally extinct in the last decade (between 2015–2018) with only two highly-related (more related than full siblings), and inbred (exhibited morphological abnormalities) individuals that could not reproduce or effectively regulate moose abundance (Hedrick *et al.* 2019), culminating in the reintroduction of nineteen wolves from October 2018–2019 (Figure 1C). Despite the long-standing research legacy on Isle Royale (Mech *et al.* 2017), little is known about the other terrestrial carnivores that inhabit the island: namely, red foxes (*Vulpes vulpes*) and American marten (*Martes americana*). While the carnivore community in Isle Royale is relatively simple (especially compared to those on the mainland of North America, Africa, or Asia), these three carnivores capture the three major ranks within the carnivore guild – large, apex carnivores (wolves), meso-carnivores (foxes), and small carnivores (martens; Prugh and Sivy, 2020). These ranks are particularly relevant to carnivore competitive interactions given the body-size mediated, hierarchical nature of carnivore communities (Donadio and Buskirk 2006). Additionally, Isle Royale is relatively well studied and the simplicity of this system lends itself to disentangle the direct and potentially mediating effects within the carnivore community.

Accordingly, the wolf reintroduction to Isle Royale presented a unique opportunity to quantify the effects of reintroducing a large, social carnivore in a before-after quasi-experimental framework while testing how a perturbation of this magnitude affects community interactions across the ecologically relevant phases of species reintroductions.

To explore the effect of the wolf reintroduction on carnivore community interactions, we non-invasively collected carnivore scats for genotyping and hair for stable isotope analysis to quantify the spatial, behavioral, trophic, and demographic consequences across three ecologically relevant phases of large carnivore reintroductions: when (a) wolves were functionally absent (Absent; 2018), (b) wolves were first reintroduced, but their social dynamics and functional return was not established (Establishment; 2019), and (c) wolf packs coalesced and functionally returned (Coalescent; 2020; Figure 1; WebPanel 1). We hypothesized that through suppression and facilitation, the apex carnivore would mediate the competitive interactions within the subordinate carnivore community, though these effects would be contingent on the phase of the reintroduction, representing a pulse perturbation to community interactions. Specifically, we predicted that the effects from the wolf reintroduction would manifest spatially and behaviorally driven by changes in trophic interactions with demographic consequences for meso- and small carnivores. We further predicted that the strongest effects from wolves to the carnivore community would be during the establishment phase and that these interactions would then weaken, supporting the phase-dependent pulse perturbation hypothesis.

Methods

For complete details on our Methods, including packages used, procedures, and model description and reporting see *WebPanel 1*. All samples were collected under approved institutional protocols (UW-Madison: A006483-A01, NPS: NPS-A006483-A01).
Briefly, we collected fox and marten scat during late-Summer/Autumn along the major trail system on the western-end of Isle Royale National Park from 2018–2020 (Figure 1A) corresponding to the area where martens have been historically detected. Beginning in late-August, each trail was hiked out-and-back a total of seven surveys, every four days. Once encountered, scats were swabbed for genetic material (i.e., for species and individual identification), georeferenced, and frozen within eight hours. Scat samples were processed in a quality-controlled pre-PCR clean-room at UW-Madison. We extracted DNA and used species-specific quantitative polymerase chain reaction (qPCR) assay for foxes and marten to verify species identify and to generate individual capture histories following Lacin Alas *et al.,* (*in Review*; WebPanel 1). To identify the potential impacts of human use, we included campsite reservations by visitors in our spatial analysis and tested for the impact of human foods in our dietary analysis.

We lacked sufficient data to conduct a dynamic multi-species occupancy model, so we used three complimentary lines of evidence to evaluate the space use and behaviors of meso- and small carnivores in response to wolves in a Bayesian framework. First, we used single-season (single-species) occupancy modeling to analyze the yearly pattern of fox and marten spatial distribution. We modeled detection and occupancy using a typical model selection approach for occupancy modeling (MacKenzie *et al.* 2006) that included survey-specific (precipitation, human use, moon phase) and site-specific (habitat heterogeneity, percent mixed forest, distance to campsites, percent forest edge, and percent pine forest) characteristics. We then used the site-specific occupancy and survey-specific detection estimates from our occupancy models in a Bayesian structural equation model (BSEM) to analyze the effects that wolves, human activity, and habitat heterogeneity had on the broad space use and specific patterns of detection of red foxes and martens. Due to limited fine-scale wolf relocation data in 2020, we modeled space use across the entire study period, but limited our behavioral analysis to 2018–2019, capturing the establishment phase of the wolf reintroduction only. We included wolf presence/absence as a covariate to capture the effects of the wolf reintroduction. Finally, to capture the spatial drivers of year-to-year colonization and extinction dynamics, we built-up dynamic single-species occupancy models for each species (Morin *et al.* 2020). For each step (detection, initial occupancy, and extinction/colonization), we tested the same site-specific and survey-specific covariates for red foxes and martens. We ran all models N = 10,000 iterations, with a burn-in of N = 2500, assessed model fit and convergence with R-hat < 1.10 and visually inspected the model diagnostics and trace plots. We used posterior predictive checks to ensure that models reasonably approximated mean values from the data and all residual errors were zero centered and normal. We identified the top model using the Deviance Information Criterion (DIC) and identified informative covariates based on the percent overlap with zero.

From collected hair samples, we analyzed stable isotopes and quantified dietary niche overlap (using standard ellipse areas [SEAc]) and the dietary specialization (ε) and similarity (s) before and after the wolf reintroduction (Newsome *et al.* 2012). Briefly, we estimated carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) bulk isotopic signatures from hair samples from wolves ($N_{2019} = 9$), red foxes ($N_{2018} = 9$; $N_{2019\text{-}2020} = 12$), and martens ($N_{2018} = 5$; $N_{2019\text{-}2020} = 4$) and estimated niche overlap with standard ellipses corrected for small sample size (SEAc). We used a Bayesian stable isotope mixing model to calculate posterior probability densities of the proportional contributions of prey to each species before and after the wolf reintroduction, using uninformative priors.

Lastly, to assess the direct effects on foxes and martens (i.e., changes in population size), we used a robust design, Pradel-seniority closed population model from the capture histories of each genetically-identified individual. We used individual capture histories (from genotypes) across the seven survey periods to estimate the conditional capture ($\hat{p}$) and recapture ($\hat{c}$) probabilities. We estimated apparent survival ($\hat{S}$) and the population growth rate (λ) between primary periods (years); we derived abundance (N) from the real parameters in our final models and ranked competing models using Akaike's Information Criterion (AIC).

Results and Discussion

We identified 599 fox ($N_{2018} = 220$, $N_{2019} = 161$, and $N_{2020} = 218$) and 64 marten ($N_{2018} = 21$, $N_{2019} = 30$, and $N_{2020} = 13$) scats from 63 individual foxes and 20 individual martens. Genotyping error rate per locus was relatively low, ranging from 1.0% to 7.0% across PCR triplicates for both foxes and martens.

Before the wolf reintroduction, foxes were the most widespread carnivore on Isle Royale – being distributed across most of our study area (Figure 2A) – whereas martens were spatially constrained (Figure 2B) and strongly associated with forest heterogeneity (WebPanel 1). The return of wolves precipitated an immediate decline in fox space use (Figure 2A, C) and detectability (WebPanel 1) while marten space use slightly increased (Figure 2A, B). After wolf packs coalesced, foxes were again distributed across the entire study area (Figure 2B) while the marten distribution decreased (Figure 2A, B), persisting in patches of high forest heterogeneity

(WebPanel 1). Consequently, marten space use was negatively influenced by foxes while detectability also decreased during surveys when foxes were observed (Figure 2). Although wolves can negatively influence marten abundance and space use (Sivy *et al.* 2017), we found that wolves exerted a net positive effect on marten space use (Figure 2C) and detectability (WebPanel 1). These interactions reinforce that the benefit small carnivores receive from decreased conflict with meso-carnivores outweigh the nominal risk from large carnivores (Donadio and Buskirk 2006; Levi and Wilmers 2012).

Human presence mediated the space use and behavior of the carnivore community on Isle Royale, the least visited National Park in the United States. Notably, fox space use was positively influenced by human activity and were more likely to be detected in higher human-visited areas (Figure 2C). Marten space use was negatively, though weakly, affected by human activity and they were more likely to colonize areas further from human campgrounds (WebPanel 1). Our analysis of trophic strategies suggests that following the wolf reintroduction, foxes had two distinct trophic strategies, they either became dissimilar generalists ($s_{\mathrm{Post}}^{1} = 0.20 \pm 0.11$ and $\varepsilon_{\mathrm{Post}}^{1} = 0.27 \pm 0.12$) consuming all diet items available (and particularly higher proportions of moose) or highly similar specialists ($s_{\mathrm{Post}}^{2} = 0.89 \pm 0.09$; $\varepsilon_{\mathrm{Post}}^{2} = 0.68 \pm 0.13$) consuming primarily human foods (Figure 3C, D). Ungulate carrion serves a dual role within carnivore communities, providing a resource subsidy that has a high caloric reward but also carries with it greater risks of agonistic interactions with dominant competitors (Sivy *et al.* 2017; Ruprecht *et al.* 2021). It appears, then, that foxes employed two strategies in the return of wolves, they either avoided conflict altogether by consuming an alternate trophic pathway (e.g., human foods) or benefited from carrion subsidies in the face of greater risk. Martens, on the other hand, did not change their foraging strategies and were classified as somewhat similar generalists ($s_{\text{Post}} = 0.50 \pm 0.20$ and $\varepsilon_{\text{Post}} = 0.29 \pm 0.12$), as they were before the wolf reintroduction, primarily consuming small prey (Figure 3E, F). Although our sample sizes are somewhat limited, we believe that we minimally sampled 25% of the functional population of foxes and martens before and after the wolf reintroduction.

Although the spatial and behavioral interactions within the carnivore guild were dynamic throughout the wolf reintroduction phases, we only detected a demographic consequence to martens. Specifically, red fox abundance and, importantly, their population growth rate did not vary throughout our study period (WebFigure 1A). On one hand, this is surprising given that wolves have been documented killing foxes (David Mech 1966); shortly following the reintroduction, carcasses of foxes killed by wolves were discovered near their den. On the other hand, a long-term weak, but positive relationship between wolf and fox abundance has been observed on the island ($\beta_{(\mu \pm \text{SE})} = 0.49 \pm 0.24$; $p = 0.05$; $R^2_{\text{Adj.}} = 0.06$; see *WebPanel* 1) and foxes are frequently observed scavenging from wolf-killed moose, suggesting slight density-mediated interactions. During wolf establishment, conflict with wolves likely increased due to increased encounter rates with naïve foxes, particularly at carcasses or as wolves were establishing packs, dens, and rendezvous sites. During the coalescent phase, however, this conflict decreased as pack territories were established and intraspecific aggression within wolves likely decreased. Foxes may have been able to offset any potential demographic consequences by employing alternative behavioral strategies to cope with the initial conflict (Figures 1 and 2). Interestingly, the spatial and behavioral responses that we observed in foxes appeared to benefit the marten population during the establishment phase ($\hat{S} = 0.81 \pm 0.22$, $\lambda = 1.35 \pm 0.40$; WebFigure 1B) and to their detriment during pack coalescence ($\hat{S} = 0.27 \pm 0.15$, $\lambda = 0.37 \pm 0.16$; WebFigure 1B), indicative of strong suppression by foxes. Martens directly compete with foxes for resources, and they are within the optimal range of interspecific conflict with the dominant red fox, furthermore, suppression of martens has been observed globally (Lindström *et al.*, 1995; *see* Prugh and Sivy, 2020).

Our observed spatial and behavioral effects from wolves and humans to red foxes – which were of similar magnitude and opposite direction – indicates that human activities may buffer interspecific conflict for meso-carnivores to the disadvantage of small carnivores, like martens. Broadly, our results suggest that human resources and space use can have a strong role in shaping carnivore community interactions, not only through changing the behavior of large carnivores (*sensu* Smith *et al.*, 2017), but by also altering the risk-reward landscape for meso- and small carnivores. Non-consumptive human recreation can alter the ecological role of large carnivores thus mediating the strength of interactions with subordinate species (Suraci *et al.* 2019). In Isle Royale, wolves were not avoiding human space use during our study, though foxes were associated with human campgrounds and some individuals specialized on human foods (consuming up to 80% human foods), suggesting the positive effect from humans to foxes was not a traditional spatial shield (*sensu* Berger, 2007). Instead, humans likely shielded foxes from interspecific aggression with wolves by providing a consequence-free, alternative resource to scavenging wolf kills. Such a resource shield could help explain the co-occurrence of competing carnivores in human landscapes. Furthermore, humans could serve to restructure carnivore community interactions by increasing the resilience of meso-carnivores to pulsed dynamics, including strong suppression from large carnivores or low prey densities. Our results reinforce that re-establishing ecological interactions (i.e., scavenging and predation risk) via apex carnivore conservation restructures carnivore communities (Prugh and Sivy 2020), however, humans can mediate, or even weaken, their efficacy by having strong opposing quiet, non-consumptive effects – particularly during the establishment of the returning carnivore.

Resistant systems exhibit a quick return towards equilibrium (Ives *et al.* 2003). Our observations, though temporally limited, suggest that the competitive interactions within the carnivore guild on Isle Royale are relatively resistant. Further and longer-term research is warranted to identify whether these effects of wolf reintroduction are, indeed, transient. Nevertheless, the rapid return of meso- and small carnivore interactions to their pre-wolf values was likely driven by the relative simplicity of the carnivore community on Isle Royale, the strong difference in niche characteristics of wolves and the subordinate carnivores, and the role of human subsidies. Our observation that the wolf reintroduction presented an initial perturbance that subsequently diminished is likely representative of large carnivore reintroductions broadly. Indeed, previous researchers have similarly observed strong and immediate effect of carnivore reintroductions both vertically, on prey and lower trophic levels (e.g., Ripple and Beschta, 2012), and horizontally, on other competing carnivores (e.g., Smith *et al.*, 2003; Swanson *et al.*, 2014). Our before after assessment of the wolf reintroduction to Isle Royale helps to define a conceptual framework for the phase dependent and community-wide effects of carnivore restoration broadly. Specifically, we predict the relative importance of suppression will be higher during the establishment phase of large carnivores, resulting in an initial pulse perturbation within carnivore guilds – that is, during the establishment phase, dominant meso-carnivores will be suppressed due to increased aggression from large carnivores as social dynamics are established, to the benefit of small carnivores. Shortly thereafter, suppression will relax during the coalescent phase – where the importance of resource partitioning will increase – and a dynamic interplay of suppression and facilitation will follow. Indeed, a pulsed response immediately following large carnivore reintroductions is not surprising given that carnivore communities are characteristically structured by interference competition (Donadio and Buskirk 2006), which we predict will be higher during establishment.

In less insular communities – for example, those in continental North America – we would nevertheless expect an initial, albeit likely more diffuse, community-wide pulsed effect. Given the greater taxonomic richness and higher overlap in body size – and consequent higher niche overlap – in mainland carnivore communities, large carnivore reintroductions will likely result in a more locally diffuse dynamic equilibrium of suppression and facilitation (Sivy *et al.* 2017; Ruprecht *et al.* 2021), resulting in a broader net facilitation to small carnivores (Levi and Wilmers 2012). Finally, given the extensive land cover change and human presence on the mainland, we predict a greater impact from humans on carnivore communities (Manlick and Pauli 2020), altering competitive dynamics by suppressing large carnivores and altering resource utilization across multiple niche axes (Rodriguez Curras *et al.* 2022). Unlike our study, the reintroduction of Iberian lynx (*Lynx pardinus*) to Spain, reduced meso- (red fox) and small (Egyptian mongoose *Herpestes ichneumon*) carnivore abundances, although this suppression was sustained (Jiménez *et al.* 2019). Iberian lynx directly suppressed the two subordinate meso-carnivores via interference competition, but also competed with both species for shared prey (Jiménez *et al.* 2019), which is not typical of large carnivores who typically specialize on large, ungulate prey. Indeed, combined negative (e.g., interference competition) and, importantly, positive (e.g., resource subsidies) effects from large carnivores result in more reticulate and complex food webs (Wilson and Wolkovich 2011), leading to dynamic, though resilient, suppression and facilitation (Prugh and Sivy 2020).

Conclusions

Conserving and restoring ecological interactions in the Anthropocene presents many challenges, and large carnivore reintroductions are a popular management tool to achieve conservation goals (Pettorelli *et al.* 2019). Our results suggest that researchers and managers should be prepared for phase-dependent and transient effects when attempting to restore community- and ecosystem-level functionality via species reintroductions. Furthermore, the return of large carnivores is occurring in novel, human landscapes and therefore may fail to restore the functional roles we desire. Accordingly, protected areas are increasingly important for reintroduction efforts. Terrestrial protected areas, however, receive 8 billion visitors every year, while National Parks in the United States see more than 280 million visitors annually (Sarmento and Berger 2017). Interestingly, we found that humans – even in the least visited National Parks – can counterbalance the effects of large carnivores and shape community interactions. Balancing the maintenance of ecological processes while providing a quality experience for park visitors (Beissinger *et al.* 2017) will also require the consideration of quiet, non-consumptive human effects, particularly for the recovery of large carnivore.

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Figures

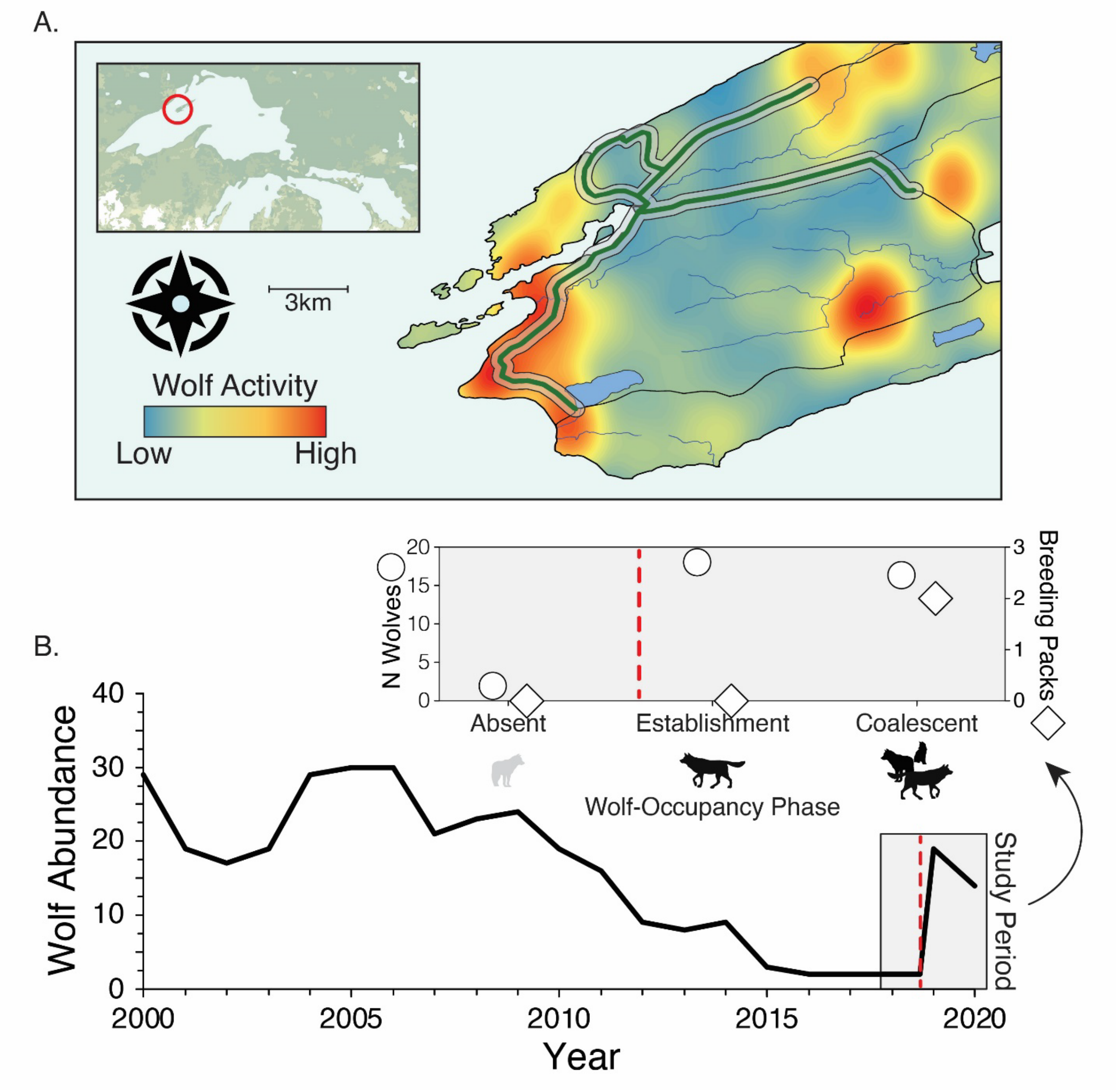
Figure 1. Trails sampled in the western-end of Isle Royale National Park, Michigan, U.S. (buffered green line) for foxes (*Vulpes vulpes*) and American martens (*Martes americana*) within wolf-activity following their reintroduction (A). Wolves on Isle Royale began declining in 2010 and 19 wolves were reintroduced in September 2018 (B). Our study captures three time periods of wolf history (insert): when wolves were functionally absent (Absent; 2018), during wolf establishment (Establishment; 2019), and when wolf packs coalesced (Coalescent; 2020). The insert shows the timing of the wolf reintroduction (dashed line), wolf abundances during our study, and number of breeding packs.

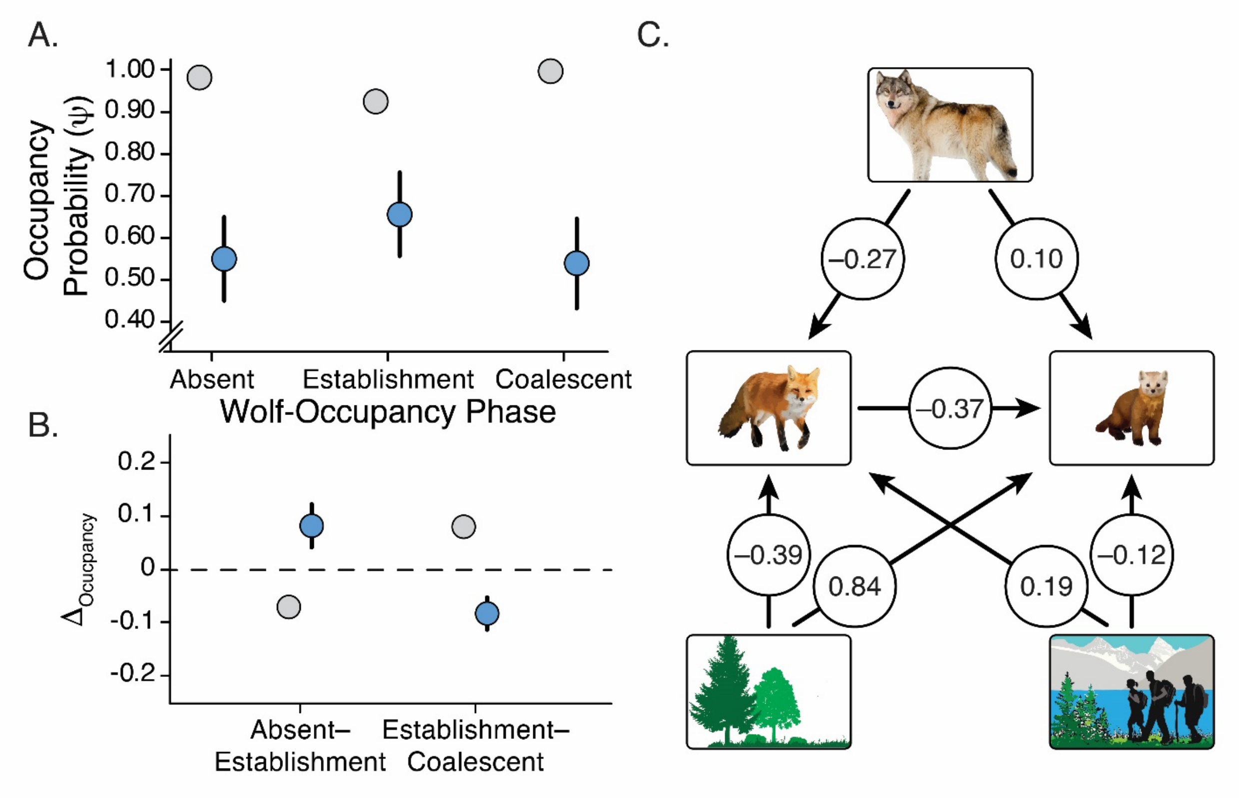
Figure 2. Yearly occupancy probability (A) and the change in occupancy across years ($\Delta_{\text{Occupancy}}$; B) for red foxes (*Vulpes vulpes*; gray) and American martens (*Martes americana*; blue). Net effects of standardized path coefficients of our final occupancy BSEM (C; effects are reported within circles), including wolves (top), foxes and martens (middle), and habitat heterogeneity and human impacts (bottom). Error bars represent 1 SD, if not shown, the error bars are smaller than the symbol.

