Ecology, 102(11), 2021, e03494
© 2021 by the Ecological Society of America

Marginal support for a trophic cascade among sympatric canids in peripheral wolf range

Nicholas L. Fowler,[1,6] Todd M. Kautz,[1] Tyler R. Petroelje,[1] Clay M. Wilton,[2] Kenneth F. Kellner,[1] Daniel J. O'Brien,[3] Bill Parsons,[4] Dean E. Beyer Jr.,[5] and Jerrold L. Belant[1]

[1]*Global Wildlife Conservation Center, State University of New York College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, New York 13210 USA*
[2]*Michigan Natural Features Inventory, P.O. Box 13036, Lansing, Michigan 48901 USA*
[3]*Wildlife Disease Laboratory, Michigan Department of Natural Resources, 4125 Beaumont Road, Room 250, Lansing, Michigan 48910 USA*
[4]*Little Traverse Bay Bands of Odawa Indians, Natural Resource Department, 7845 Odawa Circle, Harbor Springs, Michigan 49740 USA*
[5]*Wildlife Division, Michigan Department of Natural Resources, 1990 US Highway 41 S, Marquette, Michigan 49855 USA*

Citation: Fowler, N. L., T. M. Kautz, T. R. Petroelje, C. M. Wilton, K. F. Kellner, D. J. O'Brien, B. Parsons, D. E. Beyer Jr., and J. L. Belant. 2021. Marginal support for a trophic cascade among sympatric canids in peripheral wolf range. Ecology 102(11):e03494. 10.1002/ecy.3494

Abstract. Trophic cascades reportedly structure ecological communities through indirect species interactions. Though the predator–herbivore–autotroph relationship has received much attention, mechanistic evidence supporting intraguild trophic cascades is rare. We established 348 remote camera sites (1 August–5 September 2019) across seven study areas of varying wolf (*Canis lupus*) density including one study area where wolves were absent in northern Michigan, USA. Using multi-species occupancy modeling at species-relevant spatial scales, we evaluated the hypothesis that increased wolf occurrence suppresses coyote (*C. latrans*) occurrence with corresponding increased red fox (*Vulpes vulpes*) occurrence mediated by land cover edge density, human presence, and temporal partitioning. Remote cameras recorded >600,000 images and included 6,370, 10,137, and 4,876 detections of wolves, coyotes, and foxes, respectively. Fox occupancy probability was more than three times as high (0.29) at camera sites where wolves were present, relative to sites wolves were absent (0.09). Pairwise species interactions supported expected size-based dominance patterns among canids and insignificant effects were directionally consistent with reported reduced strength of top-down effects in peripheral wolf range. Increased edge density also increased co-occurrence of coyote and wolves, likely a function of increased prey availability and refugia for coyotes. Though foxes occurred in spatial proximity to wolves, competition was limited by greater temporal partitioning than observed between coyotes and foxes that were spatially segregated. Collectively, our results provide marginal support for the reported trophic cascade among wolves, coyotes, and foxes wherein top-down effects may be reduced near the edge of current wolf distributions. As predators continue to recolonize portions of their historic range, knowledge of the effects on intraguild predators has implications for species management and predicting prey population responses.

Key words: *coyote; interference competition; intraguild; niche partitioning; red fox; wolf.*

Introduction

Trophic cascades (Paine 1980) have been defined as "indirect species interactions that originate with predators and spread downward through food webs" (Ripple et al. 2016) and contribute to shaping ecological communities (Pace et al. 1999). First described empirically in aquatic systems through effects of predation (e.g., sea otters [*Enhydra lutris*] regulating urchin [*Strongylocentrotus* spp.] populations, which maintains kelp [Laminariales] forests [Estes and Palmisano 1974]), the trophic cascade concept has been extended to describe effects of altered intraguild competition among predators at lower trophic levels (Ripple et al. 2016). For example, removal of top predators reduces competition for mesopredators, which may then increase in abundance (mesopredator release) and reduce prey populations (Crooks and Soulé 1999). Intraguild predator competition may occur through interspecific killing (Case and Gilpin 1974) or interference competition where subordinate species are spatially or temporally displaced due to despotism by dominant species (Linnell and Strand 2000), which are generally larger bodied (Peterson 1996, Palomares and Caro 1999). However, when more than two intraguild predator species are competing, the occurrence and strength of competition is not always ordered by body