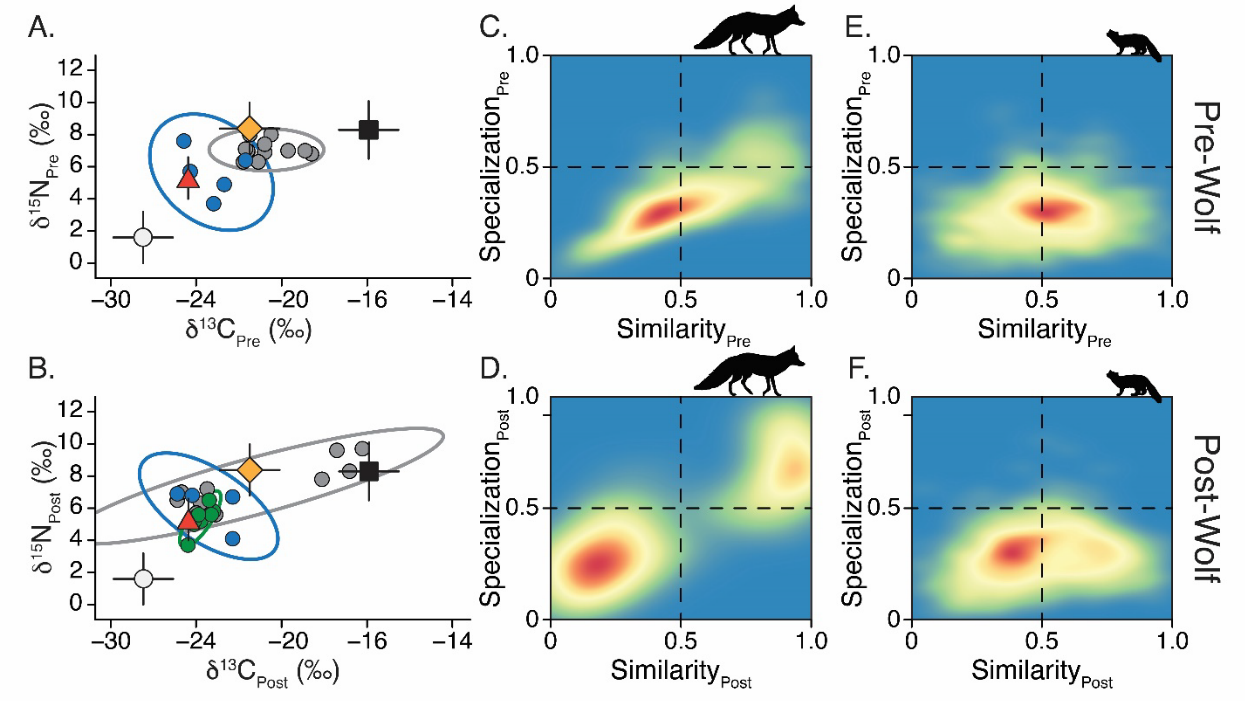
Figure 3. Carbon (δ^{13}C) and nitrogen (δ^{15}N) isotopic ellipses (SEAc) of wolves (*Canis lupus*; green), foxes (*Vulpes vulpes*; gray), and American marten (*Martes americana*; blue) before (A) and after (B) wolf reintroduction to Isle Royale. Also shown are the dietary groups available; berries (white circle), browsers (moose and snowshoe hares; red triangle), rodents and birds (gold diamond), and human foods (black square) – error bars represent 1 SD. Density plots (blue

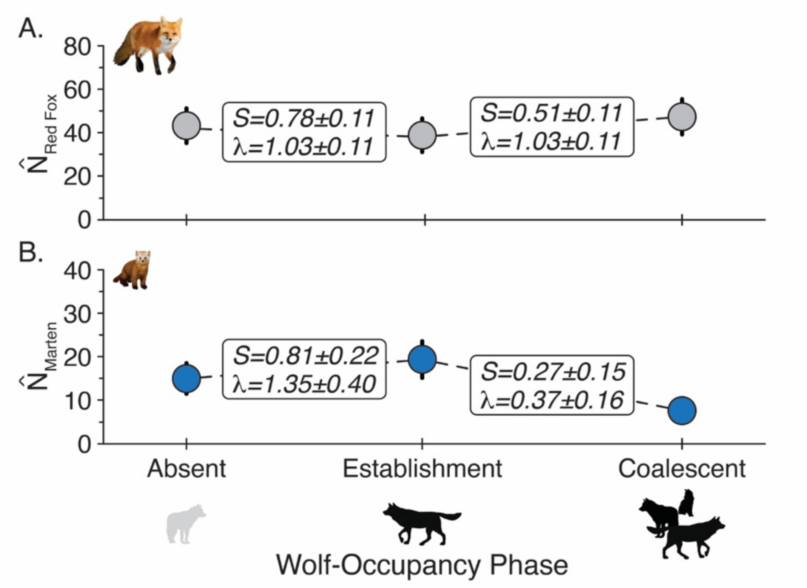
= low, red = high) of dietary Specialization (ε; y-axis) and Similarity (*s*, x-axis) indices of foxes (C and D) and martens (E and F) before and after wolf reintroduction.

Figure 4. Abundance of red fox (Vulpes vulpes; A) and American marten (Martes americana; B), including relevant demographic parameters (apparent survival [S] and population growth rate [λ]) during the absent, establishment, and coalescent phase of the wolf reintroduction to Isle Royale (see WebPanel 1 for detailed Methods). The capture probability ($\hat{p}$) of foxes was 0.17±0.03 while the recapture probability ($\hat{c}$) was 0.27±0.02. For martens, the top models included non-varying capture and recapture probabilities (p*; i.e., p = c; p*Marten = 0.15±0.03).


A.
3km
Wolf Activity
Low
High
B.
N Wolves
20
15
10
5
0
Breeding Packs
3
2
1
0
Absent
Establishment
Coalescent
Wolf-Occupancy Phase
Study Period
Wolf Abundance
40
30
20
10
0
2000
2005
2010
2015
2020
Year


A.
1.00
0.90
0.80
0.70
0.60
0.50
0.40
Occupancy Probability (ψ)
Absent
Establishment
Coalescent
Wolf-Occupancy Phase
B.
0.2
0.1
0
-0.1
-0.2
ΔOcucpancy
Absent–Establishment
Establishment–Coalescent
C.
–0.27
0.10
–0.37
–0.39
0.84
0.19
–0.12


A.
δ15NPre (‰)
δ13CPre (‰)
B.
δ15NPost (‰)
δ13CPost (‰)
0
2
4
6
8
10
12
−30
−24
−20
−16
−14
C.
D.
E.
F.
SpecializationPre
SimilarityPre
SpecializationPost
SimilarityPost
0
0.5
1.0
Pre-Wolf
Post-Wolf


A.
80
60
40
20
0
$\hat{N}_{Red Fox}$
S=0.78±0.11
λ=1.03±0.11
S=0.51±0.11
λ=1.03±0.11
B.
40
30
20
10
0
$\hat{N}_{Marten}$
S=0.81±0.22
λ=1.35±0.40
S=0.27±0.15
λ=0.37±0.16
Absent
Establishment
Coalescent
Wolf-Occupancy Phase

Supplementary Material: The pulsed effects of reintroducing wolves on the carnivore community of Isle Royale

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SI Table 3: Model selection of multi-season colonization-extinction

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Supplementary Methods

Study Area

Isle Royale (544 km^2; Figure 1) is located in north-western Lake Superior, USA (48°N, 89°W). The island currently supports a transition deciduous-to-boreal forest of fir (*Picea spp*.) and spruce (*Abies spp*.), which primarily occupy the relatively cool northeast-end and lakeshore, while temperate forest (*Acer spp., Quercus spp., Betula spp., Juniperus spp.,* etc.) defines the relatively large interior landmass. Mean monthly seasonal temperatures range from –9 °C in January to 15.8 °C in July. Mean annual precipitation is 75 cm, ranging from 54 cm to 107 cm with 40% of annual precipitation falling as snow. Lake ice formation, a primary mode of colonization to Isle Royale, has become increasingly stochastic, occurring once every 10-years (Licht *et al.* 2015). The current terrestrial carnivore community on Isle Royale is relatively simple; composed of wolves, red foxes, and American martens. The other carnivores on the island are mostly or wholly aquatic, including American mink (*Neogale vison*) and North American river otter (*Lontra canadensis*), or are highly cryptic and occur at very low densities (i.e., ermine [*Mustela erminea*]). We did not include these carnivores in our analyses because their interactions with the other terrestrial carnivores were likely minimal.

Wolves naturally colonized Isle Royale in the late 1940s and have since been nearly isolated from its source population (David Mech 1966). Shortly after their colonization, research began on the wolves and moose of Isle Royale (David Mech 1966; Peterson *et al.* 1984). Declines in wolf abundance beginning in the late 2000s prompted a prominent conservation and ethics debate regarding their reintroduction (Vucetich *et al.* 2012; Cochrane 2013), with a large-scale reintroduction project beginning in 2018, when fifteen wolves were reintroduced to Isle

Royale in an attempt to restore predation and regulate moose populations. Red foxes arrived to Isle Royale in the 1920s but were scarce until ~8-9 years after wolves colonized the island and coyotes (*Canis latrans*) were extirpated (Johnson 1970). In contrast, American martens were historically abundant on Isle Royale (Adams *et al.* 1909), but were trapped heavily until 1917, when the last recorded specimen was collected (Martin 1988). Following a 62-year hiatus, martens recolonized Isle Royale from neighboring Ontario in the early 1990s (Manlick *et al.* 2018).

The National Park Service aims to restore historical communities and ecosystem processes where appropriate, and this carnivore community appears to be an ideal candidate for reintroductions due to (i) significant turnover within the last century and (ii) an increasing concern for climate-mediated colonization barriers. The insular carnivore community on Isle Royale National Park share a complicated and dynamic history of colonization and extinction (Manlick *et al.* 2018). Furthermore, the possibility for a natural repatriation of carnivores (and other species) to the island is increasingly becoming less common because the frequency of ice-bridges connecting Isle Royale to the mainland is rapidly decreasing. This loss of gene flow is predicted to reduce genetic diversity in Isle Royale mammal populations (Manlick *et al.* 2018), the effects of which have already been realized by the wolves of Isle Royale (Vucetich *et al.* 2012), culminating in their reintroduction. Thus, population augmentation (i.e., genetic rescue) might be a necessary outcome to maintain genetic diversity and we contend that broader community interactions need to be considered before reintroduction and/or augmentation efforts. The debate over the wolf reintroductions received a great deal of attention because of conflicting human actions; the loss of gene flow between the island and mainland wolves was due to passive human actions (i.e., altering the ice dynamics on Lake Superior) and direct human intervention was proposed as a solution. However, recent research suggests that martens – one of the least likely species to colonize the island due to their small body size and limited dispersal ability in open habitats – recently colonized (Manlick *et al.* 2018). Furthermore, during 2019, one of the collared wolves crossed a solid ice bridge from Isle Royale to the mainland, suggesting the opposite could well have happened.

Reintroduction Phases

To experimentally test how the reintroduction of wolves influenced carnivore community interactions, we collected data when wolves were functionally absent from Isle Royale National Park and tracked these interactions as wolf packs established and later coalesced (Figure 1). Initially (2018), only two wolves remained on the island, a father- and brother-daughter pair that was highly inbred, exhibited morphological issues and were not reproductive (Hedrick et al., 2019). Accordingly, we considered wolves to be functionally Absent from the carnivore community; not providing suppression or trophic facilitation. The first year following the wolf reintroduction (2019), male wolves had higher movement rates (Orning *et al.* 2020) and consumed a higher proportion of beaver (Castor canadensis; MCR unpublished data). The following year (2020), the two major wolf packs within the park were established, and individuals were fully functioning within a pack dynamic: the movement rates of males were less than half from the previous year (Orning *et al.* 2020), and the wolves were consuming primarily moose. Both packs had successful litters (Figure 1), though the number of surviving individuals is not known. These key characteristics in the ecology of wolves following their reintroduction to Isle Royale provided us great confidence in conceptualizing the phases or the reintroduction.

Species and Individual Identity

Briefly, from each scat sample, we extracted DNA using QIAamp DNA micro kit (Qiagen, Valencia, California, USA) in a room dedicated to low-quality DNA samples at the University of Wisconsin-Madison following the manufacturer's protocol. We developed a species-specific quantitative polymerase chain reaction (PCR) assay for American martens and red foxes designed from previously published mitochondrial DNA (mtDNA) sequences obtained from GenBank. Samples were genotyped using a multiplex of 14 and 20 previously developed microsatellite markers for martens (Pauli *et al.* 2015; Manlick *et al.* 2018) and red foxes (Black *et al.* 2018) on an ABI 3730xl DNA analyzer (Applied Biosystems, Foster City, California, USA), and scored microsatellite alleles using GeneMapper® Software 5 (Applied Biosystems).

To account for allelic dropout and false-positive alleles, we genotyped samples in triplicate and used two replicates to confirm a heterozygous- and three replicates to confirm a homozygous-genotype at each locus. Samples that amplified at >3 loci, but <5 loci were rerun in triplicate. To minimize genotyping errors and unresolved loci (i.e., did not meet required replication), all samples that were scored from three independent PCR reactions were censored at the given locus. We assessed power to discriminate between individuals by calculating the probability of identity (PID) and the probability of identity siblings (PIDSIB) in CERVUS (Kalinowski *et al.* 2007). We further calculated the minimum number of alleles for individual identify using a genotype accumulation curve in *poppr v2.9.3* (Kamvar *et al.* 2014) that randomly samples loci and counts the number of multi-locus genotypes observed. We had enough power to identify unique individuals with a minimum of 4 loci and subsequently removed all samples that failed to amplify at <5 loci. Genotyping error rate in replicate PCR reactions was calculated by scoring errors of each within-sample run and tallying either homozygote or heterozygote errors. Once consensus genotypes were confirmed, we grouped replicate genotypes to identify unique individuals from the samples using the R package *allelematch v2.5.1* (Galpern *et al.* 2012).

Spatial and Behavioral Effects

We generated independent sampling sites along the trails by segmenting each trail into 1.0 km transects. Segments were longer than the average minimum distances between scats for foxes, the species with the highest number of detections to avoid discretization bias (Hines et al., 2010; Guillera-Arroita et al., 2017). We buffered each segment by 250m to create elliptical sites from which to infer spatial-behavioral interactions. We accounted for survey specific covariates that affected the detection process of, not only meso- and small carnivore space-use, but also our own ability to detect scats on the landscape, including the survey period, accumulated rainfall, total campsites reserved at trail-end campsites (as a proxy of human use), and a null model. To test how habitat characteristics and human activity influenced the space use and persistence of both species, we extracted ecologically relevant, site-specific variables throughout our modeling process from ground-truthed colorized infrared land cover data collected for Isle Royale National Park, including habitat heterogeneity, conifer cover, distance to human campsites, and a null model. Lastly, we used wolf collar data to generate site-specific wolf use probabilities within each detection period (to model detection) and built a kernel distribution of known locations to model wolf space use generally (to capture an occupancy response).

Wolf Space Use

Wolves were captured in Ontario, CA, and Minnesota and Michigan, USA by the National Park Service and released in Isle Royale between October, 2018–May, 2019. All reintroduced wolves were fitted with Vectronic GPS collars (VECTRONIC Aerospace, Berlin, Germany), collecting data every 4 hours. All captures and collaring of wolves followed procedures established by Sikes et al. (2016) and were internally reviewed by the NPS IACUC.

To capture the broad patterns of wolf space use in our study area (Figure 1), we combined the wolf GPS data from 2019 (thirteen individuals) and 2020 (five individuals – primarily capturing the activity patterns of wolves within our study area) during Summer/Autumn (July–October). We used a Hidden Markov model (Michelot *et al.* 2016) in the R package momentuHMM v1.5.4 (McClintock and Michelot 2018) to characterize wolf behavior using a three-behavior model following Ylitalo et al. (2021), capturing "encamped", "low-activity", and "high-activity" behaviors. We generated the utilization distribution of wolf locations using only the locations classified as low-activity (i.e., "encamped") to minimize prey-seeking or long-distance movement behaviors (Ylitalo *et al.* 2021).

To capture the fine-scale patterns of wolf space use (influencing fox or marten detection), we extracted the wolf GPS locations during the four days prior to each trail survey. Although wolves were collared upon their release on Isle Royale, all but two collars failed prior to our sampling period in 2020, leaving reliable fine-scale wolf space-use data for 2019 only. We built a Brownian bridge model using the R package adehabitatHR v0.4.19 (Calenge 2006) for each individual wolf to allow for individual-specific trajectories of movement (Horne *et al.* 2007) and extracted the mean utilization distributions of wolves within each trail segment as a site- and survey-specific measure of wolf space use within our study area.

We used a simple linear relationship between the raw wolf abundances and index of red fox abundance (Hoy et al., unpublished data) to test if a relationship between wolves and foxes has traditionally been observed.

Single Season Occupancy Modeling

To account for sampling biases that may arise from field exposure, we included the survey number as a covariate. We also included the total rainfall over the three-days prior to each survey to test for genetic quality degradation and hiker activity effects. Although Isle Royale is the least visited National Park (with ~25,000, ~26,000, and ~6,000 visitors during each year of sampling, respectively). Although visitation was lower during 2020, human use during peak visitor season overlapped with our sampling efforts, and we did not detect a substantial difference in visitation rates across years. Accordingly, we included human visitation from campsite registration records to account for human use on the landscape.

We extracted the percent of pine, mixed forest, and canopy density to test the effects of forest complexity (i.e., positive associations with high heterogeneity for martens) and resource access (i.e., positive association with edge habitat for foxes). We also include the variability (SD) of a digital elevation model to account for spatial accessibility across the island. We included the distance to campsites to measure any shield effect from humans, since wolves generally avoid areas with high human activity. Lastly, we used a utilization distribution of wolf radio-collar data during summer/fall of 2019 and 2020 as a measure of wolf space use within our study area. Although wolves were collared upon their release on Isle Royale, all but two collars failed just prior to our sampling period in 2020, leaving reliable survey-specific wolf data for 2019 only.

Specifically, we modeled occupancy at the site level using a Bernoulli distribution (i.e., $z_i \sim Bernoulli(\psi_i)$, where z_i are elements of the partially observed, true occupancy state Z, indicating whether the species is present at site i [z_i = 1] or absent [z_i = 0]); ψ_i representing the species-specific occupancy probability at each site. We modeled detection probability using a Bernoulli distribution (i.e., $y_{ij} \sim Bernoulli(z_i p_{ij})$, where y_{ij} indicates the detection frequency of the species at site i over j sampling occasions. Both the occupancy and detection probabilities were modeled using a logit link function with covariates (i.e., $logit(\psi_i) \sim \alpha_{\psi_0} + \beta_{\psi_1}\psi_i$ and $logit(p_{ij}) \sim \alpha_{p_0} + \beta_{p_1}p_{ij}$).

For each wolf-reintroduction phase (year 2018–2020), we used a single-season, single-species occupancy model (MacKenzie et al., 2002, 2006) to assess the spatial drivers of red fox and marten occupancy. To determine survey-specific heterogeneity in detection probability, we used the above-mentioned survey covariates and their additive effects as possible covariates in a detection model. We held occupancy constant (□[.]) and fit all possible models to explore the influence of the covariates on the probability of detecting each species. We then carried the best detection covariate(s) forward into a single-species single-season model, from which we determined the most important occupancy covariates for each species (not including additive effects to minimize model complexity), including a null model (□[.]).

We used an uninformative prior to model the occupancy and detection processes, using a normal distribution with Mean = 0 and SD = 0.5. We modeled occupancy at the site level using a Bernoulli distribution (i.e., $z_i \sim Bernoulli(\psi_i)$, where z_i are elements of the partially observed, true occupancy state matrix Z, indicating whether the species is present at site i [z_i = 1] or not [z_i = 0]). The parameter ψ_i represents the species-specific occupancy probability at each site. We modeled detection probability using a Bernoulli distribution (i.e., $y_{ij} \sim Bernoulli(z_i p_{ij})$, where y_{ij} indicates the detection frequency of the species at site i over j sampling occasions. Both the occupancy and detection probabilities were modeled using covariates (i.e., $logit(\psi_i) \sim \alpha_{\psi_0} + \beta_{\psi_1}\psi_i$ and $logit(p_{ij}) \sim \alpha_{p_0} + \beta_{p_1}p_{ij}$). Because individuals did not have to be continually present at a site for it to be classified as occupied, occupancy in our study should be interpreted as use.

Multi-Season Occupancy Modeling

Using the detection histories of each species, we used single-species, multi-season occupancy models to estimate the probability of detection (p), occupancy (ψ), colonization (γ), and local extinction (ε). For the multi-season occupancy modeling, we used the seven survey periods for each year to generate site-specific detection histories for each species by year and assumed sites were closed to changes in occupancy state within each year but were open between separate years (MacKenzie et al., 2006). The top covariates from each sequential step were carried forward to the final single-species multi-season occupancy model for inference. To model the state transitions (i.e., occupancy across years), we used $\psi_{i,t} \sim (1 - z_{i,t-1}) * \gamma_{i,t-1} + z_{i,t-1} * \phi_{i,t-1}$, using a Bernoulli distribution for ψ (i.e., $z_{it} \sim Bernoulli(\psi_{it})$). Within the multi-season model, we modeled detection probability using a Bernoulli distribution (i.e., $y_{ij} \sim Bernoulli(z_i p_{ij})$, where y_{ij} indicates the detection frequency of the species at site i over j sampling occasions). All probabilities (i.e., initial occupancy, detection, colonization, and extinction) were modeled using covariates (i.e., $logit(\psi_i) \sim \beta_0 + \beta_1\psi_{it}$, $logit(p_{ij}) \sim \alpha_0 + \alpha_1 p_{ijt}$, $logit(\gamma) {\sim} \varsigma_0 + \varsigma_1\gamma_{it}$, and $logit(\phi) {\sim} \delta_0 + \delta_1\phi_{it}$).

We used an uninformative prior (i.e., using a normal distribution with Mean = 0 and SD = 0.5) to model the initial occupancy, detection, colonization, and persistence processes. Furthermore, we used an uninformative prior gamma distribution (with Shape = 0.01 and Rate = 0.01) to model the temporal effects as a random variable. Like the single-season model, we modeled the initial occupancy at the site level using a Bernoulli distribution. Here, however, the parameter ψ_i represents the species-specific occupancy probability at each site, during each initial year (i.e., 2018). We assessed all model diagnostics using the R package *lattice v0.20-45* (Sarkar 2008).

Structural Equation Model

To assess spatial and behavioral processes that shape carnivore community structure in Isle Royale, we used two complimentary Bayesian structural equation models (BSEMs; (Grace, 2006) using (i) site-specific occupancy probabilities spanning 2018–2020 and (ii) survey- and site-specific detection probabilities during 2018–2019 (Joseph et al., 2016; Sivy et al., 2017). We drew upon previous literature on the interacting species (Hunter and Caro, 2008) and theoretical underpinnings of how carnivore communities are structured (Donadio and Buskirk, 2006; de Oliveira and Pereira, 2014) to guide a multivariate hypothesis of the carnivore community structure in this system. We used a global estimation approach to fit the BSEM, which compares the covariance matrices in the paths outlined in the a priori hypotheses (Grace, 2006), including the effect of red foxes on marten occupancy and detection.

Throughout this process, we used the mean estimates of site- and survey-specific fox and marten occupancy and detection from Bayesian occupancy and detection models and back transformed all occupancy and detection probabilities into log odds to linearize our data. From our single-species, single-season occupancy model (see above) of red fox and marten data, we used the average wolf utilization density, human activity, and habitat heterogeneity as site-level covariates. Apart from wolf presence, all other covariates were scaled for the BSEM and we used normal and uninformative priors (mean = 0.0, SD = 5.00). Similarly, to capture the fine-scale behavioral effects of wolves and humans, we fit a Bayesian single-species, single-season detection model of red fox and marten data, including site- and survey-specific human and wolf space-use data only for 2018 and 2019, using a null occupancy model (□[.]). Informing the BSEM with the covariate-specific priors allowed us to account for sampling variability while assessing the effects of each parameter. To account for error propagation from the occupancy and detection estimates, we used informative priors of the occupancy and detection probabilities for each species, initializing the models with mean = mean odds-occupancy (or odds-detection) and SD = SD of the estimate at the site level (and survey-specific estimate for the detection BSEM). All BSEMs were conducted using the R package *blavaan v0.4-3* (Merkle and Rosseel 2018).

We ran each final SEM model N = 10,000 iterations, with a burn-in of N = 2500 to assure model fit and convergence by assuring that all R-hat values were below 1.1 and visually inspected the model diagnostics (e.g., trace plots). We specified all models with the intercept and covariance within each species to optimize model fit. To assess the significance of each parameter estimate for our final model, we used a modification index using a cutoff of ≤5% of the distribution overlapping with 0.00, dropping any covariates that significantly overlapped zero. We assessed all model diagnostics using the R package *lattice v0.20-45* (Sarkar 2008). For interpretability, we report the mean standardized effects ($\mu_{Std.}$) and the 95% confidence interval (CI) from our BSEMs which represent the effect in proportions of standard deviations from the mean occupancy (or detection) probability for each species. Lastly, we used the Gamma-hat (BGammaHat), adjusted Gamma-hat (adjBGammaHat), and MacDonald’s centrality indices (BMc) to test for model misspecification (Garnier-Villarreal and Jorgensen 2020).

Trophic Effects

To assess how foxes and martens responded to the wolf reintroduction, we collected hair for stable isotope analysis throughout the study period from hair traps, carcasses, and trapping. Each year, we set out 6–10 non-invasive hair traps designed for foxes (Lacin Alas et al. In Review) and martens Pauli et al., (2009). All hair samples used for our stable isotope analysis were restricted to the western reaches of Isle Royale. Samples analyzed were prepared following Pauli et al. (2009). Hair samples were rinsed three times with a 2:1 chloroform-methanol solution to remove surface contaminants before being homogenized and dried for 72 h at 56 °C. All samples were weighed into tin capsules and sent to the University of New Mexico Center for Stable Isotopes using a Costech 4010 elemental analyzer (Costech) coupled to a Thermo Scientific Delta V mass spectrometer (Thermo Scientific).

We estimated niche overlap with standard ellipses corrected for small sample size (SEAc) and calculated the area of overlap between ellipses in the R package *SIBER v2.1.6* (Jackson *et al.* 2011). We used the R package *MixSIAR v3.1.12* (Stock *et al.* 2018) to estimate the percent contribution from all prey sources for foxes and martens. Using the posterior distributions of each diet item, for each species, we quantified dietary specialization (e) and similarity (s; 45). Dietary similarity and specialization: comparing the diet of an individual to an ultra-generalist and an ultra-specialist and the diet of the individual to that of the population, respectively.

Demographic Models

All demographic models were performed in the R package *RMark v2.2.*7 (Laake 2013).

SM Results

Single-Season Detection and occupancy

Red fox detection was relatively high throughout the study period (p = 0.41 [0.34, 0.47]). Importantly, during the wolf establishment phase, fox detection increased with the number of reserved campgrounds (our proxy for human use). During pack coalescence, fox occupancy increased with survey period. From our top models, only environmental factors affected marten detection (i.e., factors impacting our own ability to detect scat on the trail, rather than having some potentially important behavioral mechanism). Marten detection was relatively low (p = 0.10 [0.05, 0.17]. Specifically, we saw a decrease in marten detection with rain during the absent and establishment phase and a decrease throughout the survey period during the coalescent phase.

Habitat heterogeneity was the single most important habitat characteristic that influenced red fox (only in 2019) and marten occupancy. Throughout our study period red fox occupancy was high (ψ = 0.96 [0.90, 1.00]), while marten occupancy was relatively lower (ψ = 0.57 [0.37, 0.83]) and more variable. During the establishment phase, red fox occupancy decreased at the highest levels of habitat heterogeneity. Marten occupancy consistently increased with habitat heterogeneity, regardless of wolf introduction phase.

Colonization-Extinction

Throughout our build-up approach, we identified the best yearly covariates of detection and occupancy for foxes and martens and used those as the initial building blocks of our multi-season occupancy model. We explicitly tested the impacts of habitat heterogeneity, forest structure, and human use on the colonization and extinction process of occupancy throughout our study period. Our final multi-season occupancy model for foxes included the covariate of human use for the detection probability (0.02 [0.01, 0.04] and had constant initial occupancy, colonization, and extinction probabilities, though foxes experienced higher extinction in the coalescent phase. Our final marten model included a constant, non-varying detection across years and, unsurprisingly, an initial occupancy probability characterized by habitat heterogeneity (0.82 [-0.20, 1.90]. Interestingly, the colonization of martens increased further from human campgrounds, where foxes had lower occupancy (1.43 [-1.23, 3.67]; SI Figure 3A). As expected, marten extinction probability decreased with higher habitat heterogeneity (1.85 [-3.86, 0.59]).

BSEM (Space and Behavior)

Our global occupancy model (for our spatial BSEM) for both foxes and martens included rain and humans impacting the detection process and humans, wolves, and habitat heterogeneity impacting the occupancy (space use) process. Similarly, our global detection model (for our behavioral BSEM) for both foxes and martens included humans and wolf activity impacting the detection process and a constant occupancy process. Our spatial and behavioral BSEM models explained ~50% of the variability within the fox and marten occupancy and detection probability data, respectively. For both models, the indirect effects are inferred from the direct effects, while the net effects are the sum of direct and indirect effects (SI Table 5). Net effects for our spatial and behavioral models are reported within the main body of our manuscript.

Our spatial BSEM fit our data relatively well; all Rhat values were all < 1.1, the BRMSEA was 0.07 [0.00, 0.17], and the BMc was 0.99 [0.97, 1.00]. However, global model PPP was 0.83, suggesting that some parameters may be under-estimated. Our top model did not include a direct effect from wolves (or wolf presence) on the occupancy probability of martens. Foxes (-0.38 [-0.45, -0.30]) and humans (-0.05 [-0.11, 0.02]) had a negative direct effect on the space use of martens. Unsurprisingly, habitat heterogeneity strongly and positively influenced marten space use (0.70 [-0.76, -0.64]). Wolves (as the additive effect of wolf space use and wolf presence) had a negative effect on the space use of foxes (-0.27 [-0.45, -0.09]). Meanwhile, humans had a strong and positive effect on the space use of foxes that was in the opposite direction and a similar magnitude as the effect of wolves (0.19 [0.05, 0.33]). Lastly, foxes tended to use areas of lower habitat heterogeneity (-0.39 [-0.52, -0.26]).

Our behavioral BSEM indicated that our data fit the model well; all Rhat values were all ~ 1.0, the BRMSEA was 0.03 [0.00, 0.06], and the BMc was 0.99 [0.99, 1.00]. Global model PPP was 0.55, indicating excellent fit (parameters were not under- or over-estimated). Our top model did not include a direct effect from wolves on the detection probability of martens. Foxes negatively influenced marten detection (-0.67 [-0.74, -0.59]) while humans had a strong and opposite effect (0.58 [0.46, 0.61]). (However, this effect was largely nullified when considering the net effect [SI Table 4].) Wolves had a negative effect on red fox detection (-0.27 [-0.32, -0.22]) while humans had a strong positive effect (0.64 [0.60, 0.68]).

SIA

Before and after the wolf reintroduction, our stable isotope results suggest that foxes were primarily consuming human foods, though after the wolf reintroduction dietary estimates were much more variable (SI Table 5). Meanwhile, marten diet did not change throughout the reintroduction phases. As expected, the isotopic niche breadth of wolves was relatively narrow (SEAc = 0.63) consuming primarily moose. Fox niche breadth more than doubled following the wolf reintroduction ($\text{SEAc}_{\text{Pre}} = 2.04$ compared to $\text{SEAc}_{\text{Post}} = 9.51$). Marten dietary niche breadth remained constant before and after the wolf reintroduction ($\text{SEAc}_{\text{Pre}} = 7.02$ and $\text{SEAc}_{\text{Post}} = 6.71$). Niche overlap between foxes and martens was low, but nearly doubled after wolves were reintroduced ($\text{Overlap}_{\text{Pre}} = 0.12 \pm 0.07$ then $\text{Overlap}_{\text{Post}} = 0.23 \pm 0.08$).

Initially, foxes were all generalists ($s_{\text{Pre}} = 0.53 \pm 0.21$ [Mean ± SD] and $\varepsilon_{\text{Pre}} = 0.36 \pm 0.14$; Figure 3C) and consumed a wide range of food items. Foxes exhibited a strong, negative correlation between the consumption of small mammals and human foods ($r = -0.89$) and berries ($r = -0.80$), and between browsers and berries ($r = -0.81$). Martens were classified as somewhat similar generalists ($s_{\text{Pre}} = 0.51 \pm 0.19$ and $\varepsilon_{\text{Pre}} = 0.29 \pm 0.12$; Figure 2E) and did not exhibit any strong correlation between diet items ($r < \pm 0.70$). There were no strong correlations between the diet items of foxes following the wolf reintroduction ($r < \pm 0.70$).

Demography

Our final model suite for our demographic analysis included eight models for each species, including four models varying p and c and four models with p = c. The top model for foxes included a year-varying survival probability. Although a null model was within 2.0 AIC from our top model, we used our top model for inference because the posterior of the beta-coefficient of survival () overlapped 0.0 with <5% of runs, suggesting including this parameter was informative. The top model for martens included a year-varying survival and population growth rate (λ; SI Table 4). Like our fox model, the null model for martens was within 2.0 AIC, however, we deemed the beta-coefficients for both covariates to be informative (<5% overlap with 0.0). The capture probability ($\hat{p}$) of foxes was 0.17 [0.11, 0.25] while the recapture probability ($\hat{c}$) was 0.27 [0.22, 0.31]. Meanwhile, the capture and recapture probability were equal and constant across years for martens ($\hat{p} = \hat{c} = 0.15$ [0.10, 0.22]).

Wolf-Fox Relationship

We found evidence of a slight positive relationship between wolf abundance and red fox abundance ($t = 2.02$, p-value = 0.05; $\beta_{\mu\ [95\%\ \mathrm{CI}]} = 0.48$ [0.001, 0.97]), suggesting some density mediation.

SI Tables

SI Table 1. Model selection of detection models for red foxes (*Vulpes vulpes*) and martens (*Martes americana*).

2018 Detection Model Summary				Covariate Information				
Red Fox	DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
p(rain), y(.)	450.67	0.00	0.37	-0.55	0.43	-1.40	0.25	0.10
p(.), y(.)	**450.79**	**0.12**	**0.35**				–	
p(survey), y(.)	452.41	1.74	0.15	-0.03	0.06	-0.13	0.08	0.30
p(humans), y(.)	452.74	2.07	0.13	0.00	0.01	-0.02	0.03	0.40
Marten	DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
p(rain), y(.)	**188.34**	**0.00**	**0.89**	**-1.55**	**0.89**	**-3.35**	**0.08**	**0.03**
p(humans), y(.)	193.46	5.12	0.07	0.03	0.03	-0.02	0.08	0.13
p(.), y(.)	194.78	6.44	0.04				–	
p(survey), y(.)	199.15	10.81	0.00	-0.17	0.11	-0.39	0.05	0.05

2019 Detection Model Summary				Covariate Information				
Red Fox	DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
p(humans), y(.)	**433.96**	**0.00**	**0.73**	**0.02**	**0.01**	**0.00**	**0.04**	**0.01**
p(.), y(.)	436.81	2.85	0.17				–	
p(survey), y(.)	439.19	5.23	0.05	-0.08	0.06	-0.19	0.04	0.09
p(rain), y(.)	439.56	5.60	0.04	-0.22	0.32	-0.86	0.41	0.25

Marten	DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
p(rain), y(.)	214.81	0.00	0.49	-1.29	0.73	-2.83	0.03	0.03
p(.), y(.)	**215.44**	**0.63**	**0.36**	–				
p(survey), y(.)	217.67	2.86	0.12	-0.04	0.1	-0.24	0.16	0.38
p(humans), y(.)	219.95	5.14	0.04	-0.02	0.02	-0.07	0.02	0.20

2020 Detection Model Summary				Covariate Information				
Red Fox	DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
p(survey), y(.)	**449.10**	**0.00**	**0.87**	**-0.16**	**0.06**	**-0.27**	**-0.05**	**0.00**
p(rain), y(.)	454.09	4.99	0.07	1.52	1.12	-0.67	3.84	0.09
p(.), y(.)	455.13	6.03	0.04	–				
p(humans), y(.)	456.78	7.68	0.02	0.00	0.01	-0.02	0.02	0.43
Marten	DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
p(.), y(.)	**139.25**	**0.00**	**0.31**	–				
p(survey), y(.)	139.54	0.29	0.27	-0.30	0.14	-0.60	-0.05	0.01
p(humans), y(.)	140.07	0.82	0.21	-0.04	0.03	-0.09	0.01	0.06
p(rain), y(.)	140.07	0.82	0.21	0.89	1.35	-1.79	3.44	0.25

SI Table 2. Model selection at occupancy stage for red foxes (*Vulpes vulpes*) and martens (*Martes americana*).

2018 Occupancy Model Summary				Covariate Information				
Red Fox	DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
p(.), y(Hab. Het.)	448.90	0.00	0.28	0.35	0.71	-1.39	1.49	0.26
p(.), y(Edge)	449.46	0.56	0.21	-0.33	0.69	-1.57	1.19	0.28
p(.), y(Camps)	449.85	0.95	0.17	0.32	0.73	-1.1	1.71	0.42
p(.), y(Mix Forest)	450.61	1.71	0.12	0.20	0.67	-1.01	1.64	0.39
p(.), y(Pine)	450.63	1.73	0.12	0.14	0.49	-0.78	1.13	0.40
p(.), y(.)	**450.79**	**1.89**	**0.11**				–	
Marten	DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
p(rain), y(Hab. Het.)	**181.75**	**0.00**	**0.92**	**0.75**	**0.56**	**-0.31**	**1.9**	**0.05**
p(rain), y(Mix Forest)	186.68	4.93	0.08	0.6	0.56	-0.4	1.84	0.12
p(rain), y(.)	194.78	13.03	0.00				–	
p(rain), y(Camps)	195.20	13.45	0.00	-0.46	0.64	-1.77	0.79	0.21
p(rain), y(Pine)	196.68	14.93	0.00	-0.17	0.45	-1.1	0.85	0.31
p(rain), y(Edge)	197.58	15.83	0.00	-0.08	0.66	-1.29	1.38	0.42

2019 Occupancy Model Summary				Covariate Information				
Red Fox	DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
p(humans), y(Hab. Het.)	**420.33**	**0.00**	**0.98**	**-1.36**	**0.81**	**-3.08**	**0.11**	**0.04**
p(humans), y(Pine)	428.86	8.53	0.01	0.5	0.47	-0.36	1.49	0.13

p(humans), y(Mix Forest)	431.10	10.77	0.00	0.73	0.65	-0.46	2.07	0.12
p(humans), y(Edge)	434.99	14.66	0.00	0.38	0.54	-0.67	1.49	0.23
p(humans), y(Camps)	435.49	15.16	0.00	-0.12	0.57	-1.21	1.06	0.41
p(humans), y(.)	439.39	19.06	0.00				–	
Marten	DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
p(rain), y(Hab. Het.)	**187.67**	**0.00**	**1.00**	**1.70**	**0.81**	**0.33**	**3.46**	**0.01**
p(rain), y(Mix Forest)	204.30	16.63	0.00	0.71	0.52	-0.16	1.92	0.06
p(rain), y(Camps)	208.72	21.05	0.00	0.72	0.63	-0.36	2.08	0.11
p(rain), y(Edge)	209.79	22.12	0.00	-0.39	0.82	-1.91	1.46	0.28
p(rain), y(.)	213.92	26.25	0.00				–	
p(rain), y(Pine)	217.77	30.10	0.00	0.23	0.49	-0.66	1.38	0.32

2020 Occupancy Model Summary				Covariate Information				
Red Fox	DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
p(survey), y(Mix Forest)	448.00	0.00	0.24	0.43	0.75	-0.92	1.95	0.30
p(survey), y(Hab. Het.)	448.54	0.54	0.18	-0.38	0.75	-2.01	0.88	0.33
p(survey), y(Camps)	448.69	0.69	0.17	-0.26	0.70	-1.55	1.19	0.34
p(survey), y(.)	**448.74**	**0.74**	**0.17**				–	
p(survey), y(Edge)	449.05	1.05	0.14	0.03	0.64	-1.15	1.39	0.49
p(survey), y(Pine)	449.78	1.78	0.10	0.02	0.46	-0.83	1.00	0.49
Marten	DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0

p(.), y(Hab. Het.)	**122.77**	**0.00**	**0.96**	**2.00**	**0.90**	**0.46**	**3.93**	**0.01**
p(.), y(Pine)	129.68	6.91	0.03	0.70	0.60	-0.36	2.04	0.09
p(.), y(Edge)	133.93	11.16	0.00	0.25	0.93	-1.45	2.15	0.39
p(.), y(Camps)	134.02	11.25	0.00	0.69	0.74	-0.71	2.31	0.16
p(.), y(Mix Forest)	139.65	16.88	0.00	0.20	0.69	-1.06	1.69	0.40
p(.), y(.)	141.17	18.40	0.00	–				

SI Table 3. Model selection at colonization-extinction stage for red foxes (*Vulpes vulpes*) and martens (*Martes americana*). Models not shown did not converge.

Red Fox	Colonization Models				Covariate Estimates				
		DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
	g(.)	**1330.55**	**0.00**	**0.38**	–				
	g(Pine)	1331.41	0.86	0.25	-0.09	1.44	-2.93	2.78	0.47
	g(Hab. Het.)	1331.92	1.37	0.19	0.12	1.39	-2.70	2.85	0.45
	g(Mixed)	1332.16	1.61	0.17	-0.05	1.44	-2.88	2.70	0.49
	Extinction Models				Covariate Estimates				
		DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
	y.pine	1329.75	0.00	0.60	0.07	1.32	-2.58	2.70	0.47
	f(.)	**1330.55**	**0.80**	**0.40**	–				

	y.canv	1354.36	23.81	0.00	0.37	1.43	-2.46	3.06	0.39

	Colonization Models				Covariate Estimates				
		DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
Marten	**g(Camps)**	**461.43**	**0.00**	**0.79**	**1.22**	**1.49**	**-2.13**	**3.94**	**0.18**
	g(Mixed)	464.33	2.90	0.18	0.65	1.58	-2.64	3.56	0.32
	g(.)	468.23	6.80	0.03				–	
	g(Hab. Het.)	485.22	23.79	0.00	-1.04	1.34	-3.58	1.96	0.19
	Extinction Models				Covariate Estimates				
		DIC	DDIC	DICwt	Mean	SD	2.50%	97.50%	% overlapping 0
	Hab. Het.	**457.82**	**0.00**	**0.88**	**-1.72**	**1.36**	**-4.21**	**1.40**	**0.10**
	Camps	462.06	4.24	0.11	0.42	1.41	-2.64	3.06	0.34
	Pine	466.85	9.03	0.01	0.29	1.40	-2.86	2.87	0.37
	(.)	468.23	10.41	0.00					

SI Table 4. Model selection of demographic models

Red Fox Models	npar	AIC	DeltaAIC	weight
ϕ(~time)𝜆(.)p(.)c(.)	**5**	**986.75**	**0.00**	**0.27**
ϕ(.)𝜆(~time)p(.)c(.)	5	986.92	0.16	0.25
ϕ(.)𝜆(.)p(.)c(.)	4	987.76	1.01	0.16
ϕ(~time)𝜆(~time)p(.)c(.)	6	987.94	1.19	0.15
ϕ(~time)𝜆(.)p=c(.)	4	989.81	3.05	0.06
ϕ(.)𝜆(~time)p=c(.)	4	990.66	3.91	0.04
ϕ(.)𝜆(.)p=c(.)	3	990.84	4.09	0.04
ϕ(~time)𝜆(~time)p=c(.)	5	991.40	4.65	0.03

Marten Models	npar	AIC	DeltaAIC	weight
ϕ(~time)𝜆(~time)p=c(.)	**5**	**273.03**	**0.00**	**0.28**
ϕ(~time)𝜆(~time)p(.)c(.)	6	273.59	0.55	0.21
ϕ(.)𝜆(~time)p=c(.)	4	274.51	1.47	0.13
ϕ(.)𝜆(.)p=c(.)	3	274.74	1.70	0.12
ϕ(.)𝜆(~time)p(.)c(.)	5	275.21	2.18	0.09
ϕ(.)𝜆(.)p(.)c(.)	4	275.83	2.80	0.07
ϕ(~time)𝜆(.)p=c(.)	4	276.24	3.20	0.06
ϕ(~time)𝜆(.)p(.)c(.)	5	277.37	4.33	0.03

SI Table 5. Final identified spatial (top) and behavioral (bottom) Bayesian Structural Equation Model results for red foxes (*Vulpes vulpes*) and American marten (*Martes americana*).

	Species	Interaction	Estimate	SE	Lower CI	Upper CI
Spatial BSEM	Marten	Intercept	1.476	0.122	1.237	1.715
		Fox	-0.375	0.036	-0.446	-0.304
		Humans	-0.045	0.031	-0.106	0.016
		Canopy	-0.697	0.031	-0.758	-0.635
	Fox	Intercept	3.675	0.225	3.234	4.116
		Wolf	-0.106	0.076	-0.256	0.044
		Humans	0.188	0.073	0.045	0.331
		Canopy	0.387	0.067	0.255	0.518
		Wolf Presence	-0.162	0.076	-0.311	-0.012
	Net Effects	Wolf on Marten	0.100	0.037	0.028	0.172
		Wolf on Fox	-0.267	0.092	-0.447	-0.087
		Human on Marten	-0.116	0.042	-0.197	-0.034
		Canopy on Marten	-0.842	0.021	-0.882	-0.801

	Species	Interaction	Estimate	SE	Lower CI	Upper CI
Behavioral BSEM	Marten	Intercept	-8.734	0.196	-9.117	-8.351
		Fox	-0.666	0.039	-0.741	-0.59
		Humans	0.538	0.039	0.463	0.614
	Fox	Intercept	-2.574	0.068	-2.706	-2.441

		Wolf	-0.273	0.026	-0.324	-0.222
		Humans	0.639	0.019	0.602	0.677
	Net	Wolf on Marten	0.182	0.02	0.142	0.221
		Human on Marten	0.113	0.037	0.039	0.186

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Carnivore community reassembly provides a test of Eltonian niche conservatism

Running Title: Eltonian niche conservatism in carnivora

Authors and Affiliations

Mauriel Rodriguez Curras[1*], Philip J. Manlick[2], and Jonathan N. Pauli[1]

[1]University of Wisconsin-Madison, Department of Forest & Wildlife Ecology, Madison, WI, USA.