Manuscript received 13 December 2020; revised 5 May 2021; accepted 19 May 2021; final version received 22 July 2021.
Corresponding Editor: Evan L. Preisser.
[6] E-mail: nl.fowler@outlook.com

size (Rosenzweig 1966, Palomares and Caro 1999, Caro and Stoner 2003). Levi and Wilmers (2012) suggested Fretwell and Barach's (1977) hypothesis regarding food chain length and parity may apply to competition among predators and that when odd numbers of species compete, the most subordinate predators may benefit from interference competition between two more dominant predators through the principles of trophic cascades. Despite the logic of this relationship there is little empirical evidence and a mechanistic demonstration has not been reported.

Interference competition and inverse density relationships are reported between gray wolves (*Canis lupus*) and coyotes (*C. latrans*; Berger and Gese 2007, Merkle et al. 2009), and coyotes and red foxes (*Vulpes vulpes*, hereafter foxes; Gosselink et al. 2007, Levi and Wilmers 2012) in North America. Competition between species is reportedly mediated by resource partitioning related to habitat heterogeneity (Berger and Gese 2007, Mueller et al. 2018), human disturbance (Mech 2017), and temporal partitioning (Gosselink et al. 2003). However, studies that have concurrently evaluated abundance and distribution of wolves, coyotes, and foxes are rare. Using a 30-yr time series data set of scent station data in Minnesota, USA, Levi and Wilmers (2012) observed a negative relationship between coyote and fox abundance in areas where wolves were absent. But, where wolves were present, coyote and fox abundance had no relationship in forested habitat, and wolf and fox abundance exhibited a positive relationship (Levi and Wilmers 2012). Similarly, analysis of fur return data across Canada indicated greater fox than coyote fur returns where wolves were present and greater coyote than fox fur returns where wolves were absent and in areas near the edge of wolf distributions (i.e., "transition zones"; Newsome and Ripple 2015). It is postulated that intensity of top-down effects of wolves on subordinate canids may be reduced near the edge of current wolf distributions (i.e., transition zones) due to high immigration potential of coyotes (Newsome and Ripple 2015). Despite these apparent regional (Levi and Wilmers 2012) and continental (Newsome and Ripple 2015) scale trophic cascades, we are unaware of evidence that demonstrates fine-scale mechanistic release from competition for foxes facilitated by wolves limiting or displacing coyotes.

We used multi-species occupancy modeling and diel activity patterns to evaluate the hypothesis that presence of wolves results in shifts in occurrence of coyotes and foxes due to the cascading effects of competition (Newsome and Ripple 2015). We tested our hypothesis in areas where wolves were present and absent in the Upper and Lower Peninsulas of Michigan, USA. Where wolves were present, we predicted that occupancy of coyotes at camera sites would be lesser during occasions when wolves occurred, and that occupancy of foxes would be lesser during occasions when coyotes occurred. From this, we further predicted that fox occupancy would be greater during occasions when wolves occurred. In areas where wolves were absent, we predicted camera site occupancy of foxes would be lesser during occasions when coyotes occurred. Under both scenarios, we predicted that increased land cover edge density (indexing habitat heterogeneity) would reduce interference competition between species, facilitating co-occurrence. We also predicted increased human presence would reduce occurrence of wolves and coyotes and increase occurrence of fox. We predicted species with high spatial co-occurrence would exhibit greater temporal niche partitioning than species that were spatially segregated.