[2]Pacific Northwest Research Station, USDA Forest Service, Juneau, Alaska, 99801 USA

*Corresponding Author: Mauriel Rodriguez Curras; mrodriguezcu@wisc.edu

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Abstract

The repatriation of species is common, especially in conservation efforts aimed at restoring trophic interactions. Whether the Eltonian niches of restored species are conserved in reassembled ecological communities is largely unknown. Within mammalian carnivores, we hypothesized that the Eltonian niches of sympatric competitors would be structured by trophic facilitation from subsidies provided by large carnivores (i.e., carrion) and humans (i.e., food subsidies). Using stable isotopes ($d^{13}C$, $d^{15}N$), we quantified the Eltonian niches of an apex predator, the grey wolf (*Canis lupus*) and two subordinate guild members, coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*), from Michigan, USA across three periods that differed in community composition: a "functional" carnivore community (1910-1930), a "departed" community which lacked wolves (1950-1970), and a "reassembled" carnivore community featuring wolves as well as human food subsidies (2000-2020). In functional and reassembled communities, wolves constrained the niche space of coyotes via resource facilitation, regardless of human presence, such that coyotes consumed ~50% more deer in the presence of wolves. Without wolves, coyotes exhibited an isotopic and dietary niche breadth ~2-5× greater (3.33±0.74‰^{2}) than in the functional (0.64±0.11‰^{2}) and reassembled (1.66±0.63‰^{2}) communities. Conversely, we found that the niche breadth of foxes was conserved across the functional (1.91±0.41‰^{2}) and departed (1.98±0.75‰^{2}) communities but quadrupled in the presence of human resource subsidies (7.52±1.95‰^{2}). Notably, we found that trophic facilitation by wolves and resource subsidies from humans altered the foraging strategies of individuals, resulting in disparate foraging strategies for foxes. Our results highlight that Eltonian niche conservatism in carnivore communities is driven by resource subsidies, both from the provisioning of carrion by large carnivores to meso-carnivores and from human foods

subsidizing small carnivores. More broadly, our work suggests that large carnivore repatriation can restore some species interactions, while human resource subsidies can strongly decouple competitive interactions.

Introduction

Niche theory provides a foundation for understanding competitive interactions (Grinnell 1917, Elton 1927, Hutchinson 1957). Competitors influence the critical components of a species niche (Case and Gilpin 1974), impacting resource utilization and trophic interactions (Macarthur and Levins 1967). Niche conservatism – the tendency of species to retain ecological characteristics across space and time – has emerged as a useful framework for ecologists to understand the roles of species within communities following the loss of community members (Peterson et al. 1999), the introduction of non-native invaders (Larson et al. 2010), and the putative replacement of species' ecological roles (Clark et al. 2021). Compared to past research on phylogenetic (the tendency of related species to exhibit a similar niche space; Losos 2008) and Grinellian (the retention of species-habitat associations through space and time; Wiens and Graham 2005, Soberón 2007) niche conservatism, Eltonian niche conservatism has only recently been explored in depth (Larson et al. 2010, Manlick et al. 2019, Medina and Almeida-Neto 2020). This limited advance could be due to the original nuanced definition of the Eltonian niche that emphasized the roles of species within the communities they lived in, namely their "relations to food and enemies" and the comparison of a species niche to "trades or professions or jobs in a human community" (Elton, 1927; *see* Dussault, 2022). Elton further posited that the roles of species within their respective communities and ecosystems should be regarded as context-dependent characteristics rather than phylogenetic properties of organisms (Elton 1927). Eltonian niche conservatism, then, should be addressed in the context of community and trophic interactions between species – testing if species interactions, *per se*, are conserved as the environmental context changes.

The predictable characteristics of mammalian carnivore communities make them a useful model for understanding Eltonian niche conservatism. Large carnivores (Mammalia, Carnivora) shape ecological communities through both predation (Estes *et al.*, 2011) and competitive interactions (Holt and Polis, 1997). Carnivore communities are hierarchically structured by body size, whereby species that are between 2–5× larger than their competitors may physically harm or behaviorally displace subordinates (Palomares and Caro 1999, Donadio and Buskirk 2006). However, large carnivores may also provide meso- and small carnivores predictable and year-round scavenging opportunities through carrion (Wilmers et al. 2003, Roemer et al. 2009), especially during resource scarcity (Pereira et al. 2014). Not surprisingly, dietary overlap is a leading driver of interspecific competition and intraguild predation (Palomares and Caro 1999, Donadio and Buskirk 2006). Thus, resource provisioning by large carnivores draws subordinate carnivores into implicitly risky foraging locations – forcing decisions between food and safety. This hierarchical and nested structure of carnivore communities produces a dynamic interplay between suppression (e.g., interspecific killing) and facilitation (e.g., carrion subsidies; Prugh and Sivy, 2020; Ruprecht *et al.*, 2021) where competitive interactions are predicated by body size.

Resources provisioned by large carnivores, generally in the form of ungulate carrion, are increasingly recognized as an important driver of community interactions (Wilson and Wolkovich 2011, Pereira et al. 2014, Perrig et al. 2023). These resources percolate through food webs (Selva and Fortuna 2007), supporting extensive networks of reticulate interactions, especially obligate and facultative scavenging (Wilson and Wolkovich 2011). Resource provisioning from large carnivores impact competition among subordinate species and, in some cases, offset the effect of suppression (Wilmers et al. 2003, Wilson and Wolkovich 2011).

Indeed, carcasses provisioned by large carnivores can facilitate resource partitioning in carnivore communities by alleviating exploitative competition for small mammals (Sivy et al. 2018). Alternatively, human food subsidies in the form of agriculture, domestic livestock, and human refuse can alter competition within carnivore communities (Newsome et al. 2015a, Manlick and Pauli 2020) and alter the co-existence dynamics between meso- and small carnivores (Murray et al. 2015, Pluemer et al. 2019). Determining how changes in large carnivore presence and increasing resource subsidies from humans influence dietary partitioning among carnivores is needed to better understand carnivore community dynamics, especially where carnivore abundance is expected to change as a result of anthropogenic activities (Chapron et al. 2014).

One of the most widely reestablished large carnivores, the wolf (*Canis lupus*), is expected to have substantial top-down impacts on their primary prey and other carnivores at the community-level (Levi and Wilmers 2012, Ripple and Beschta 2012, Flagel et al. 2017). While previous research has focused on the top-down consequences of large carnivore extirpations and repatriations, less research has assessed how the functional return of large carnivores impacts the competitive interactions and niche characteristics of subordinate carnivores (though see Rodriguez Curras et al. *In Press*). As large carnivores return to human landscapes (Chapron et al. 2014), it is critical to consider the impact of humans on the functional relationships that large carnivores could restore, and how they might deviate from our expectations. To our knowledge, however, no research has explicitly tested if the Eltonian niches of carnivores are conserved following the repatriation of a large carnivore to a landscape with increasing human use.

To explore the consequences of large carnivore extirpation and subsequent recovery on Eltonian niche conservatism in subordinate carnivores, we quantified the resource use and trophic interactions between wolves, coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*) across the Upper Peninsula (UP), Michigan, USA over 100 years of community change. Most notably, wolves were functionally extirpated from the UP by approximately 1950, before reestablishing populations in the early 1990s (Beyer et al. 2009, Hendrickson and Robinson 1975). In addition, the UP saw an exponential increase in tourism and housing density – though not necessarily a change in total population size – over this period (Radeloff et al. 2005), likely altering the resource landscape via human food subsidies to wildlife (IPBES 2019, Manlick and Pauli 2020). Specifically, to understand how community reassembly and human disturbance interact to drive carnivore trophic relationships and Eltonian niches, we used bulk tissue stable isotope analysis of museum specimens and harvested carnivores to quantify diets and niche overlap during three ecologically relevant time periods: (i) a functional carnivore community with wolves (1910-1930), (ii) the community following the extirpation of wolves (which we refer to as "departed" throughout; 1950-1970), and (iii) the reassembled carnivore community featuring wolves and high human subsidies (2000-2020). Within the context of Eltonian niche conservatism, we expect that the drivers of carnivore community interactions – specifically, suppression and facilitation – would be consistent through time. Accordingly, we hypothesized that the Eltonian niches of subordinate carnivores are structured by trophic facilitation, with different responses to resources provisioned by large carnivores and human food subsidies for meso- and small carnivores, respectively. Specifically, we predicted that the Eltonian niche of coyotes would be conserved in the presence of wolves due to facilitation – that is, coyote niche breadth would be narrower in the presence of wolves due to a higher proportion of deer carrion in their diet. Conversely, we did not expect carrion subsidies to support foxes given that dominant meso-carnivores like coyotes can monopolize this resource (Sivy et al. 2018). Specifically, we predicted that the Eltonian niche of foxes is more strongly mediated by nonwolf subsidies – that is, fox niche breadth would expand due to increased subsidies provided by humans. Accordingly, we expected dietary overlap between coyotes and foxes to be highest when wolves were absent due to a lack of carrion provisioning. Human use has been shown to increase dietary overlap between carnivores while simultaneously increasing co-occurrence due to exceedingly high convergence on human food subsidies (Manlick and Pauli 2020), so we expected the total community niche breadth to increase through time, which could lead to an increase in dietary overlap through time as human impacts increase. Finally, we predicted that dietary specialization would be highest for coyotes in the presence of large carnivores due to an increase in the consumption of deer, while human subsidies would drive higher diet variability.

Methods

Study Area

The Upper Peninsula (UP) of Michigan, USA is characterized by boreal forest and mixed conifer and deciduous stands, with interspersed agricultural lands. The dominant vegetative community has been strongly influenced by human intervention during the last two centuries (Radeloff et al. 2005), with primary succession following industrial logging in the 19th century shifting landcover (Karamanski 1989). The region is highly seasonal, with mean temperatures ranging from −14°C in winter with up to 450cm of snowfall and 25°C in summer with an average annual precipitation between 812–864mm. Land-use change over the past century has attenuated in the UP relative to the broader Great Lakes Region, while key prey like white-tail deer (*Odocoileus virginianus*) have increased in abundance (see SM and SM Figure 1). Following the crash in deer populations across North America, the UP was considered a white-tail deer refugia in the United States prior to modern management practices (Webb 2018). Although moose (Alces alces) – the only other substantial prey for wolves in the UP – occurred throughout the 20th century, their populations have been exceedingly low (i.e., <200 individuals; (Beyer, D. E., Winterstein, S. R., Lederle, P. E. 2011), thus likely not significantly contributing to carnivore diets. The mammalian community has remained relatively stable, other than the extirpation of wolves in the middle of the century, and sympatric carnivores include black bears (*Ursus americanus*), Canada lynx (*Lynx canadensis*), bobcats (*Lynx rufus*), American badgers (*Taxidea taxus*), fishers (*Pekania pennanti*), American marten (*Martes americana*), least weasels (*Mustela nivalis*), striped skunks (*Mephitis mephitis*), racoons (*Procyon lotor*), and gray foxes (*Urocyon cinereoargenteus*). Nevertheless, we were particularly interested in the canids within this community where we would expect the strongest competitive interactions due to their taxonomic relatedness, body size distributions, and diet (including theoretical, Donadio and Buskirk 2006, and empirical (Levi and Wilmers 2012, Ripple et al. 2013, Newsome and Ripple 2014). Generally, we were interested in testing the dynamics among the three most tightly coupled competing carnivores who serve as an ideal model for facilitation-suppression dynamics.

Design, Data Collection, and Preparation

We measured bulk tissue carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes from hair and bone collagen for 74 ($N_{Fox} = 24$, $N_{Coyote} = 35$, $N_{Wolf} = 15$), 31 ($N_{Fox} = 9$, $N_{Coyote} = 22$), and 65 ($N_{Fox} = 17$, $N_{Coyote} = 17$, $N_{Wolf} = 31$) individuals in the functional, departed, and reassembled carnivore communities, respectively. Functional and departed community and samples were acquired from museum specimens while reassembled community samples were acquired from published data by Manlick and Pauli (2020) and include samples from fur auctions, museum collections, and collared animals. In addition, we sampled hair from historical (1920-1930; N = 35) and contemporary (2010-2020; N = 76; *see* Carlson *et al.*, 2014) prey specimens to quantify isotopic variability in prey for each time period (*see SM Methods*). We rinsed hair samples three-times with 2:1 chloroform methanol solution to remove surface oils, homogenized them with scissors, and dried samples for 72 hours at 50°C (Pauli et al. 2009). Bone collagen samples were demineralized in 0.1N HCL, rinsed 5× with deionized water, and then lipid extracted in 2:1 chloroform methanol for three days and dried for ≥ 72 hours at 50°C before homogenization in a mill mixer. Carbon and nitrogen isotope values were measured using a Costech 4010 Elemental Analyzer (Valencia, CA) coupled to a Thermo Scientific Delta V Plus (Bremen, Germany) isotope ratio mass spectrometer with internal reference materials calibrated against international reference standards (V-PDB for $\delta^{13}C$ and atmospheric N for $\delta^{15}N$). The within-run standard deviation for internal reference materials was <0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. All measurements were conducted at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM, USA). Prior to analyses and comparisons, we corrected all stable isotope samples for the Suess effect to pre-industrial values (c. 1750s) using data from Dombrosky (2020; Elliott Smith *et al.*, 2020). Because the variability within time periods was equal to or less than the analytical precision of the mass spectrometer ($\delta^{13}C_{SD} < 0.20$‰), we used an average value of the Suess-correction for all samples collected from the functional (historic, 1910-1930; −0.45±0.05‰), departed (mid-century, 1950-1970; −0.77±0.15‰) and reassembled (contemporary, 2000-2020; −1.81±0.12‰) communities, respectively. All bone collagen samples exhibited high quality with C:N ratios within the acceptable range (C:N = 3.2±0.3; (DeNiro 1985, Guiry and Szpak 2021).

Analyses

To test the mechanisms driving dietary variation across species and time periods, we used $\delta^{13}C$ and $\delta^{15}N$ values to estimate (a) isotopic niche breadth and pairwise isotopic niche overlap in 'δ-space' (Layman et al. 2007, Newsome et al. 2007, Jackson et al. 2011) and (b) the proportional assimilation of putative prey and dietary overlap based on stable isotope mixing models (i.e., 'p-space'; Parnell *et al.*, 2010). First, we quantified isotopic niche breadth and overlap – a proxy for dietary niche breadth and competition, respectively – as the 95% standard ellipses areas (B ‰^{2}) of each species (within time periods) and the overlap between species in each time period and across time periods for each species in the R package *SIBER v 2.1.6* (Parnell et al. 2010). We ran 3 chains of 300,000 iterations and removed the first 200,000 iterations as burn-in and then thinned posterior samples to every 10th sample. We calculated the total isotopic niche breadth (SEA_δ ‰^{2}) and the area of overlap between ellipses within each time-period. To quantify isotopic niche overlap, we used the single metric of niche overlap (O_δ) defined by overlap as the proportion of non-overlapping area of the two ellipses being compared relative to the non-overlapping area, $O_\delta = O_{x-y}/\left(\left(B_x + B_y\right) - O_{x-y}\right)$, where O_{x-y} (= O_{y-x}) is the overlap between Species 1 and 2, B_x is the niche breadth of Species 1 and B_y is the isotopic niche breadth of Species 2; the resulting value ranges from 0 (no overlap) to 1.0 (complete overlap). Consistent niche breadth among meso- or small carnivores provided changes in the environmental context would support Eltonian niche conservatism, though the drivers leading to a lack of conservatism likely change for individual species. Furthermore, increased isotopic niche overlap among subordinate carnivores in the absence of wolves would support that facilitation mediates these interactions (i.e., trophic facilitation decreases competitive overlap between meso- and small carnivores; Sivy et al. 2018). Finally, increasing isotopic niche breadth through time – especially a shift encompassing higher δ^{13}C values – would indicate higher consumption of human foods.

To determine the proportional assimilation of dietary groups for each species across time periods we used a species and time period-specific suite of concentration dependent mixing models using the R package *simmr 0.4.5* (Parnell 2019). First, we tested differences between historic and contemporary prey samples collected across the UP and northern Wisconsin (see SM: Methods) to test for baseline isotopic shifts through time. We used a PERMANOVA in the R package *vegan 2.6-2* (Oksanen et al. 2022) and found no evidence for isotopic differences in putative prey sources ($p>0.15$ for all comparisons), so we combined historic and contemporary prey data for all downstream analyses. To account for potential human resource subsidies in carnivore diets, we also included isotopic ratios from anthropogenic sources, including trophic-corrected human hair isotope values to account for refuse and domestic prey (Hülsemann et al. 2015, Newsome et al. 2015b). Finally, we included berries that would be available during the hair growth period typical of canids (i.e., spring-early-summer; Korhonen *et al.*, 1984) and aggregated isotopically indistinct prey items, using a k-means clustering algorithm (Phillips et al. 2014) in the R package *NbClust v3.0.1* (Charrad et al. 2014). We identified 4 isotopically distinct and biologically meaningful prey groups representative of the UP: (1) berries (e.g., *Rubus spp.* and *Ragaria spp.),* (2) white-tail deer, (3) small prey (e.g., mice [*Peromyscus spp*.], voles [*Myodes gapperi*], squirrels [*Glaucomys sabrinus* and *Tamiascirus hudsonicus*], and grouse [*Bonasa umbellus*]), and (4) human foods (see SM for further details).

We estimated proportional dietary inputs of species at the population- and individual-level by running 3 chains of 300,000 iterations and removed the first 200,000 iterations as burn-in and then thinned posterior samples to every 100th sample. We used uniform (i.e., even dietary proportions 1/N-sources = 0.25) priors throughout the modelling process (Parnell et al. 2010, Stock et al. 2018) with the exception of wolves. Because they are known to be large ungulate specialists in the region (Petroelje et al. 2019), we used loosely informed priors for wolves based on past work in the Great Lakes region (Petroelje et al. 2019): Human Foods = 0.13 ± 0.06, Deer = 0.67 ± 0.13, Small Prey = 0.13 ± 0.06, and Berries = 0.08 ± 0.06. We used [C] and [N] data of berries ([C] = 0.48; [N] = 0.01), deer ([C] = 0.47; [N] = 0.14), and small prey ([C] = 0.47; [N] = 0.14) from Carlson *et al.*, (2014) and data from Hopkins and Ferguson (2012) for the concentrations of anthropogenic-derived sources ([C] = 0.53; [N] = 0.07). Lastly, we used trophic discrimination factors of 2.0‰ (±0.5) and 3.5‰ (±0.5) for δ^{13}C and δ^{15}N for all hair and 3.2‰ (±0.5) and 3.5‰ (±0.5) for δ^{13}C and δ^{15}N for all bone collagen samples, respectively (Roth and Hobson 2000, Stephens et al. 2022). However, because we sampled small prey and deer hair and not muscle, we adjusted our δ^{13}C discrimination factors by –0.5‰ for those prey groups based on tissue specific discrimination factors (Roth and Hobson 2000, Newsome et al. 2015b).

We first quantified prey use at the population level by grouping each canid species by time-period and estimated proportional use of the four potential prey sources (berries, deer, small prey, and human foods). At the population level, higher deer consumption for meso- or small carnivores in the presence of wolves would support our prediction of trophic facilitation by wolves. Furthermore, high deer consumption (i.e., carrion provisioning) in the face of altered human use would suggest that scavenging is a highly conserved trophic strategy. Then, we analyzed individuals separately to quantify consumption of each prey group and tested the impacts of community context on dietary variability. For the population- and individual-level models, we identified model convergence using the Gelman–Rubin diagnostic value $\hat{R} < 1.01$ and the effective sample size of each estimate >5000. Because our estimates of dietary proportions are posterior distributions, we calculated the probability of directionality (PD) in the R package *bayest v1.4* (Kelter 2020), testing the consumption of each diet item was greater (or lower) across community context (represented as PD(Community_1< [or >]Community_2). PD values range from 0.5 – indicating identical posterior distributions – and 1.0 – indicating no overlap in posterior distributions.

We estimated dietary niche breadth and overlap using our dietary proportion estimates of individuals across time periods. First, we performed a non-metric multi-dimensional scaling (NMDS) analysis on all median individual-level diet estimates across time periods in the R package *vegan 2.6-2* (Oksanen et al. 2022) using the Bray-Curtis dissimilarity distances. We included the median estimates of prey use for each individual carnivore across all time periods to be able to compare dietary overlap between species and across time. Using the two axis scores from our NMDS, we again used the R package SIBER to calculate the standard ellipse area in p-space (SEA_p unitless) and the total dietary niche overlap (O_p). We again report the proportion of non-overlapping area of the two ellipses being compared relative to the non-overlapping area, ranging from 0 (no overlap) to 1.0 (complete overlap). To quantify the foraging strategies of individuals within each population in each time period, we used the individual proportional estimates of prey groups to quantify dietary specialization (ε) and similarity (s) indices and visually inspected the density plots (Newsome et al. 2012). Here, ε varies between 0 (an ultra-generalist) and 1 (an ultra-specialist) and s varies between 0 (exactly dissimilar from the population) and 1 (exactly similar to the population). Accordingly, the density plots can be subdivided into four quadrants: dietary specialists ($\varepsilon>0.50$) with diets dissimilar to the population ($s<0.50$; dissimilar-specialists), dietary specialists with diets similar to the population ($s>0.50$; similar-specialists), dietary generalists ($\varepsilon<0.50$) with diets dissimilar to the population (dissimilar-generalists), and dietary generalists with diets similar to the population (similar-generalists; Newsome *et al.,* 2012). We classified dietary specialization and similarity from the posterior estimates of individual diets and generated density plots to classify the foraging strategies at the population level based on where the density distributions using a kernel function (Newsome et al. 2012) – foraging strategies are qualified as unique if there is little overlap between high density centers. Finally, we used a similarity percentage analysis in the R package *vegan 2.6-2* (Oksanen et al. 2022) to determine percent contribution of each prey group to the dissimilarity in diet composition among groups based on a Bray–Curtis dissimilarity matrix calculated from the estimates of each of prey group.

Results

Isotopic Niche Breadth and Overlap

The isotopic niche breadth of wolves in the reassembled carnivore community was ~250% greater than the historically (‘functional’) observed value, increasing from 1.12±0.31‰^{2} to 2.99±0.56‰^{2} (Figure 1). Coyotes had a narrower niche breadth when wolves were present in the functional (0.64±0.11‰^{2}) and reassembled (1.66±0.63‰^{2}) communities, respectively, compared to the simplified community when wolves were absent (3.33±0.74‰^{2}; Figure 1). Alternatively, red foxes had a relatively narrow isotopic niche breadth within the functional (1.91±0.41‰^{2}) and departed (1.98±0.75‰^{2}) communities, while isotopic niche breadth in the reassembled community was nearly 4× larger (7.52‰±1.95‰^{2}). We found that the total breadth of the carnivore community increased through time due to increasing human resource subsidies in the UP (Functional = 1.24±0.15‰^{2}, Departed = 3.20±0.60‰^{2}, and Reassembled = 4.49±0.57‰^{2}).

The highest proportional isotopic overlap we observed was in the absence of wolves ($O_{\delta\text{-Departed}}$ = 0.38±0.09) and isotopic niche overlap between coyotes and foxes was lowest in the reassembled community, despite increased human subsidies ($O_{\delta\text{-Reassembled}}$ = 0.23±0.07; Figure 1). Isotopic niche overlap between wolves and coyotes decreased from the functional ($O_{\delta\text{-Functional}}$ = 0.44±0.12) to reassembled ($O_{\delta\text{-Reassembled}}$ = 0.37±0.09) communities, as did overlap between wolves and foxes ($O_{\delta\text{-Functional}}$ = 0.49±0.12; $O_{\delta\text{-Reassembled}}$ 0.38±0.09; SM Figure 1).

Dietary Contributions, Dietary Niche Overlap, and Foraging Strategies

Wolves consumed >60% deer and their diets were relatively similar through time, though they consumed slightly higher proportion of human food subsidies contemporarily (increasing from ~20% to 30%; Figure 2). Coyotes consumed ~200% more deer when wolves were present on the landscape (Figure 2) leading to a narrower dietary niche (Figure 3). Specifically, deer consumption was much greater in the functional (0.32±0.06) and reassembled (0.43±0.13) carnivore community than in the departed community (0.18±0.12; $PD_{(\text{Functional}>\text{Departed})}$ = 0.85 and $PD_{(\text{Reassembled}>\text{Departed})}$ = 0.92; Figure 2). Interestingly, coyotes consumed higher proportions of deer in the reassembled community than the functional community ($PD_{(\text{Reassembled}>\text{Functional})}$ = 0.78), while foxes consumed similar proportions of deer regardless of carnivore community context (0.18±0.09, 0.11±0.11 and 0.17±0.11 in the functional, departed, and reassembled communities, respectively; Figure 2).