Study Area

We conducted the study across seven areas in Michigan, USA, which includes part of the current contiguous southern distribution limit of wolves (Fig. 1; Boitani et al. 2018). Six areas (Crystal Falls [CF], Silver Mountain [SM], West Iron County [WIC], Little Girl's Point [LGP], Lake Gogebic [LG], Dickinson County [DC]) were in the Upper Peninsula (UP) of Michigan in areas with varying wolf density (Michigan Department of Natural Resources [MDNR], Appendix S1: Fig. S1; O'Neil 2017) and one area (Little Traverse Bay Bands of Odawa Indians [ODA]) in the northern Lower Peninsula of Michigan (LP) where wolves are absent and geographically separated by Lake Michigan and Lake Huron. All study areas were predominantly forested (DataS1: Study Area Means.csv); dominant tree species included eastern white cedar (*Thuja occidentalis*), eastern hemlock (*Tsuga canadensis*), and balsam fir (*Abies balsamea*) in lowlands, and pine (*Pinus* spp.), aspen (*Populus* spp.), maple (*Acer* spp.), and birch (*Betula* spp.) in uplands. At the smaller spatial scale used in this study, total housing density was greatest in the LGP and least in the SM study area. Land cover edge density (indexing habitat heterogeneity) was greatest in the CF and least in the ODA study area. Where wolves were present, wolf density appeared greatest in the SM and least in the DNC study area. Site-specific (see camera sites and covariates) and mean study-area-specific estimates of covariates and weather during the study period reported in DataS1: Study Area Means.csv and DataS1: Site Covariate Estimates.csv.

Methods

Camera sites and covariates

During 1 August–5 September 2019, we established 290 remote cameras (model sn84G, Stealth Cam, Grand Prairie, Texas, USA) at sites in the six UP study areas where wolves were present, and 58 remote cameras (model BTC-8A, Browning, Birmingham, Alabama, USA) at sites in the 1 LP study area where wolves were absent (Fig. 1). Cameras were affixed to trees about 50 cm above ground and >1 km ($\bar{x}$= 1.6 km, standard deviation [SD] = 0.42) apart along non-primary roads,

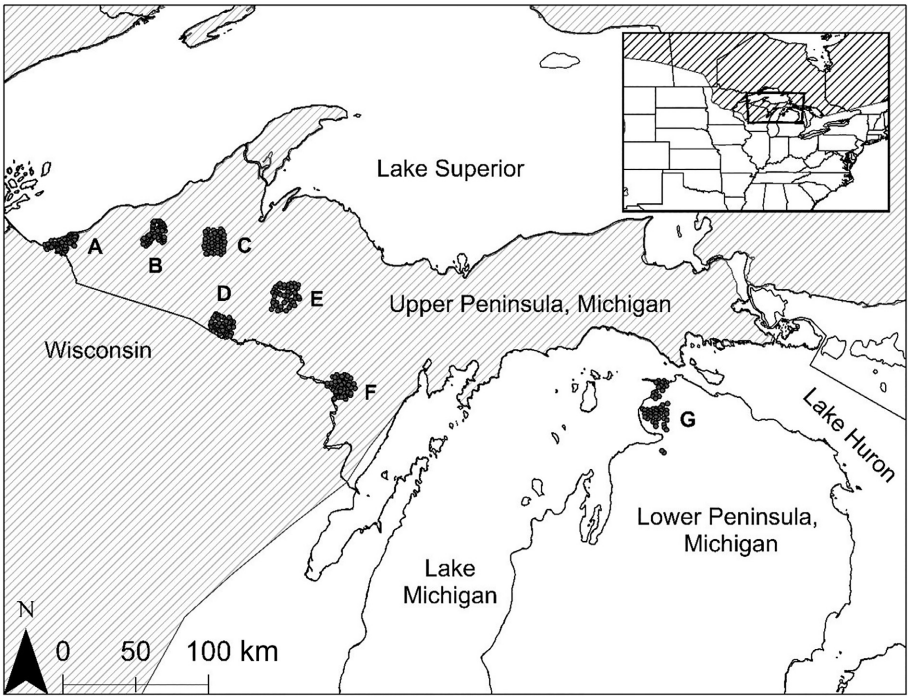

FIG. 1. Locations of study areas (denoted by letters) and remote camera sites (represented as dots) used to assess patterns in multi-species occupancy and diel activity of gray wolves (*Canis lupus*), coyotes (*C. latrans*), and red fox (*Vulpes vulpes*), in Michigan, USA, 1 August–5 September 2019. A, Little Girl's Point (n = 50); B, Lake Gogebic (n = 49); C, Silver Mountain (n = 50); D, West Iron County (n = 46); E, Crystal Falls (n = 47); F, Dickinson County (n = 48); G, Little Traverse Bay Band of Odawa Indians (n = 58; wolves absent). Inset shows black rectangle denoting location of study area, dashed lines show current wolf distribution (Boitani et al. 2018).

animal trails, and small clearings to detect carnivores (Kohn et al. 2001) and minimize vegetative obstruction. In the LP study area only, a scent attractant (Caven's Gusto, Minnesota Trapline Products, Pennock, MN, USA) was used to improve detection. Cameras recorded three or five images when triggered (0.4 and 0.7 s between images, respectively) with 5-minute or 30-minute delays in the UP and LP study areas, respectively. We then sub-sampled the UP data to a 30-min delay to match LP data. Identification of species in images was performed by the authors and trained technicians. A species was considered detected at a site during each observation period by ≥1 image.

Recent work has emphasized the need for ecological relevance in choice of scale when using multi-species occupancy models (Devarajan et al. 2020). We used an observation period (temporal scale) of 24 h that began at 15:00 and ended at 14:59 the following day, coinciding with diel activity patterns of collared wolves and coyotes in the UP (Petroelje et al. 2021) and camera detections of canids in this study (Fig. 4). To estimate spatial scale, we calculated the mean daily distance between the first and last locations of wolves (n = 36) and coyotes (n = 34) affixed with global positioning system collars (15-minute relocation interval) during July–August 2010–2019 in the UP as part of a parallel study (e.g., Petroelje et al. 2020, 2021). We estimated mean daily distance values of 4.8 and 2.7 km for wolves and coyotes, respectively, which agrees with patterns of reduced space use with decreased body size in mammals (Tucker et al. 2014). Next, we created circular buffers around all sites with radii corresponding to mean daily distances for each species. Within each buffer we estimated the area weighted sum of seasonal and permanent housing density (Stewart et al. 2007, United States Census Bureau 2010) and land cover edge density of land covers considering eight ordinal directions as the ratio of total edge length of observed land cover types and buffer area (Hesselbarth et al. 2019, Jin et al. 2019).

Multi-species occupancy modeling

The six UP study areas and the one LP study area had both methodological (camera details, scent lure used in LP) and biological differences (wolves present in UP and absent in LP). Thus, we assessed species occupancy and pairwise interactions with separate multi-species occupancy analyses (Rota et al. 2016), one for the UP areas that included all three species, and one for LP area that included only coyote and red fox. Within each of these analyses, methodology was consistent. For each analysis, we defined seven candidate occupancy models: (1) a null

model with all intercept-only occupancy and interaction parameters, (2) a model that incorporated effects of edge density on first-order occupancy parameters, (3) a model that incorporated effects of human presence on first-order occupancy parameters, and (4) a model combining edge density and human presence, (5) the edge density model with effects also on each pair of two-species interactions, (6) the human presence model with effects on two-species interactions consistent with direct dominance relationships, (7) and a global model. Consistent with our hypotheses focused on pairwise interactions, we did not estimate the three-way interaction term across species (Rota et al. 2016). All models assumed unique, but constant, detection probabilities for each species.