Although the magnitude of isotopic and dietary niche breadth differed, the percent changes across time periods were indistinguishable, corroborating the isotopic niche breadth results (SM Table 5). Indeed, the NMDS diagnostics suggest good representation of the proportional data with no risk of drawing false inference (maximum residual error = 0.00032;

Stress = 0.085). Estimates of dietary overlap revealed limited wolf-coyote and wolf-fox overlap ($O_p \leq 0.05$). Like the observed isotopic niche overlap, the estimated dietary niche overlap between coyotes and foxes was highest in the absence of wolves, increasing by ~600% when wolves were absent ($O_{p\text{-Functional}} = 0.07 \pm 0.06$, $O_{p\text{-Departed}} = 0.43 \pm 0.15$) and then decreasing following community reassembly ($O_{p\text{-Reassembled}} = 0.05 \pm 0.02$). Generally, we observed a reciprocal pattern in the directional niche space overlap between species whereby the species with the largest dietary niche space greatly overlapped with the species of the narrower niche breadth (SM Table 6).

Human foods were the leading cause of dietary dissimilarity among foxes at the individual-level in the functional and reassembled communities, accounting for >40% of the total dissimilarity among individuals, while consumption of small prey drove dissimilarity in the departed community (SM Table 7). Coyote dissimilarity was driven by the consumption of deer in the departed and reassembled communities, while it was driven by human foods in the functional community (SM Table 7). Lastly, deer consumption drove variation in wolf diets accounting for ~42.5% of the dissimilarity among individuals (SM Table 7). Considering diets across communities, dietary dissimilarity was significantly high for foxes when comparing the functional and departed diets to the reassembled carnivore community (SM Table 8). Meanwhile, coyote diets were most dissimilar relative to the departed community, but similar when wolves were present (SM Table 9). Lastly, wolf diets were relatively similar during the functional and reassembled community (SM Table 10).

The trophic strategies of both wolves and foxes were largely synchronous through time, becoming most variable in the presence of high human use (Figure 3). Wolves were predominantly classified as highly similar ($s \geq 0.75$) and generalists ($\varepsilon \approx 0.40$; Figure 3).

Alternatively, coyotes were classified as dietary generalists throughout (all $\varepsilon \leq 0.25$), though their trophic strategy was more variable, and they exhibited more dissimilar diets when wolves were absent ($s_{Departed} = 0.73 \pm 0.12$) compared to the functional ($s_{Functional} = 0.88 \pm 0.09$) and reassembled ($s_{Reassembled} = 0.84 \pm 0.10$) communities (Figure 3). Notably, foxes were dietary generalists ($\varepsilon = 0.22 \pm 0.09$) when the carnivore community was functionally intact, but two divergent foraging strategies emerged in the reassembled community whereby some individuals were quantified as dietary generalists ($\varepsilon < 0.35$), while others were classified as dietary specialists ($\varepsilon > 0.50$; Figure 3).

Discussion

We quantified the diets of sympatric canids in the UP of Michigan over a century of ecological change to assess Eltonian niche conservatism and the consistency of trophic relationships through time. Reassembled carnivore community interactions were markedly different than the historic community and shaped by both large carnivore provisioning and human food subsidies. Indeed, we found that wolves structured the diets of meso-carnivores like coyotes by facilitating access to deer carrion, resulting in the release of competition for smaller carnivores like red foxes. Furthermore, we show that humans can decouple competitive interactions within carnivore guilds by providing exceptionally high quantities of resource subsidies, especially to small carnivores. Notably, individual-level analysis of trophic strategies provided a means to make inference on the competitive pressure for individuals and human habituation exhibited by small carnivores, such as the red fox. Our results are consistent with recent studies illustrating the plasticity of mammalian carnivore diets, and we highlight two contrasting mechanisms that can overwhelm Eltonian niche conservatism depending on body size.

Eltonian niche conservatism

Given Elton's (1927) emphasis on the functional role of a species within a community, Eltonian niche conservatism is contingent on the context of the community itself (Dussault 2022). Grinnellian niches have been hypothesized to be more labile than Eltonian niches (Larson et al. 2010), indicating that restored communities should maintain a similar structure to their historical counterparts. Accordingly, we hypothesized that large carnivores anchor the ecological interactions between meso- and small carnivores via resource facilitation; ultimately, these interactions cascade to shape the services that meso- and small carnivores provide to the broader community. Supporting our hypothesis, we found high levels of deer consumption by coyotes when wolves were present in the functional and reassembled carnivore communities (Figure 2), resulting in lower dietary overlap – and presumably competition – between coyotes and foxes (SM Table 5). These results are supported by past empirical studies (Wilmers et al. 2003, Mark Elbroch and Wittmer 2012, Pereira et al. 2014), but further reinforce that scavenging resources facilitated by large carnivores is a highly viable strategy for meso-carnivores despite the potential interspecific conflict (Wilmers et al. 2003, Wilson and Wolkovich 2011, Ruprecht et al. 2021). This strategy appears conserved when large carnivores are present, regardless of environmental context or human use. Our framing differs from Eltonian niche conservatism as it has previously been tested, where conservatism is a lack of variation in the diet of a species across a geographical range (Manlick et al. 2019). Rather, we aimed to realign this modern concept with Elton's traditional conceptualization of the species niche (Elton, 1927; *see*

Dussault, 2022). In our present framing of Eltonian niche conservatism, the facilitation of deer to coyotes when wolves are present was, indeed, conserved. Although the use of other prey groups slightly varied between historic and modern samples (Figure 2), dietary overlap and the trophic strategies of coyotes were most similar in the presence of wolves (Figures 2 and 3), supporting Eltonian niche conservatism in the presence of wolves regardless of environmental context. This was not the case for foxes, however, who became more individually varied in trophic strategy and diet in the reassembled carnivore community (Figure 2 and 3). The Eltonian niche of foxes, instead, was conserved in the departed and functional carnivore communities, suggesting that coyotes most strongly impact the foraging strategies of foxes as opposed to wolves. Notably, foxes exhibited an increasing disparity in foraging strategies through our study period, which coincided with increasing human food subsidies (Figure 3). Globally, foxes are the most cosmopolitan carnivore and exhibit high variability in trophic strategies (Henry 1996), so it is not surprising that they have the behavioral and trophic flexibility necessary to expand their Eltonian niches when presented with novel opportunities such as human foods.

Facilitation and Competition

Globally, large carnivores provide >1,000 kg of carrion per individual per year to scavengers, with large allocations to meso-carnivores (Prugh and Sivy 2020). Although coyotes are effective predators of deer fawns, accounting for as much as 25% of fawn mortalities in the UP (Duquette et al. 2014), we found that coyotes consumed ~50% more deer when wolves were present, thereby shaping the dietary niche of coyotes (Figure 2). This was especially surprising in the context of the functional community (1900-1920), as deer and wolf abundances were lowest during this time period (SM Figure 1); although deer and wolf abundances were relatively lower in the functional community, we nevertheless detected high levels of trophic facilitation to coyotes in the form of deer carrion. Competitive interactions within carnivore communities are structured by body size differences between species (Donadio and Buskirk 2006) but agonistic interactions can be mitigated by minimizing overlap in resource use (Wilson and Wolkovich 2011, de Oliveira and Pereira 2014). Consequently, resource facilitation by large carnivores can lead to decreased competition between meso- and small carnivores via two mechanisms. First, provisioned carrion can decrease the impact of exploitative competition for a shared and limited resource base (Levi and Wilmers 2012, Allen et al. 2015). For example, resources provisioned by large carnivores are often high-quality and preferred (and monopolized) by large-bodied meso-carnivores (Wilson and Wolkovich 2011, Prugh and Sivy 2020), while small-bodied carnivores scavenge depending on the relative availability of alternative resources (Pereira et al. 2014). Indeed, in the presence of wolves, we found evidence that coyotes consumed much higher proportions of deer ($PD_{(Coyote>Fox)} = 0.90$ and $PD_{(Coyote>Fox)} = 0.93$ in the functional and departed communities, respectively; Figure 2). Further, small-bodied carnivores are often superior exploitative competitors (Polis et al. 1989, Holt and Polis 1997), thereby allowing them to avoid interference altogether by targeting lower quality (and hence low risk) resources (Robinson *et al.*, 2014; Smith *et al.*, 2023). Indeed, foxes exhibited the greatest isotopic and dietary niche breath in each community and our analysis of directional dietary overlap suggested that foxes exploited the niche space of their larger, interspecific competitors (SM Table 6). Our results suggest that although coyotes shifted their diets following the extirpation of wolves (i.e., the departed community), red fox diet did not change (Figures 1 and 2). Second, facilitation by large carnivores can disproportionately impact large-bodied meso-carnivores via ‘fatal attraction’ to scavenging (Sivy et al. 2017). This higher reliance on provisioned resources by large-bodied meso-carnivores (like we found in coyotes; Figure 2) can enhance agonistic encounters with apex predators with population-level demographic consequences (Ruprecht et al. 2021), which has been observed in the UP (Fowler et al. 2021). These interactions, in turn, can release small-bodied meso-carnivores from competition with dominant meso-carnivores, and explain the indirect positive effects that large carnivores have on small carnivores. While we did not test this hypothesis directly, wolves in our study area suppress coyote occupancy, with positive effects on fox occurrence (Fowler et al. 2021). Our study suggests that provisioning by large carnivores facilitates dietary partitioning between sympatric meso- and small carnivores and may be the proximate mechanism that mediates the release of foxes from competition.

Although foxes consumed nontrivial proportions of deer (~0.16±0.11, likely from scavenging), this may place them at risk of interference with both wolves and coyotes. Indeed, wolves and coyotes are known to displace foxes from their kills and carrion, respectively (Gese et al. 1996, Palomares and Caro 1999), suggesting that temporal partitioning might be important for deer consumption in red foxes – either avoiding the times that large and meso- carnivores are present or accessing carrion when the larger bodied species have given up (Fowler et al. 2021). Likewise, human resource subsidies can also release foxes from competition by providing a resource not tethered to immediate negative, competitive interactions (Pluemer et al. 2019). Indeed, foxes and coyotes have been found to co-occur at higher frequencies in the presence of humans – largely due to the consumption of human foods (Newsome et al. 2015a, Mueller et al. 2018). The divergent foraging strategies that red foxes developed following community reassembly (Figure 3) shows the emergence of alternate strategies that competitors can utilize to co-occur with their larger competitors. Finally, the individual-level shift to novel resources (i.e., human foods) can result in a reprieve of competitive pressure for some species, such as foxes, with consequences that can cascade through communities and food webs (Schell et al. 2021, Rodriguez Curras et al. 2022).

Human impacts to competitive interactions

Over the last century, the total human population of the UP has remained relatively stable (~300k), accompanied by a rural-to-urban migration, ≥ 50% decrease in agricultural lands (US Census Data), and a growing tourism industry (MEDC 2022). In the last 50 years, State and National Parks in the UP have reported park-visitor increases between 200–300% (NPS IRMA); today the UP receives >6 million tourists a year (MEDC). Accompanying the change in industry, many of the UP forests have recovered from the excessive logging in the late-1800s and much of the UP has become designated as National or State Forest, designed for recreational tourism. The land-use changes in the UP over the past century have largely resulted in forest succession, with ecological processes resembling natural and undisturbed systems (Anderson et al. 2023). Nevertheless, we found that the isotopic niche breadth of the carnivore community increased through time (Figure 1) and was accompanied by an increase in the consumption and specialization on human foods, especially in foxes (Figures 2 and 3). Although meso- and small carnivores exhibit great dietary plasticity across their ranges (Gittleman 1989) and can persist in contemporary human landscapes by consuming high levels of human foods (Newsome et al. 2015b, Manlick and Pauli 2020), there is limited evidence that human food subsidies drive individual specialization (Manlick and Newsome 2021). Our work adds to the growing body of literature showing that human foods can increase individual specialization in carnivores – particularly small carnivores like foxes – with putative downstream consequences to the impacts of suppression and facilitation. The human food system is particularly ‘leaky’, with an estimated one-quarter to one-third of food produced for human consumption lost or wasted each year (The World Bank, 2014). Given the environmental context in the UP, we suspect the increasing dietary niche breadth and human food consumption has been due to an influx of human foods via refuse rather than agriculture (Manlick and Pauli 2020) or landscape homogenization. Our results, then, suggest that protecting and restoring community interactions cannot be accomplished by only protecting land from development and homogenization, and more emphasis should be placed on minimizing 'leakage' from human to natural food webs.

The niche expansion of the reassembled carnivore community was not reflected by coyotes, who possessed a narrower isotopic and dietary niche relative to the departed community (Figures 1 and 2). Indeed, wolves appeared to constrain the dietary niche of coyotes via the facilitation of high-quality resources, as niche breadth was not impacted by human subsidies (Figure 2). Canids are well equipped to exploit human landscapes because of their body size, dietary flexibility, and low risk they pose to humans (Kuijper et al. 2016), so it was surprising that coyotes did not more strongly track anthropogenic resources. At the highest human densities, consumption of human foods by contemporary coyotes has been found to be as high as 50% (Newsome et al. 2015b, Manlick and Pauli 2020), which is comparable to our estimates of the highest proportion of human foods in coyote diets (~40%). However, this value is much lower than the overall consumption of human foods by foxes, where numerous individuals consumed >60% human food subsidies. Alternatively, human food resources were the leading cause of dietary dissimilarity among coyotes and foxes (SM Table 4), exemplifying the disproportionate importance of exploiting these resources. The use of human food subsidies by meso- and small carnivores can also result in behavioral changes with variable fitness consequences (Murray et al. 2015, Newsome et al. 2015a). On one hand, human food subsidies can actually increase co-occurrence among competing carnivores like coyotes and foxes (Mueller et al. 2018, Pluemer et al. 2019). On the other, human resource subsidies can also lead to the collapse of predator-prey (Rodewald et al. 2016, Parsons et al. 2022) and community interactions (Sapolsky and Share 2004, Manlick and Pauli 2020), as well as increased disease transmission (Murray et al. 2015) and ecological traps (Moss et al. 2016, Lamb et al. 2017). Given the current repatriation of large carnivores to human-dominated landscapes (Chapron et al. 2014), there is an urgent need to assess the degree to which human subsidies decouple interactions like facilitation and suppression that are predicted to be highly conserved.

Conclusion

Re-establishing trophic interactions has become a global ecological priority (Dobson et al. 2009, Estes et al. 2011), with anticipated benefits to biodiversity (Terborgh 2015) and ecosystem functionality (Ritchie et al. 2012). Carnivore restoration (particularly of large carnivores) has been promoted as an effective management tool to re-establish community interactions and lost functional roles (Pettorelli et al. 2019), particularly by mediating consumer–resource dynamics and top-down forcing (Ritchie et al. 2012, Ripple et al. 2014). However, ecologists still do not fully understand how the restoration of large carnivores will affect community-level processes and ecological functions (Ritchie et al. 2012, Pettorelli et al. 2019), particularly in the human-dominated landscapes of the Anthropocene (Chapron et al. 2014). Understanding and applying the concepts of Eltonian niche conservatism within the context of large carnivore repatriation is important because it can inform managers of the projected functional roles of reintroduced carnivores in novel ecosystems. Furthermore, applying this conceptualization to individuals within a broader population can refine the use of limited conservation resources to maximize impact and also provide a greater mechanistic understanding of ecological processes. In the context of Eltonian niche conservatism, we predict that horizontal interactions such as facilitation of carrion can be conserved among carnivores like wolves and coyotes, though these relationships could be decoupled by high resource subsidies from humans. Ultimately, as large carnivores repatriate their former ranges into cotemporary human-dominated landscapes we caution managers to expect variable outcomes, and our findings suggest that the realized functional roles of carnivores may be undermined by human food subsidies that permeate contemporary ecosystems.

Acknowledgements

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Figures

Figure 1. Standard ellipse area (SEAc; 95%) of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values for wolves (*Canis lupus*; gray), coyotes (*Canis latrans*; blue), and red foxes (*Vulpes vulpes*; brown) across the functional (1910-1930; A), departed (1950-1970; B), and reassembled (2000-2020; C) carnivore community in the Upper Peninsula of Michigan.

Figure 2. Posterior distribution of assimilated human foods, deer (*Odocoileus virginianus*), small prey (e.g., Cricetids, Leporids, and Phasianidae; see Methods), and berries (*Rubus spp.*) from wolf (*Canis lupus*; dark grey), coyote (*Canis latrans*; blue), and red fox (*Vulpes vulpes*; light grey) tissues estimated via stable isotope mixing model (A–C). Note that we used uniform proportions (0.25) as priors for coyotes and foxes and informative priors for wolves based on a diet of ~70% deer. Population-level dietary overlap from the stable isotope mixing model results of individual (median) diet represented using non-metric multidimensional scaling (NMDS; D–F). Assimilated diet and dietary overlap are shown across the functional (1910-1930; A), departed (1950-1970; B), and reassembled (2000-2020; C) carnivore community in the Upper Peninsula of Michigan.

Figure 3. Foraging strategies represented as density plots of individual dietary similarity (x-axis) and specialization (y-axis) of wolves (*Canis lupus*; A–C), coyotes (*Canis latrans*; D–F), and red foxes (*Vulpes vulpes*; G–I) in the respective functional (1910-1930; A, D, and G), departed (1950-1970; E and H), and reassembled (2000-2020; C, F, and I) carnivore community in the Upper Peninsula of Michigan. Dashed lines represent the qualitative cutoffs identifying dissimilar individuals and generalists (ε and $s < 0.50$) and similar individuals and specialists (ε and $s > 0.50$).

Figure 1.

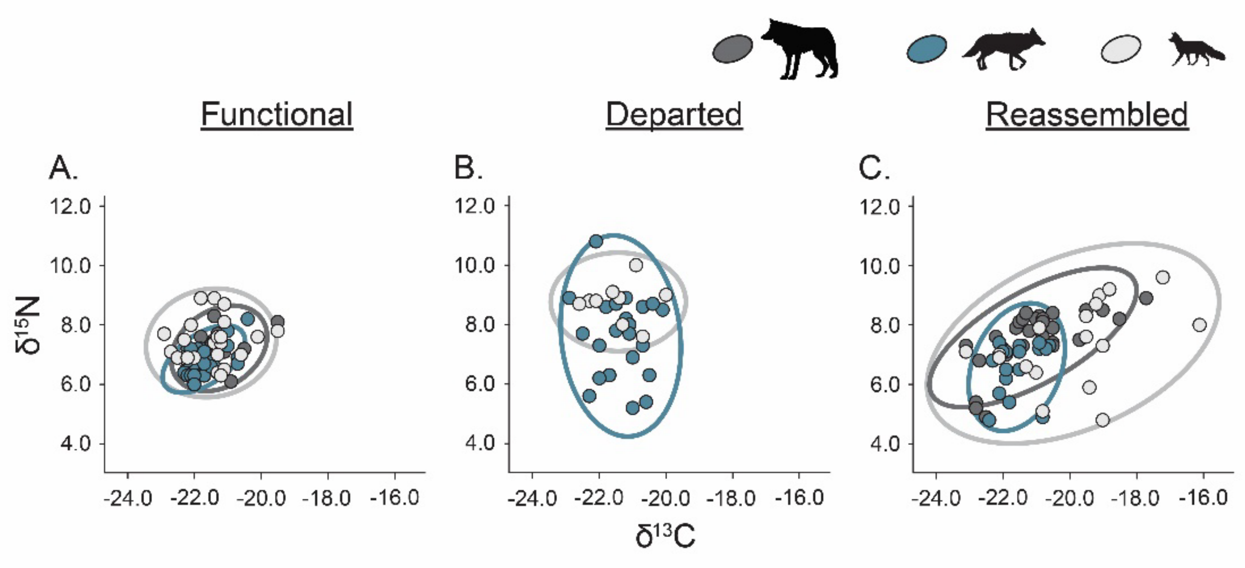

Functional
Departed
Reassembled
A.
B.
C.
12.0
10.0
8.0
6.0
4.0
δ15N
-24.0
-22.0
-20.0
-18.0
-16.0
δ13C

Figure 2.

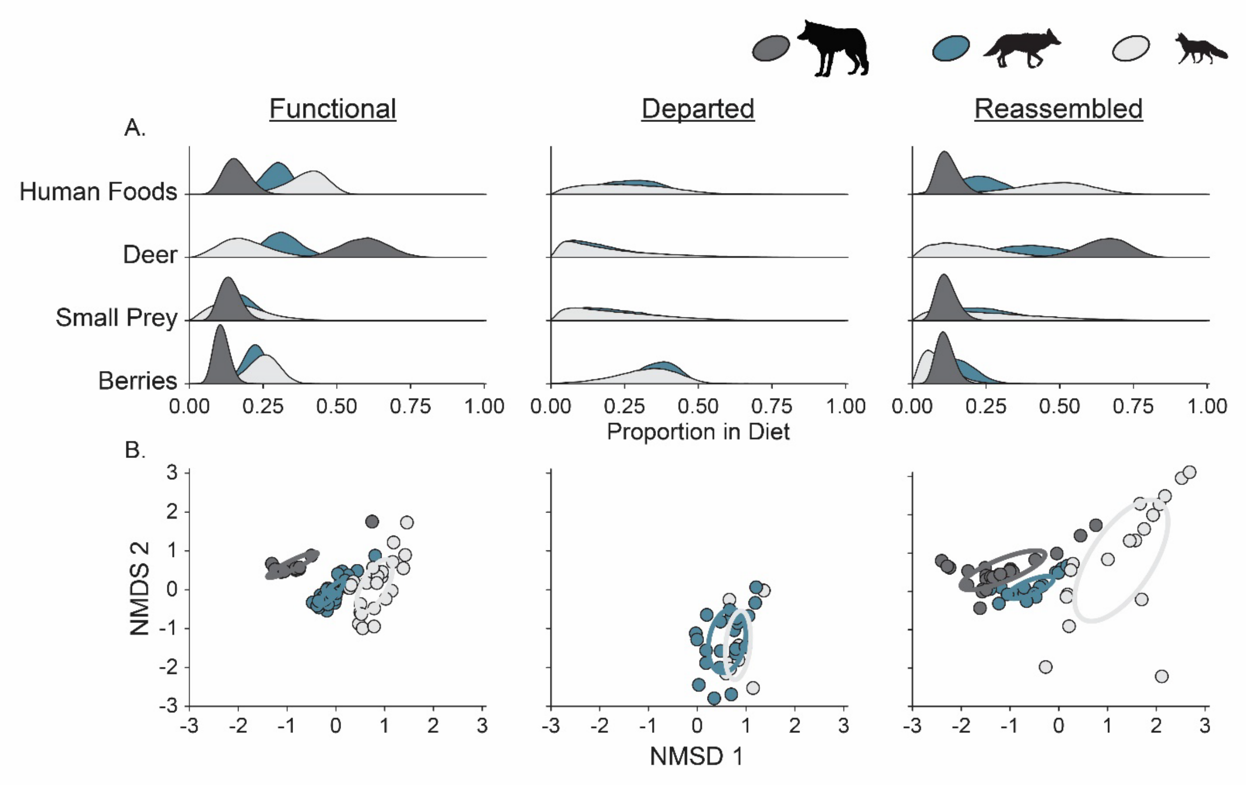
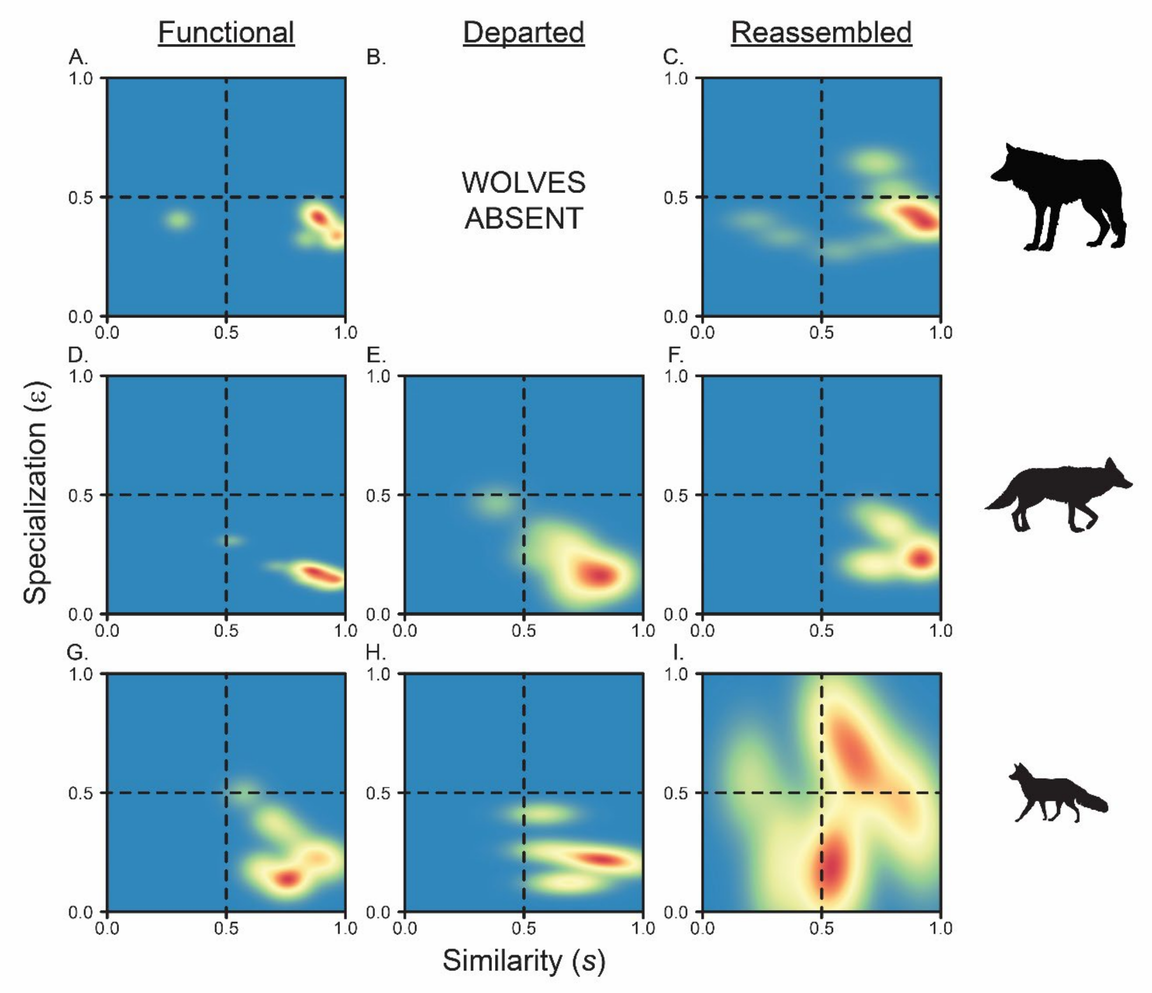

Functional
Departed
Reassembled
A.
Human Foods
Deer
Small Prey
Berries
0.00
0.25
0.50
0.75
1.00
Proportion in Diet
B.
NMDS 2
3
2
1
0
-1
-2
-3
NMSD 1

Figure 3.


Functional
Departed
Reassembled
A.
B.
C.
D.
E.
F.
G.
H.
I.
WOLVES ABSENT
Specialization (ε)
Similarity (s)
0.0
0.5
1.0

Supplementary Materials: Carnivore community reassembly provides a test of Eltonian niche conservatism

SM Methods

Prey groups

To test whether a baseline shift had occurred in the Upper Peninsula of Michigan during our sampling period – which would influence the prey samples collected for our analysis – we collected contemporary samples of deer mice (Peromyscus maniculatus), white-tailed deer (Odocoileus virginianus), snowshoe hares (Lepus americanus), red-backed voles (Myodes gapperi), and Eastern meadow voles (Microtus pennsylvanicus) and sampled these same species from museum samples collected from 1910-1920. Contemporary and museum samples were collected across a representative area of the UP to minimize potential spatial biases as spatial sampling could affect the trophic niche of species. We used a PERMANOVA in the R package vegan 2.6-2 (Oksanen et al., 2022) and found no evidence for isotopic differences in putative prey sources ($p>0.15$ for all comparisons). Accordingly, we combined all prey sources across time periods for our downstream analysis of proportional diet space (see Methods). We contend that the samples that we collected of prey widely represent the major foraging groups available to carnivore in the UP of Michigan.

To get a robust estimate of human food sources (Methods) we used a $N = 10,000$ bootstrapping approach using trophically corrected human hair data from Hulsemann et al. 2015, Newsome et al. 2015 on the national level. Our reasoning, similar to Newsome et al. 2015, was to include a general human signature and trophically correct this signature to get the estimated, broadly categorized diet of humans.

Trophic discrimination factors (TDFs)

Whereas TDFs have been shown to not strongly vary across feeding guilds, there is a significant difference across tissues sampled for $\delta^{13}C$ (Stephens et al., 2022). Accordingly, we included tissue specific TDFs in our mixing models (see Methods).

Results

Our mixing models revealed the proportion of important prey groups for carnivores in the UP (Figure 2) with relative good fit (SM Table 2). Notably, because mixing model results always sum to 1.0, we observed correlation among the posterior distribution of our prey groups. Specifically, berries and human foods were broadly positively correlated within each species and time period (generally highest for coyotes [0.60-0.75], followed by wolves [0.44-0.53], and finally foxes [0.20-0.60]). Small prey and deer exhibited a modest (-0.10–-0.80) – though highly variable – negative relationship across time periods for coyotes and foxes, while small prey was positively associated with human foods for wolves (0.33-0.45).

Our choice to include a prior for wolves influenced the results from our mixing models. Generally, in our mixing models without a prior, the consumption of deer decreased by 15-30% while it was generally associated with an increase in berries and human foods. However, the use of priors for wolves makes ecological sense given their strong selection for ungulate prey biomass (Petrolje et al., 2019).

SM Tables

SM Table 1. Diet samples collected from museum (primarily for historic samples), collected for this study, and used from previous studies that we incorporated into our analysis.

	UP Historic		UP Modern		Wisc. Modern			
Row Labels	d13C	d15N	d13C	d15N	d13C	d15N	N	Source
Rubus spp. and *Ragaria spp.*					–28.5±1.4	–3.1±1.4	5	Modern Carlson et al. 2014
Blarina brevicauda					–21.5±0.5	3.7±0.7	11	Modern Carlson et al. 2014
Bonasa umbellus					–24.0±0.8	3.5±0.6	7	Modern Carlson et al. 2014
Glaucomys sabrinus					–20.0±0.2	2.3±0.8	3	Modern Carlson et al. 2014
Lepus americanus	–22.4±1.2	4.02±1.4					5	Historic Sampled
Microtus pennsylvanicus	–24.2±0.6	4.5±1.7					9	Historic Sampled
Myodes gapperi	–21.4±1.0	4.0±1.0			–22.0±1.2	4.3±1.2	18	Historic Sampled = 10; Modern Carlson et al. 2014 = 8
Odocoileus virginianus	–24.1±1.3	3.6±1.5			–23.6±1.3	2.7±0.7	26	Historic Sampled = 8; Modern Carlson et al. 2014 = 18
Peromyscus leucopis					–22.9±0.8	3.4±0.6	4	Modern Carlson et al. 2014
Peromyscus maniculatus	–22.5±2.0	4.6±1.5	–21.5±1.1	2.1±1.5	–21.7±1.2	3.2±0.4	29	Historic Sampled = 10; Modern Carlson et al. 2014 = 9; Modern Sampled = 10
Sorex cinereus					–21.4±1.0	3.9±0.5	5	Modern Carlson et al. 2014
Tamiasciurus hudsonicus					–21.6±0.9	2.4±1.2	12	Modern Carlson et al. 2014
Aves					–20.2±0.4	6.1±0.4	4	Modern Carlson et al. 2014

SM Table 2. Mixing model diagnostics including pD (var(deviance)/2), Deviance, and the minimum effective sample size from our Bayesian mixing models in simmr. The Rubin-Gelman statistic (R-Hat) for all models was 1.001.

	pD	Deviance	Min. Effective N
Wolf			
Functional	36.4	70.93±8.53	9500
Reassembled	9.3	202.25±4.31	14000
Coyote			
Functional	5.3	122.28±3.25	5600
Departed	4.5	129.20±3.00	6100
Reassembled	4.4	80.83±2.98	19000
Red Fox			
Functional	4.6	113.59±3.03	14000
Departed	9.7	56.63±4.40	15000
Reassembled	4.2	129.22±2.90	12000

SM Table 3. Probability of directionality (PD) comparing diet groups within species and across each time period in our study.

Wolves	*Functional-Reassembled*
Human Foods	0.74
Deer	0.58
Small Prey	0.62
Berries	0.53

Coyotes	Functional-Departed	Functional-Reassembled	Departed-Reassembled
Human Foods	0.67	0.84	0.85
Deer	0.85	0.77	0.91
Small Prey	0.69	0.66	0.54
Berries	0.54	0.88	0.80

Foxes	Functional-Departed	Functional-Reassembled	Departed-Reassembled
Human Foods	0.66	0.60	0.54
Deer	0.73	0.57	0.65
Small Prey	0.56	0.70	0.70
Berries	0.50	0.98	0.95

SM Table 4. Probability of directionality (PD) comparing diet groups within each time period and across species in our study.

Functional	*Wolf-Coyote*	*Wolf-Fox*	*Coyote-Fox*
Human Foods	0.75	0.92	0.86
Deer	0.99	1.00	0.90
Small Prey	0.75	0.74	0.51
Berries	1.00	1.00	0.69

Departed			*Coyote-Fox*
Human Foods			0.71
Deer			0.69
Small Prey			0.67
Berries			0.64

Reassembled	*Wolf-Coyote*	*Wolf-Fox*	*Coyote-Fox*
Human Foods	0.80	0.76	0.88
Deer	0.85	0.99	0.93
Small Prey	0.89	0.90	0.62
Berries	0.95	0.86	0.80

SM Table 5. Isotopic (SEA_d) and proportional (SEA_p) dietary overlap for each species and time period.

Functional

	Red Fox	Coyote	Wolf
Red Fox	SEA_p = 3.90±0.81 SEA_d = 1.91±0.41	O_p = 0.07±0.06	O_p = 0.004±0.01
Coyote	O_d = 0.32±0.08	SEA_p = 0.85±0.15 SEA_d = 0.64±0.11	O_p = 0.001±0.004
Wolf	O_d = 0.49±0.12	O_d = 0.44±0.12	SEA_p = 1.70±0.51 SEA_d = 1.12±0.31

Departed

	Red Fox	Coyote
Red Fox	SEA_p = 4.50±1.8 SEA_d = 1.98±0.75	O_p = 0.43±0.15
Coyote	O_d = 0.38±0.09	SEA_p = 6.30±1.4 SEA_d = 3.33±0.74

Reassembled

	Red Fox	Coyote	Wolf
Red Fox	SEA_p = 23.00±6.50 SEA_d = 7.52±1.95	O_p = 0.05+0.02	O_p = 0.07±0.03

Coyote	$O_d = 0.23 \pm 0.07$	$SEA_p = 1.90 \pm 0.43$ $SEA_d = 1.66 \pm 0.63$	$O_p = 0.16 \pm 0.09$
Wolf	$O_d = 0.38 \pm 0.09$	$O_d = 0.37 \pm 0.09$	$SEA_p = 5.60 \pm 0.98$ $SEA_d = 2.99 \pm 0.56$

SM Table 6. Directional isotopic (O_d) and dietary (O_p)

Functional

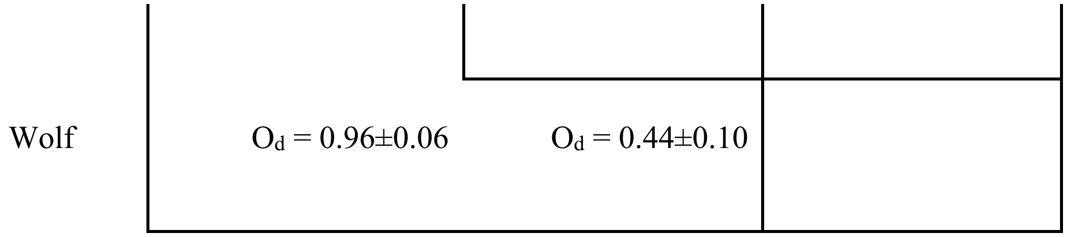
	Red Fox	Coyote	Wolf
Red Fox		$O_d = 0.33 \pm 0.08$	$O_d = 0.54 \pm 0.15$
Coyote	$O_d = 0.92 \pm 0.09$		$O_d = 0.80 \pm 0.14$
Wolf	$O_d = 0.90 \pm 0.12$	$O_d = 0.48 \pm 0.14$	

Departed

	Red Fox	Coyote
Red Fox		$O_d = 0.79 \pm 0.14$
Coyote	$O_d = 0.45 \pm 0.13$	

Reassembled

	Red Fox	Coyote	Wolf
Red Fox		$O_d = 0.22 \pm 0.07$	$O_d = 0.38 \pm 0.10$
Coyote	$O_d = 0.98 \pm 0.05$		$O_d = 0.77 \pm 0.11$


Wolf
$O_d = 0.96 \pm 0.06$
$O_d = 0.44 \pm 0.10$

SM Table 7. Drivers of dietary dissimilarity within the time periods of our study for red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), and gray wolves (*Canis lupus*) from our proportional contributions of each prey group we analyzed (human foods, berries, deer, and small prey). Notice that the dissimilarity for each species within time periods is not ranked but ordered – the cumulative sum shows the importance of rank.

	Red Fox		Coyote		Wolf	
Functional	Ratio	Cumulative Sum	Ratio	Cumulative Sum	Ratio	Cumulative Sum
Human Foods	1.32	0.40	1.11	0.42	0.73	0.87
Berries	1.31	0.59	1.44	0.94	1.13	0.95
Deer	1.44	0.91	1.31	0.69	1.00	0.45
Small Prey	1.27	1.00	1.27	1.00	1.10	1.00
Departed						
Human Foods	1.33	0.62	1.41	0.56		
Berries	1.30	1.00	1.42	1.00		
Deer	1.64	0.89	1.36	0.28		
Small Prey	1.18	0.33	0.96	0.82		
Reassembled						
Human Foods	1.44	0.47	1.40	0.75	0.86	0.81
Berries	0.94	1.00	1.50	0.89	1.16	0.92
Deer	1.46	0.90	1.48	0.40	1.09	0.42
Small Prey	1.16	0.73	1.14	1.00	1.26	1.00

SM Table 8. Drivers of dietary dissimilarity across time periods for red foxes (*Vulpes vulpes*) from our proportional contributions of each prey group we analyzed (small prey, human foods, deer, and berries).

Functional–Departed	Ratio	Cumulative Sum	p-value
Human Foods	1.56	0.35	0.89
Small Prey	1.63	0.67	0.01
Berries	1.45	0.85	1.00
Deer	1.53	1.00	0.81
Functional–Reassembled			
Human Foods	1.42	0.39	0.01
Berries	1.91	0.65	>0.01
Small Prey	0.94	0.85	0.40
Deer	1.58	1.00	0.01
Departed–Reassembled			
Human Foods	1.28	0.40	0.01
Berries	1.27	0.67	>0.01
Small Prey	1.38	0.89	0.04
Deer	1.51	1.00	0.39

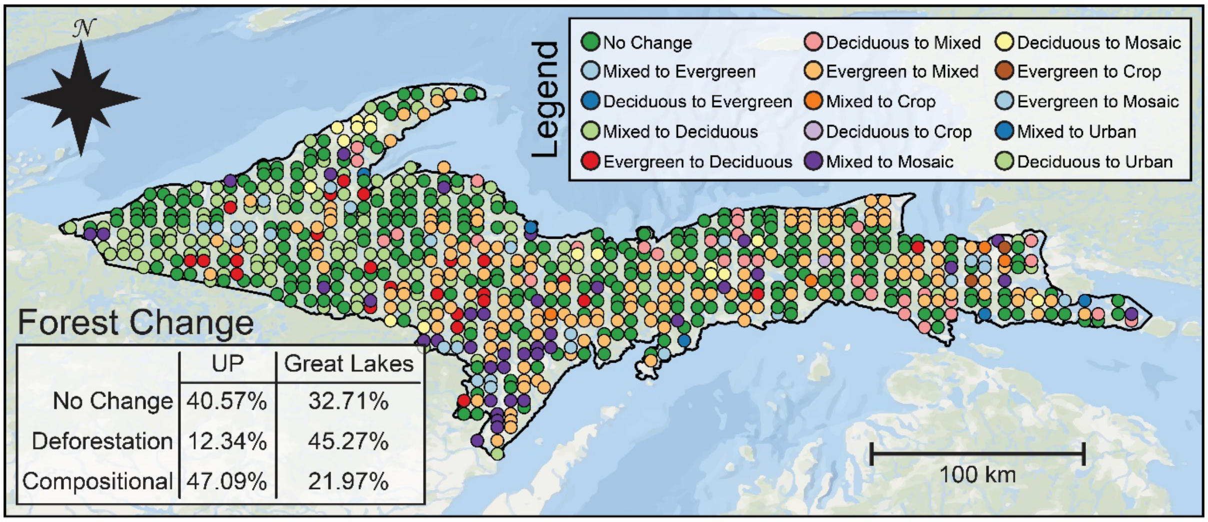
SM Table 9. Drivers of dietary dissimilarity across time periods for coyotes (*Canis latrans*) from our proportional contributions of each prey group we analyzed (small prey, human foods, deer, and berries).

Functional–Departed	Ratio	Cumulative Sum	p-value
Deer	3.21	0.44	>0.01
Berries	1.39	0.69	>0.01
Human Foods	1.30	0.87	0.29
Small Prey	0.82	1.00	>0.01
Functional–Reassembled			
Human Foods	1.42	0.35	0.05
Berries	1.98	0.65	0.98
Deer	1.26	0.93	1.00
Small Prey	1.10	1.00	1.00
Departed–Reassembled			
Deer	2.90	0.43	>0.01
Berries	2.24	0.75	>0.01
Human Foods	1.35	0.90	0.26
Small Prey	0.86	1.00	>0.01

SM Table 10. Drivers of dietary dissimilarity across time periods for gray wolves (*Canis lupus*) from our proportional contributions of each prey group we analyzed (small prey, human foods, deer, and berries).

Functional–Reassembled	Ratio	Cumulative Sum	p-value
Human Foods	0.96	0.40	0.52
Deer	1.08	0.80	0.83
Berries	1.06	0.91	0.83
Small Prey	1.16	1.00	0.13

SM Figures



Forest Change

	UP	Great Lakes
No Change	40.57%	32.71%
Deforestation	12.34%	45.27%
Compositional	47.09%	21.97%

	Functional	Departed	Reassembled
Human Population[1]	306,515	304,186	315,175
Acres in Agriculture[1]	662,148 (2.2%)	1,431,666 (4.8%)	495,646 (1.7%)
Primary Industry[1]	Logging/Mining	Mining/Tourism	Tourism
Copper[2]	150-250 MLb/yr	50-125 MLb/yr	30-40 Mlb/yr
Iron Ore[2]	10-20 MMT/yr*	15-30 MMT/yr*	30-40 MMT/yr*
Deer Abundance[3]	~30,000-60,000	~250,000-350,000	~250,000-350,000
Wolf Abundance[4]	150-250	0	500-700

SM Figure 1. Forest compositional change in the Upper Peninsula of Michigan (including forest change in the Great Lakes Region [Michigan, Wisconsin, and Minnesota] as a reference) from Pre-Human to Contemporary forests (Map) and highlight of the change in key sectors (human demography, industry, and deer and wolf abundances) through our study period (Table).

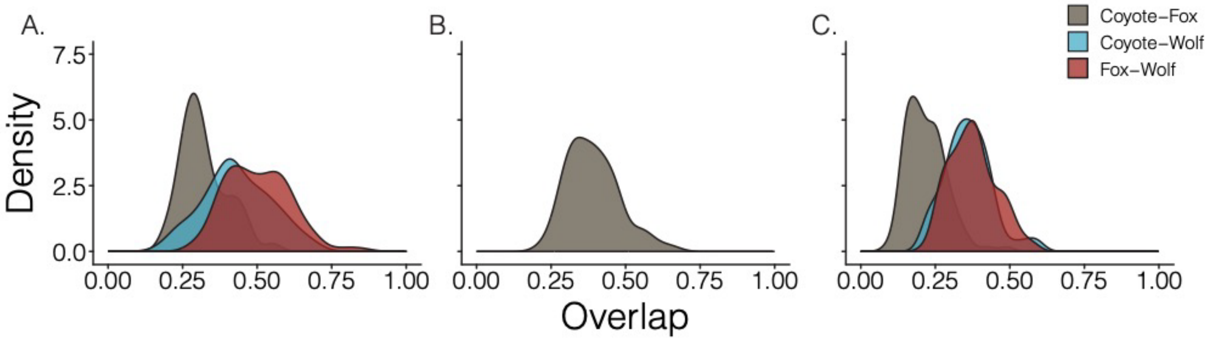
[1] US Census Bureau, Census.gov

[2] The Mineral Industry of Michigan U.S. Geological Survey, USGS.gov

[3] John Ozoga, Whitetails of the U.P., woods-n-waternews.com

[4] Michigan Department of Natural Resources, Michigan.gov

SM Figure 2. Pairwise isotopic niche breadth overlap between wolves (*Canis lupus*), coyotes (*Canis latrans*), and red foxes (*Vulpes vulpes*).



Trophic facilitation and resource subsidies structure the seasonal diets of meso-carnivores

Running Tittle: Seasonal dietary subsidies

Authors and Affiliations

Mauriel Rodriguez Curras[1*] and Jonathan N. Pauli[1]

[1] University of Wisconsin-Madison, Department of Forest & Wildlife Ecology, Madison, WI, USA.

*Corresponding Author: Mauriel Rodriguez Curras; mrodriguezcu@wisc.edu

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Abstract

Resource subsidies are a powerful force in the dynamics of community interactions. In natural communities, carrion subsidies from large carnivores are an important supplement to meso-carnivores in times of resource scarcity. Human recreation and resultant food subsidies are also often a seasonal resource and generally restricted to warmer seasons in northern latitudes. Isle Royale National Park features a simple community of interacting species and wolves (*Canis lupus*) were reintroduced in 2018 to restore predation to the over-abundant moose (*Alces alces*) population and horizontal interactions to the other carnivores on the island, particularly the red fox (*Vulpes vulpes*). Additionally, human visitation to the park is strongly seasonal; the park is closed to recreation for 6-months of the year. We quantified the diets of red foxes in Isle Royale National Park, MI, USA during summer and winter using a combination of scat and stable isotope analysis to assess the degree of seasonality in their diet and the degree of trophic facilitation from wolves and resource subsidies from humans. We hypothesized that meso-carnivore dietary seasonality is mediated by trophic facilitation from large carnivores and resource subsidies from humans. We found that fox diets were 46% more diverse in summer than winter and that dietary overlap across seasons was relatively low (0.30±0.02). Further, foxes consumed higher proportions of human foods (0.26±0.04) and berries (0.36±0.10) during summer, while they switched to consuming predominantly small prey (0.22±0.06) and especially large browsers (0.71±0.07) during winter. Seasonality strongly influenced red fox diet (Cowell's M/P = 0.93±0.02) and we found strong support for yearly periodicity (max Wavelet Power = 1.2 at yearly intervals) in fox diet, suggesting that trophic facilitation from wolves and resource subsidies from humans are complementary and operate asynchronously throughout the year. Our results suggest that asynchronous dual subsidies from restored large carnivores during winter and

human recreation during summer can lead to an increase to the overall nutritional landscape for plastic meso-carnivores, which can ultimately accelerate the rise of the meso-predator.

Introduction

Resource subsidies play a central role in consumer-resource interactions and community dynamics (Polis and Strong 1996, Huxel and McCann 1998). By creating alternative flows of energy to food webs, subsidies can stabilize food web dynamics by providing reticulate interactions (Teng and McCann 2004, Wilson and Wolkovich 2011). Alternatively, high inputs or significant preference for subsidies can lead to decoupling trophic interactions thereby serving to destabilize food webs (Nevai and van Gorder 2012). Indeed, very high levels of resource subsidies have been shown to precipitate spillover predation (Oksanen 1990), apparent competition (Polis and Hurd 1995), and otherwise trophic instability (Huxel and McCann 1998).

Large carnivores provide critical resource subsidies to obligate and facultative scavengers (Wilson and Wolkovich 2011), especially during times of resource scarcity (Pereira et al. 2014). The reintroduction of carnivores is a commonly employed strategy with the goal of restoring the ecological fabric of communities (Wolf and Ripple 2018), including the horizontal interactions to carnivore communities and resource subsidies to scavengers (Rodriguez Curras et al. 2024a). Interestingly, however, much like predator-prey dynamics, the subsidies provided from carnivores are often seasonal in nature – shaped by bottom-up resource pulses (Yang et al. 2008) or phenological punctuations (e.g., calving, Berger et al. 2008, or spawning, Deacy et al. 2017). For example, pronghorn fawns born in early summer are especially vulnerable to predation, and a variety of predators incorporate fawns in their diet in early summer (Berger et al. 2008). Moreover, although resource subsides from large carnivores are ubiquitous for facultative scavengers (i.e., meso- and small carnivores; (Wilson and Wolkovich 2011), they are especially important in times of resource scarcity (e.g., winter in northern latitudes, Pereira et al. 2014). Accordingly, the subsidies that large carnivores facilitate to subordinate species are highly seasonal in natural systems and exhibit pulsed dynamics in terms of meso- and small carnivore reliance, which can serve to stabilize community interactions across the year (Levy et al. 2016).

Carnivores can cope with seasonal variation in resource availability through flexibility in their feeding strategies, ranging from strict predation, to mostly scavenging, and even becoming omnivorous (Pereira et al. 2014). However, species that rely on trophic facilitation (i.e., scavenging) are forced to weigh the benefits of a free meal against the risk of intraguild aggression (Lima and Bednekoff 1999, Ruprecht et al. 2021). Scavenging draws subordinate carnivores into implicitly risky places for foraging, forcing decisions between food and safety (i.e., a fatal attraction; Prugh and Sivy 2020). The multi-faceted modes by which carnivores compete are necessarily dependent on bottom-up processes (Prugh and Sivy 2020) and thus seasonal variability should ultimately shape these interactions. Although seasonal dynamics have been reported for large carnivores (e.g., Durant et al. 2004, Cusack et al. 2017, Deacy et al. 2017), the broader impacts of seasonal dynamics should be most pronounced for generalist species that can feed across multiple trophic channels (Polis et al. 1989, Huxel and McCann 1998) and integrate complementary resources such as facultative scavenging and omnivory (Pereira et al. 2014).

Human food subsidies in the form of agriculture, domestic livestock, and human refuse can alter competition within carnivore communities (Newsome et al. 2015b, Manlick and Pauli 2020, Rodriguez Curras et al. 2024a) and alter the co-existence dynamics between meso- and small carnivores (Murray et al. 2015, Pluemer et al. 2019). Like trophic facilitation by large carnivores, human food subsidies are dynamic in space and time (Brauman et al. 2020, Rodriguez Curras et al. 2024b). For example, cities may represent one extreme, where resources are available throughout the year, thereby leading to high levels of co-occurrence (Moll et al.

2018, Mueller et al. 2018). However, human food subsidies, too, can exhibit highly seasonal pulses in natural systems in the form of harvesting, calving, and recreation (Wilmers et al. 2003, Brauman et al. 2020), and these dynamics can cause wide-reaching impacts to a variety of predators (Wilmers et al. 2003, Gilbert et al. 2022). Accordingly, determining how changes in trophic facilitation by large carnivore and human resource subsidies influence the diets of carnivores is needed to better understand carnivore community dynamics, especially where large carnivore abundances are expected to change as a result of anthropogenic activities.

Asynchronous resource pulses shape species interactions and mediate community structure (Armstrong et al. 2016), and carnivores are especially responsive to resource pulses (Wilson and Wolkovich 2011). Northern latitudes feature especially high resource pulses during spring and summer due to ephemeral primary production and synchronized prey births. Human resource subsidies may further amplify this resource pulse in the form of resource subsidies associated with recreation. During winter, resources are especially scarce and meso-predators rely on carrion subsidies from large carnivores, which essentially function as a resource pulse due to their relative availability. Although the broad impacts of human resource subsidies are relatively well-understood (Manlick and Pauli 2020, Rodriguez Curras et al. 2024), the impact of these asynchronized dual resource subsidies (e.g., trophic facilitation from large carnivores and resource subsidies from humans) for the ‘rise of the meso-predator’ (Prugh et al. 2009) may be an underappreciated force structuring carnivore communities and raising the baseline populations of meso-carnivores. However, the degree to which asynchronous resource subsidies – from humans in summer and large carnivores in winter – percolate into meso-carnivores remains unknown.

Herein, we quantified the seasonal diet of red foxes (*Vulpes vulpes*) in Isle Royale National Park, MI, USA using a combination of scat and stable isotope analysis. We analyzed diets seasonally and collected whiskers of red foxes for stable isotopes to recreate the diets of foxes throughout the year. We hypothesized that meso-carnivore dietary seasonality is mediated by resource subsidies. Specifically, we predicted that wolves provide carrion subsidies to red foxes, especially during times of low resource availability (i.e., winter). Alternatively, we predicted that humans provide resource subsidies to foxes during summer, which would lead to individuals developing alternative foraging strategies. Lastly, we predicted that these alternative forms of resource subsidies would coincide with highly seasonal diets for foxes as Isle Royale exhibits high seasonality in terms of resource availability and human recreation.

Methods

Study Area

Isle Royale (544 km2; Figure 1) is located in north-western Lake Superior, USA (48°N, 89°W). The island currently supports a transition deciduous-to-boreal forest of fir (Picea spp.) and spruce (Abies spp.), which primarily occupy the relatively cool northeast-end and lakeshore, while temperate forest (*Acer spp., Quercus spp., Betula spp., Juniperus spp.,* etc.) defines the relatively large interior landmass. Mean monthly seasonal temperatures range from –9 °C in January to 15.8 °C in July. Mean annual precipitation is 75 cm, ranging from 54 cm to 107 cm with 40% of annual precipitation falling as snow. The current terrestrial carnivore community on Isle Royale is relatively simple; composed of wolves, red foxes, and American martens. The other carnivores on the island are mostly or wholly aquatic, including American mink (*Neogale vison*) and North American river otter (*Lontra canadensis*), or are highly cryptic and occur at very low densities (i.e., ermine [Mustela erminea]). We did not include these carnivores in our analyses because their interactions with the other terrestrial carnivores were likely minimal as they occur at low densities (Rodriguez Curras et al. 2024).

Wolves were reintroduced to Isle Royale in 2018 to manage the parks erupting moose (*Alces alces*) population. Immediately following this reintroduction, foxes were shown to strongly respond by developing two alternative foraging strategies, consuming either high proportions of wolf-killed carrion or human resource subsidies (Rodriguez Curras et al. 2024b). However, Isle Royale is closed to human recreation from September 15 – April 15, limiting potential resource subsidies from humans to the summer months – which could strongly influence the importance of asynchronized resource subsidies for foxes.

Data Collection

Beginning in late-August through late-September and mid-February through early-March, we hiked the four major trails on the western-end of the island (the Feldtmann [24km], Huginnin [20km], Greenstone [22km], and Minong [18km]) and the Windigo area. During summer, we surveyed each trail a total of seven times, with a four-day interval between sampling efforts, while we sampled each trail three times, with a four-day interval during winter. We collected data in Summer of 2020 and 2023 and Winter of 2021 and 2022. When a scat was encountered, we swabbed the exterior of the scat with a sterile cotton applicator (Thermo Fisher Scientific, USA) and placed the applicator in a 15ml Falcon tube (Thermo Fisher Scientific, USA) filled with desiccant. We collected the scat sample in a 50ml tube, recorded the location (UTM), and stored frozen within 8 hours of collection. Genetic species identity was accomplished following Lacin-Alas et al. (2024). Briefly, we extracted DNA from all scat samples using Qiagen QIAamp

DNA micro kits (QIAGEN, Valencia, CA) in a dedicated pre-PCR room and included a negative control for each extraction batch. We identified samples to species from a species-specific portion of mitochondrial DNA (mtDNA).

From September 2021 through February 2024, we captured 16 red foxes using foothold traps, box traps, and cable restraints (N_{Winter}=8 and N_{Summer}=8; 6 females and 10 males) and fur and whisker samples were collected for stable isotope analysis. The total number of individual foxes we captured represents ~35% of the fox population in our study area (Rodriguez Curras et al. 2024). All protocols were approved by the Institutional Animal Care and Use Committee at the University of Wisconsin-Madison and the National Park Service (A006483).

Data Preparation

Scat

We rinsed (using a detergent; Alconax Inc. NY, USA), dried at 65°C overnight (~ 12 hours), and filtered (through a fine mesh) each scat sample prior to analysis. We used a dissecting and light microscope to identify the undigested material to the finest possible taxonomic level (except for birds and arthropods) using keratinous or bone fragments (i.e., skulls, mandibles, teeth, and claws), guard hair coloration, banding patterns, and medulla characteristics and comparing samples to a reference voucher specimen library (Carlson et al. 2014). We recorded the presence-absence (i.e., occurrence) of each species or item (e.g., seeds and plant material), accordingly, the sum of occurrences exceeded 100% because we frequently found more than one food item in each scat.

Stable isotopes

Red fox whiskers grow at a constant rate (Robertson et al. 2013, Mutirwara et al. 2018) of 0.43±0.10 mm/day (McLaren et al. 2015). Accordingly, we segmented whiskers to a length of 7 cm to balance the weight required for accurate bulk stable isotope analysis (0.5-0.6 mg) and sufficient temporal resolution to reconstruct diets across seasons; each sample, then, represented ~18 days. Fur and whisker samples were rinsed three times with 2:1 chloroform: methanol solution, homogenized with surgical scissors, and then dried at 55°C for a minimum of 72 hours following previously described methods (Pauli et al. 2009).

We measure the carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values were measured using a Costech 4010 Elemental Analyzer (Valencia, CA) coupled to a Thermo Scientific Delta V Plus (Bremen, Germany) isotope ratio mass spectrometer with internal reference materials calibrated against international reference standards (V-PDB for $\delta^{13}C$ and atmospheric N for $\delta^{15}N$). The within-run standard deviation for internal reference materials was <0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ values. All measurements were conducted at the University of California-Davis (Davis, CA, USA).

Data Analyses

We used all scat samples collected to generate a naïve frequency of occurrence of each diet item (e.g., Carlson et al. 2014). In addition, we also used a bootstrap sample within each season to account for within-individual pseudo-replication. We resampled the dataset N = 10,000 times using each draw to calculate the frequency of occurrence to capture variation of diet at the population level. We further quantified Hill's diversity and evenness metrics (Hill 1973) to test changes in diet use across seasons in the R package *chemodiv v0.3.0* (Petrén et al. 2023). To compare diversity and evenness across seasons, we calculated the total density overlap of the bootstrap draws in the R package *overlapping v.2.1* (Pastore et al. 2022).

To test the mechanisms driving dietary variation through time (i.e., seasonally, at the population- and individual-level), we used δ^{13}C and δ^{15}N values to estimate the isotopic niche breadth and isotopic niche overlap in ‘δ-space’ (Layman et al. 2007, Newsome et al. 2007, Jackson et al. 2011) and the proportional assimilation of putative prey and dietary overlap based on stable isotope mixing models (i.e., 'p-space'; Parnell et al. 2010). First, we used an ANOVA to test the differences in δ^{13}C and δ^{15}N at the population level across seasons. We quantified isotopic niche breadth within seasons and overlap across seasons at the population-level – a proxy for dietary niche breadth and competition, respectively – using the 95% standard ellipses areas (SEAs) in the R package *SIBER v 2.1.6* (Parnell et al. 2010). We ran 3 chains of 300,000 iterations and removed the first 200,000 iterations as burn-in and then thinned posterior samples to every 10th sample. To quantify isotopic niche overlap, we used the single metric of niche overlap (O_δ) defined by overlap as the proportion of non-overlapping area of the two ellipses relative to the non-overlapping area, $O_\delta = O_{W-S}/\left((B_W + B_S) - O_{W-S}\right)$, where $O_{S\text{-}W}$ (= $O_{W\text{-}S}$) is the overlap across seasons, B_W is the niche breadth of foxes in winter and B_S is the isotopic niche breadth during summer; the resulting value ranges from 0 (no overlap) to 1.0 (complete overlap).

To quantify the influence of individual diet to the population-level, we estimated the niche breadth of the 16 subsampled individuals in relation to total, population-wide niche space in both isotopic- and resource-space following Bolnick et al. (2003). In this formulation, the contribution of individual diet to the population can be quantified by the ratio of the within-individual component (WIC) of niche width to the total niche width (TNW) of the population, expressed as WIC/TNW. Low WIC/TNW values suggest that individuals contribute little to the overall population diet, thereby suggesting high individual specialization. This measurement of diet specialization differs from the designation of diet specialists vs diet generalists related to the evenness in the distribution of resource contributions, sensu Newsome et al. (2012a; see below), and provides an index of individual diet flexibility relative to the population. We calculated WIC/TNW from Bayesian standardized ellipse areas corrected for small sample size (SEA's) in both isotopic- and resource-space using the R package SIBER (Jackson et al., 2011). Models were run using similar parameters as those above to quantify SEAc's. We compared SEAc's for each of the 16 subsampled individuals to the total fox dietary niche estimated from bulk hair samples.

To determine the proportional assimilation of dietary groups of foxes across seasons we used concentration-dependent mixing models using the R package *simmr 0.4.5* (Parnell 2019). For all prey endmembers, we used previously collected (Rodriguez Curras et al. 2024) dietary samples analyzed for bulk $\delta^{13}C$ and $\delta^{15}N$. To account for potential human resource subsidies in carnivore diets, we also included isotopic ratios from anthropogenic sources, including human refuse and domestic prey (Hülsemann et al. 2015, Newsome et al. 2015a). We included berries that would be available during the hair growth period typical of canids during the summer only (i.e., spring-early-summer; Korhonen et al. 1984) and aggregated isotopically indistinct prey items, using a k-means clustering algorithm (Phillips et al. 2014) in the R package *NbClust v3.0.1* (Charrad et al. 2014). We identified 4 isotopically distinct and biologically meaningful prey groups representative of Isle Royale: (1) berries ($\delta^{13}C$ = -29.1±1.4, $\delta^{15}N$ = -1.9±1.4; e.g., Rubus spp. and Ragaria spp.), (2) browsers ($\delta^{13}C$ = -27.0±0.5, $\delta^{15}N$ = 1.8±1.3; moose and snowshoe hares [Lepus americanus]), (3) small prey ($\delta^{13}C$ = -24.4±2.1, $\delta^{15}N$ = 4.8±1.5; e.g., beaver [*Castor canadensis*], mice [*Peromyscus maniculatus*], red squirrels [*Tamiascirus* *hudsonicus*], Arthropods, and birds [e.g., *Leuconotopicus villosus* and *Dendroica spp.*]), and (4) human foods ($\delta^{13}C = -19.5\pm1.3$, $\delta^{15}N = 5.5\pm1.5$; based on data from Hülsemann et al. 2015, Newsome et al. 2015a). Putative prey samples included: moose (N = 17), beaver (N = 5), snowshoe hare (N = 7), red squirrel (N = 5), deer mice (N = 7), passerine birds (N = 15), arthropods (N = 9), and berries (N = 23).

We estimated proportional dietary inputs of species at the population- and individual-level by running 3 chains of 300,000 iterations and removed the first 200,000 iterations as burn-in and then thinned posterior samples to every 10th sample. We used informative priors based on our scat analysis to inform our model (Parnell et al. 2010, Stock et al. 2018). During summer, we used standardized priors of 0.40±1.08, -1.43±1.98, 0.07±0.55, and 0.95±0.52 while for winter, we accounted for the park closure between September 15 and April 15 and used standardized priors of 1.87±0.23, 2.77±0.57, -3.42±1.05, and -1.21±0.83 for small prey, browsers, human foods, and berries, respectively. We used [C] and [N] data of berries ([C] = 0.48; [N] = 0.01), browsers ([C] = 0.47; [N] = 0.14), and small prey ([C] = 0.47; [N] = 0.14) from Carlson et al., (2014) and data from Hopkins and Ferguson (2012) for the concentrations of anthropogenic-derived sources ([C] = 0.53; [N] = 0.07). Lastly, we used diet-specific trophic discrimination factors of $\Delta^{13}C=2.5$ and $\Delta^{15}N=3.4$ for all hair and whisker samples (Roth and Hobson 2000, Stephens et al. 2022) with the exception of human foods. However, because we sampled small prey and browser hair and not muscle, we adjusted our $\Delta^{13}C$ discrimination factors by –1.0‰ for those prey groups to account for tissue specific discrimination factors (Roth and Hobson 2000, Newsome et al. 2015a). We used trophic discrimination factors of $\Delta^{13}C=2.0$ and $\Delta^{15}N=3.5$ for human foods following Newsome et al. (2015a).

We first quantified prey use at the population level by grouping each individual within summer and winter and estimated proportional use of the four potential prey sources (berries, browsers, small prey, and human foods). Then, we analyzed individual whisker segments separately to quantify consumption of each prey group at each represented window (~18 days) and tested the impacts of individuals on dietary variability through the seasons. For each analysis, we identified model convergence using the Gelman–Rubin diagnostic value $\hat{R} < 1.01$ and the effective sample size of each estimate >5000. Because our estimates of dietary proportions are posterior distributions, we calculated the probability of directionality (PD) in the R package *bayest v1.4* (Kelter 2020), testing the consumption of each diet item was greater (or lower) across seasons (represented as PD(Summer < [or >] Winter). PD values range from 0.5 – indicating identical posterior distributions – and 1.0 – indicating no overlap in posterior distributions. We estimated dietary niche breadth and overlap using our posterior dietary proportion estimates of individuals across seasons in the R package *nicheROVER v.1.9.0* (Swanson et al. 2015).

To quantify the foraging strategies of individuals within each season, we used the individual proportional estimates of prey groups to quantify dietary specialization (ε) and similarity (s) indices and visually inspected the density plots (Newsome et al. 2012). Here, ε varies between 0 (an ultra-generalist) and 1 (an ultra-specialist) and s varies between 0 (exactly dissimilar from the population) and 1 (exactly similar to the population). Accordingly, the density plots can be subdivided into four quadrants: dietary specialists (ε>0.50) with diets dissimilar to the population (s<0.50; dissimilar-specialists), dietary specialists with diets similar to the population (s>0.50; similar-specialists), dietary generalists (ε<0.50) with diets dissimilar to the population (dissimilar-generalists), and dietary generalists with diets similar to the population (similar-generalists; Newsome et al., 2012). We classified dietary specialization and similarity from the posterior estimates of individual diets and generated density plots to classify the foraging strategies at the population level based on where the density distributions using a kernel function (Newsome et al. 2012) – foraging strategies are qualified as unique if there is little overlap between the density kernels.

To quantify dietary overlap across seasons for both our scat and stable isotope analysis, we estimated Pinaka's index of niche overlap (Pianka 1974) in the R package pgirmess v2.0.3 (Giraudoux 2024) using a bootstrap estimate of N = 10,000. We also used a non-parametric test to test for differences in diet use across seasons in the R package *npvm v2.4.0* (Ellis et al. 2017). Finally, we used a similarity percentage analysis in the R package *vegan v2.6-2* (Oksanen et al. 2022) to determine percent contribution of each prey group to the dissimilarity in diet composition among groups based on a Bray–Curtis dissimilarity matrix calculated from the estimates of each of prey group.

To test for seasonality using our stable isotope data, we used contingency (Colwell's M; Colwell 1974), the standardized role of seasonality in relation to overall predictability (Contingency/Contingency+Constancy; M/C+M), and wavelet analysis to independently identify dominant temporal cycles and characterize the predictability of seasonal red fox diet. From a standard definition of seasonal predictability – the regularity of recurrence of the annual distribution of events – we quantified predictability as the proportion of timesteps over the time series with significant power at the 26-week frequency (i.e., two-week intervals in similar accordance to our stable isotope data). Accordingly, we measured the degree to which a given distribution recurs from year to year. Put simply, this measures how consistent the annual repeatability of the red fox diet patterns is. First, we used a time series analysis in the R package

MARSS v.3.11.9 (Holmes et al. 2024) and recreated a ten-year dataset from our data to account for individual variability and pseudoreplication. To calculate contingency and constancy, we used the R package *hydrostats v.0.2.9* (Bond 2022). To perform the wavelet analysis, we used the R package *WaveletComp v.1.1* (Rösch and Schmidbauer 2018). We used the Morlet wavelet which represents a sine wave modulated by a Gaussian function (Torrence and Compo 1998). Finally, we tested for temporal autocorrelation between summer and winter in the base stats package in R (R Core Team 2024). Critically, explicitly testing seasonality from time-series data does not use any prior categorization (i.e., pre-defined seasonal events) to inform the analysis, so it is a powerful tool to test for periodicity in time-series data, which has not been previously applied to trophic ecology. All analyses were performed in *R* (R Core Team 2024).

Results

Scat Analysis

During winter, foxes consumed significantly higher proportions of moose ($O<0.001$) and snowshoe hares ($O = 0.001±0.0006$), while in summer, they consumed significantly higher proportions of squirrels ($O = 0.004±0.002$), birds ($O<0.001$), arthropods ($O<0.001$), and berries ($O<0.001$; Figure 1A). Fox diet was more diverse in summer (6.29±0.14) than winter (4.31±0.31; $O<0.001$; Figure 1B). Lastly, fox winter (0.75±0.07) and summer (0.70±0.02) diets were similarly evenly distributed ($O=0.37±0.01$, given the resources available (i.e., no insects or berries were consumed during winter; Figure 1C). Dietary overlap between summer and winter was relatively low (0.30±0.02) and diets across seasons were significantly different (non-parametric bootstrap test $p<0.01$). The leading causes of dietary dissimilarity across seasons (accounting for the cumulative sum in dissimilarity ≥ 0.75) for foxes was in the consumption of berries, arthropods, moose, and, lastly, birds (SM Table 1).

Stable Isotopes

The nitrogen isotopic composition ($\delta^{15}N$) of foxes was higher in summer (6.33±0.70‰) than winter (5.21±0.83‰; $p<0.01$) though we did not detect a difference for carbon ($\delta^{13}C$; boxplots in Figure 2A). Furthermore, the isotopic niche breadth (SEA) of foxes that was broader in summer (2.71±0.40‰^{2}) than winter (1.88±0.30‰^{2}; $p<0.01$; Figure 2A). At the population level, isotopic niche overlap between summer and winter was low (0.30±0.04). Our measure of WIC/TNW was similar for both summer and winter (0.29±0.03 and 0.33±0.05, respectively; Figure 2B).

Foxes consumed higher proportions of human foods (0.26±0.04) and berries (0.36±0.10) during summer (compared to 0.04±0.05 and 0.03±0.02, respectively during winter), while consuming higher proportions of small prey (0.22±0.06) and browsers (0.71±0.07) during winter (compared to 0.14±0.04 and 0.31±0.06, respectively during summer; Figure 3A and B). From our individual-level mixing model results, dietary overlap was somewhat higher for summer (0.67±0.21) compared to winter (0.60±0.20; SM Figure 1). Using the individual estimates of diet from our mixing models, Pianka's index of niche overlap between summer and winter was relatively low (0.46±0.04). During summer, foxes were generally qualified as dietary generalists (0.47±0.16) while they were quantified as dietary specialists (0.58±0.09) during winter (Figure 4). Alternatively, foxes were qualified as exhibiting more similar diets during winter (0.79±0.14) than summer (0.53±0.21; Figure 4). Nevertheless, we observed higher variability in dietary strategies during summer compared to winter (Figure 4). Lastly, the trophic strategies of foxes had little overlap across seasons (O = 0.16; Figure 4).

Using $\delta^{15}N$ as a proxy for seasonal diets (Figure 5A and B), we detected strong positive autocorrelation throughout winter and negative autocorrelation between summer and winter (Figure 5C). Yearly Colwell's predictability (P; 0.89±0.02) and contingency (M; 0.77±0.02) were both high, while constancy (C) was low (0.13±0.03; Figure 5D). Furthermore, the contribution that seasonality contributed to predictability (M/M+C) was high 0.87±0.03 (Figure 5A). Similarly, we estimated a strong seasonal impact (M/P; 0.93±0.02; Figure 5D). Our wavelet analysis (Figure 5D) demonstrated high peaks in power corresponding to yearly periodicity (Figure 5D). We also observed support for minor peaks in periodicity occurring at ~8 two-week intervals (coinciding with the differences between summer and winter) and ~4 two-week intervals (coinciding with the differences observed within seasons; Figure 5D).

Discussion

Summer diets were markedly different from winter diets, reflected by the higher consumption of berries and human foods and browsers and small prey, respectively. Indeed, we found that berries, arthropods, and human foods were the most dominant diet items during summer while moose and snowshoe hares were the most dominant in winter. Notably, we found that seasonal resource subsidies significantly contributed to red fox diets, and we were able to recreate red fox diets with a significant degree of certainty knowing the time of year. Our results provide a mechanistic understanding of the seasonal diets of meso-carnivores, and we highlight the seasonal resource subsidies that drive trophic strategies and community interactions that shape carnivore communities.

Dietary Seasonality

The asynchronous availability of resources classically provides constant resources to carnivores, such as red foxes (e.g., small prey and berries during summer and snowshoe hares and scavenging during winter). Dietary flexibility (i.e., distinct foraging strategies) should promote community stability by allowing reliance on relatively abundant resources while decoupling from declining prey. Temporal compartmentalization, dormancy, migration, coupling, and omnivory are potentially widespread mechanisms by which species respond to temporal variation and help sustain energy flow (McCann et al. 2005, White and Hastings 2020). We found that summer diets were generally more diverse than winter diets, when foxes exhibited high dietary similarity, coinciding with a high reliance on moose (i.e., scavenging) and snowshoe hares (Figures 1 and 2). This is not surprising because berries, arthropods, and birds are ephemeral in Isle Royale, and only present in summer. Further, we often found multiple diet items in the scats of foxes during summer (e.g., berries and mice, insects and squirrels, etc.), though we did not observe this in winter. Likely, as foxes were consuming larger prey items in winter, there was no need to seek alternate prey to meet their nutritional or energetic demands. This suggests a temporal component to dietary specialization (e.g., Figure 4), whereby multiple feeding bouts on a singular prey (or carrion) can contribute to greater dietary specialization and similarity at the individual level. Not surprisingly, our stable isotope analysis suggested a higher contribution of human foods during summer, which can be attributed to the park closing to visitors from September 15 – April 15. Theoretically, seasonal changes of species interactions are optimized to minimize both the variation in persistence conditions and unnecessary dietary changes that can be energetically costly for individuals (Saavedra et al. 2016). Indeed, from theoretical to empirical studies, seasonality is central to ecosystem function and stability and widespread across ecosystem (McMeans et al. 2015). Our results suggest that the diets of meso-carnivores (e.g., foxes) can be highly dynamic and largely driven by availability and human resource subsidies in summer and trophic facilitation in winter; supporting a coupling between carnivore diets to species composition and environmental seasonality, likely resulting from long-term adaptations to cope with seasonal changes by seeking the most available resources to reduce energetic constraints.

Seasonally Dynamic Fatal Attraction

Although the degree to which trophic facilitation impacts competitive interactions between carnivores has received widespread attention (Prugh and Sivy 2020), few studies quantify the degree to which suppression and facilitation contribute to competitive interactions in a seasonal context, broadly (but see, Johnson and Franklin 1994, Pereira et al. 2014, Torretta et al. 2016). Our stable isotope analysis showed that foxes relied ~3x more on browser biomass during winter than summer (Figure 2) and we detected moose in ~500% more scats during winter. Given the broad empirical support of the fatal attraction hypothesis (Prugh and Sivy 2020), our results imply that the impacts of suppression would be highest during winter, (i.e., the time of the year that subordinate carnivores are mostly reliant on trophic facilitation). Our findings imply that such seasonal effects, clearly detectable in this insular food web featuring quiet non-consumptive human recreation, may be particularly important for the persistence of species in natural settings (e.g., islands and habitat fragments) where small populations require management to avoid extinction. Indeed, winter (or times of resource scarcity, generally), can represent a bottleneck for carnivores which are often reliant on decreasing resources and, simultaneously, trophic facilitation, which can lead to costly encounters with dominant guild members (i.e., wolves). Models that account for species interactions, then, must account for seasonality at the risk of underrepresenting the strength of suppression or facilitation (or both) and the impacts they can have on persistence. Although we do not have the data to test for the numerical responses of meso-carnivores, our results suggest a functional response in the form of shifting diets to include more carrion in winter.

Resource Subsidies

Due to the disproportionate impacts that carnivores have on community- to ecosystem-level processes (Ritchie et al. 2012), restoring the functional role of carnivores has been classified as a priority for conservation efforts (Pettorelli et al. 2019). Large carnivore reintroductions are traditionally implemented to restore top-down effects (i.e., predator–prey relationships and cascading consequences; Estes et al. 2011), however, large carnivores also structure carnivore communities via horizontal community interactions (de Oliveira and Pereira 2014), ranging from suppression (via competitive exclusion) to facilitation (via resource subsidies) for other carnivores in similar trophic positions (Prugh and Sivy 2020, Rodriguez Curras et al. 2024a). In Isle Royale, the reintroduction of wolves restored resource subsidies to foxes (Rodriguez Curras et al. 2024a), which we show are a critical component of fox diet during winter (e.g., Figures 1, 2, and 5). Resource subsides have been previously shown to stabilize community interactions (Polis and Hurd 1995), and our results suggest these anticipated interactions have, indeed, been restored. In addition to suggesting that facilitation from wolves has been restored to this ecosystem of conservation concern, our results further illuminate how strong seasonality sets the stage for seasonal changes in diet, species interactions, and human resource subsidies.

Human recreation can strongly alter competitive dynamics within carnivores via resource subsidies (Manlick and Pauli 2020, Rodriguez Curras et al. 2024a). The two forms of subsidies that we observed (trophic facilitation from wolves and resource subsidies from humans) likely have dissimilar impacts on competitive interactions. While we have highlighted the interplay of trophic facilitation with interspecific conflict, human foods offer a resource that is relatively free of immediate risk (though see, Murray et al. 2015 for a discussion on alternate forms of risk). This relatively low-risk resource offered by humans can lead to increased variability in resource availability during summer, which can negatively impact communities in highly seasonal environments by increasing the summer survival of individuals beyond the background carrying capacities. Even in a relatively undisturbed ecological community – Isle Royale – with high seasonal variation, the trophic strategies that we observed in foxes were exceedingly variable throughout the year (Figure 5), which could lead to trophic instability over time. Factors that alter or inhibit the capacity of species to decouple from declining resources would be predicted to destabilize food webs (McMeans et al. 2015). Accordingly, resource synchrony via changes in resource subsidies by humans could lead to food web instability over time (McMeans et al. 2015). Altered seasonal signals could also collapse the current spectrum of environmental variation upon which different species have set up their temporal niches, threatening coexistence in addition to food web stability. In conjunction with the fatal attraction hypothesis, human resource subsidies can break-down risk-taking behaviors and create a feedback loop with trophic facilitation whereby meso-carnivores take exceedingly greater risks to meet their energetic demands during times of resource scarcity due to (i) inflated population sizes or (ii) liberal risk-management. Alternatively, the highly seasonal activity of humans in northern latitudes may decrease the disparity in resources across seasons, thereby leading to lower variability in trophic dynamics which could augment species abundances beyond their traditional carrying capacities. In combination with returning large carnivores and the ecosystem services they provide (e.g., trophic facilitation), we believe the resource subsidies that humans provide in northern latitudes (which have previously been underappreciated) could be a potential mechanism behind the 'rise of the meso-predator' (Prugh et al. 2009).

Conclusion

Understanding seasonal variations in resource use is important for predicting how species interactions cascade through carnivore communities (Pereira et al. 2014). Globally, large carnivores are repatriating their historical communities (Chapron et al. 2014) while reintroducing large carnivores is a widely adopted strategy to restore ecological interactions (Wolf and Ripple 2018). As large carnivores return, the resource subsidies they provide to obligate and facultative scavengers is predicted restore community stability. Simultaneously, human resource subsidies associated with summer recreation – even in one of the least visited National Parks in the United States – are exceedingly widespread across northern latitudes. Indeed, human food subsidies that permeate into natural systems through recreation can create a novel asynchronous resource that is relatively free of risk, which can threaten the existing abiotic signals and, in turn, the biotic processes and functions that are built around them. The impacts from asynchronized human and large carnivore resource subsidies likely play an underappreciated role in structuring contemporary carnivore communities, which will strongly shape community interactions as large carnivores recover throughout their historical ranges.

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Figures

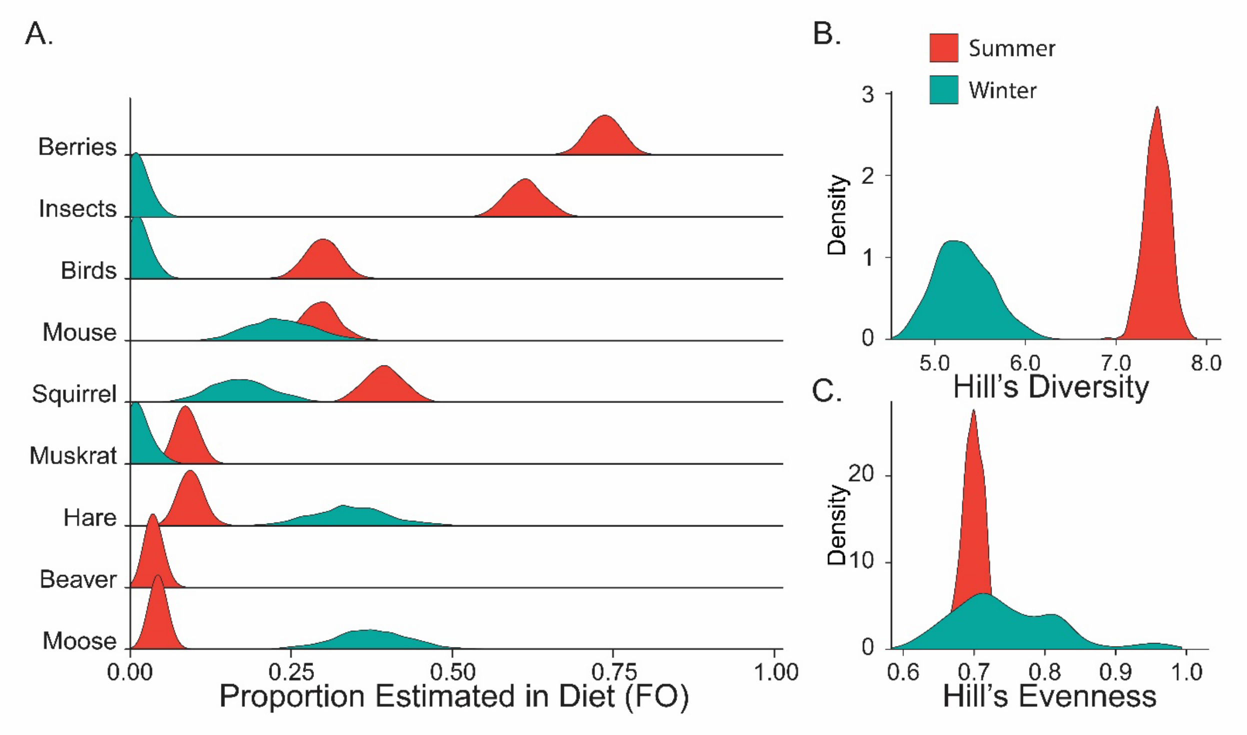

Figure 1. Frequency of occurrence of different items in diet of red fox (*Vulpes vulpes*) during summer (red) and winter (green; A). Hill's diversity (B) and evenness (C) for summer and winter. Hill's diversity accounts for the incorporation of diet items, while evenness accounts for the availability of the total resources.

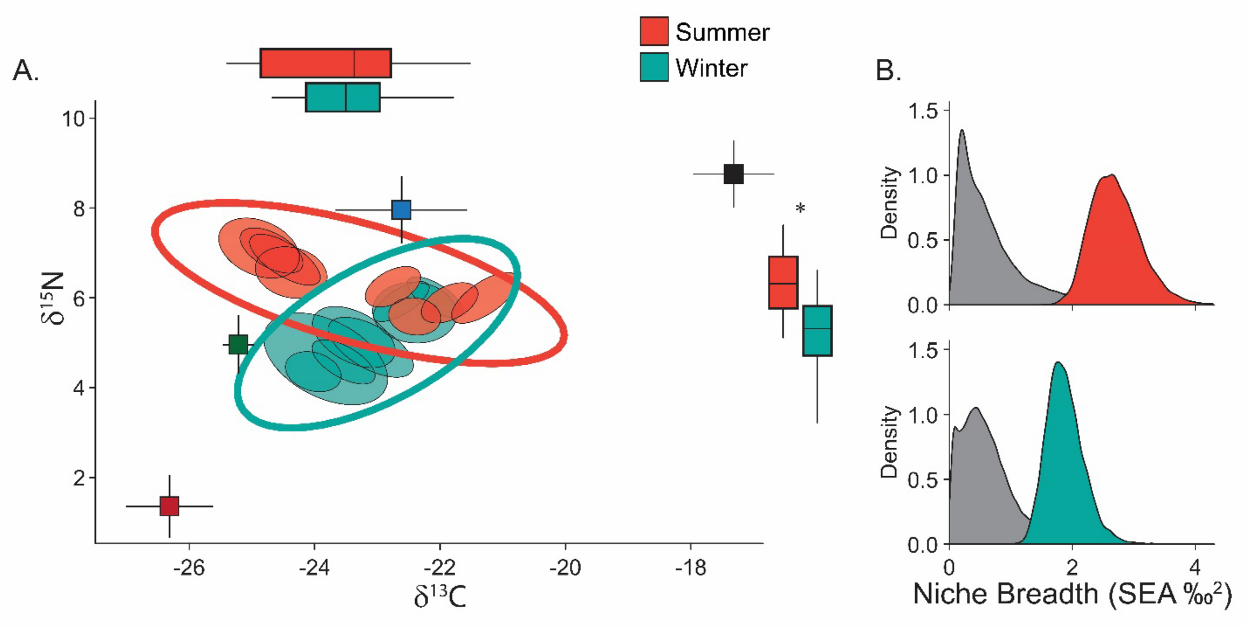

Figure 2. Standard ellipse areas of red fox (*Vulpes vulpes*; $N_{Summer} = 8$, $N_{Winter} = 8$) isotopic niche quantified by $\delta^{13}C$ and $\delta^{15}N$ at the population- (ellipse outlines) and individual- (filled ellipses) level during summer (red) and winter (green) including the mean (squares) and SD (lines) of each isotopically corrected prey item (see Methods): berries (red square; $\delta^{13}C = -29.1 \pm 1.4$, $\delta^{15}N = -1.9 \pm 1.4$), browsers (green square; $\delta^{13}C = -27.0 \pm 0.5$, $\delta^{15}N = 1.8 \pm 1.3$), small prey (blue square; $\delta^{13}C = -24.4 \pm 2.1$, $\delta^{15}N = 4.8 \pm 1.5$), and human foods (black square; $\delta^{13}C = -19.5 \pm 1.3$, $\delta^{15}N = 5.5 \pm 1.5$; A). The associated box plots along the x- and y-axes show the differences between $\delta^{13}C$ and $\delta^{15}N$ across seasons (the asterisk denotes statistical significance of $p < 0.05$; A). Isotopic niche breadth of foxes during summer (red distribution) and winter (green distribution) with the associated within-individual variability (grey) for each season (B).

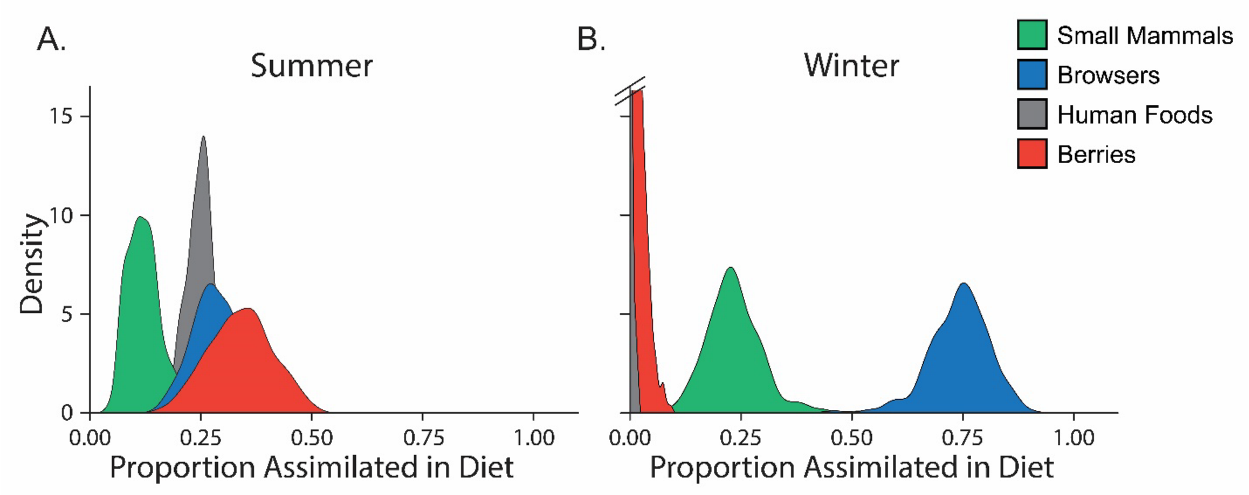

Figure 3. Proportion of assimilated diets of red foxes (*Vulpes vulpes*) during summer (A) and winter (B) from our mixing models using four putative prey groups (small prey – green, browsers – blue, human foods – gray, and berries – red).

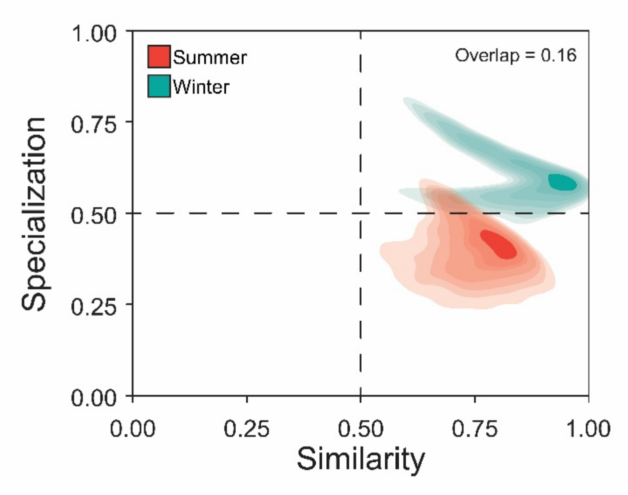

Figure 4. Foraging strategies of foxes (*Vulpes vulpes*) quantified as similarity (x-axis) and specialization (y-axis) during summer (red) and winter (green). The kernels shown are the 95% confidence kernels (transparent colors) ranging to the core kernels during each season.

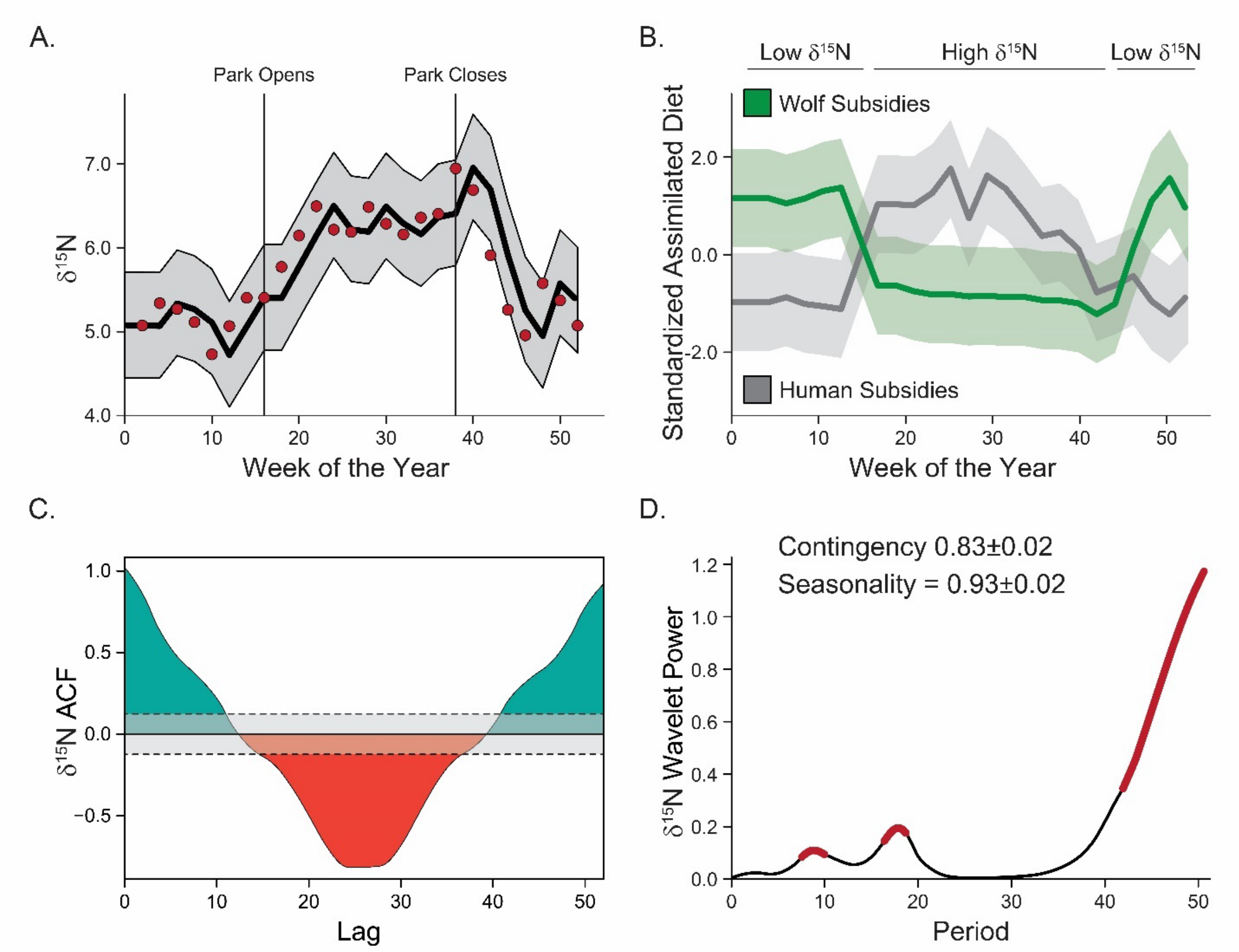

Figure 5. (A) Nitrogen stable isotope ($\delta^{15}N$) data of red foxes (*Vulpes vulpes*) collected from whiskers represented as the average value across individuals at the two-week period (red points); the black line with associated 95% confidence intervals are fitted values from our autoregressive model. (B) Time-series standardized proportion (and 95% confidence intervals) of assimilated resource subsidies from wolves (green) and humans (gray) of red foxes from our individual mixing models using whisker samples; above the graph, we show the corresponding relative $\delta^{15}N$ values to corresponding time periods. (C) Seasonal auto-correlation function (ACF) of the yearly reconstructed $\delta^{15}N$ data of red foxes showing associated positive and negative autocorrelation across winter (green) and between summer and winter (red), respectively. (D)

Wavelet power across recursive periods and the associated contingency (Cowell's M) and seasonality (Cowell's M/P) showing strong support for yearly periodicity and strong seasonality.