For all models, edge density and human presence covariates were calculated for the corresponding species-relevant buffer size. As subordinate canids may spatially avoid dominant canids (Mueller et al. 2018, Svoboda et al. 2019), we estimated covariates at the dominant canid daily movement scale in species interaction models. To account for potential spatial autocorrelation between camera sites, we included latitude and longitude as covariates on first-order occupancy parameters in all models (Rota et al. 2016). All covariates were normalized before analysis. We ranked models using the Akaike information criterion (AIC; Burnham et al. 2011) and considered significance at $\alpha < 0.15$ concordant with AIC_c (AIC corrected for sample size) model selection (Arnold 2010). Models were fit using the "unmarked" package (Fiske and Chandler 2011) in R version 4.0.2 (R Core Team 2020).

As intraguild carnivores may partition niche space spatially and temporally, we estimated overlap in diel activity periods between species by the coefficient of overlap, Δ_4 (0 = no overlap, 1 = complete overlap) via kernel density functions (Ridout and Linkie 2009) from camera detections. We compared overlap in diel activity of species between the UP and LP study areas. We estimated 95% confidence intervals of Δ_4 estimates with 1,000 iterations and considered significance when confidence intervals did not overlap.

Results

Raw detection statistics

Cameras recorded 687,197 total images across study areas ($\bar{x}$ per study area = 98,171) and of these 6,370 were identified as wolves ($\bar{x}$ [excluding LP] = 1,062), 10,137 as coyotes ($\bar{x}$ = 1,448), and 4,876 as fox ($\bar{x}$ = 696) (Fig. 2).

Upper Peninsula occupancy model results

Across the 290 UP camera sites where wolves were present, wolves were detected at least once at 37% of sites, coyotes at 50% of sites, and foxes at 18%. Both coyotes and wolves were detected at least once at 18% of sites and both wolves and foxes were detected at least once at 11% of sites. Both coyote and fox were detected at least once at 8% of sites.

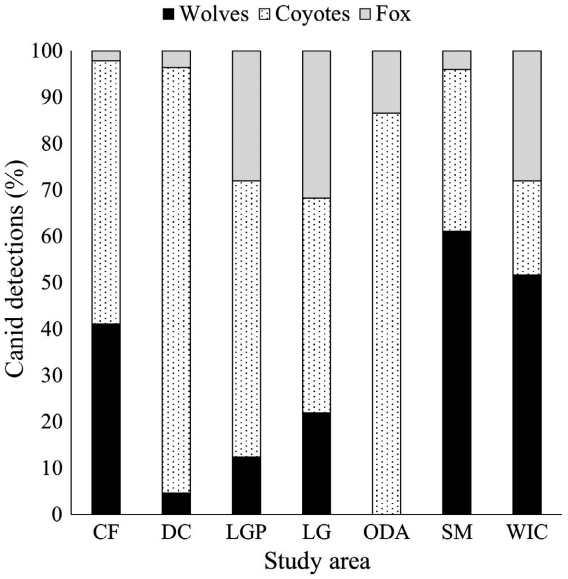

Fig. 2. Percentages of total remote camera detections by species among study areas used to assess patterns in multi-species occupancy and diel activity of gray wolves (*Canis lupus*), coyotes (*C. latrans*), and red fox (*Vulpes vulpes*), in Michigan, USA, 1 August–5 September 2019. LGP, Little Girl's Point (total number of images obtained [*n*] = 95,214); LG, Lake Gogebic (*n* = 115,936); SM, Silver Mountain (*n* = 70,812); WIC, West Iron County (*n* = 136,004); CF, Crystal Falls (*n* = 70,158); DC, Dickinson County (*n* = 61,907); ODA, Little Traverse Bay Band of Odawa Indians (*n* = 137,706; wolves absent).

The top-ranked wolf, coyote, and fox interaction model included edge density effects on first-order occupancy parameters and two-species interactions (Table 1). Based on the top-ranked model, wolf occurrence did not influence coyote occupancy probability, and coyote occurrence did not influence fox occupancy probability. However, fox occupancy probability was more than three times greater at sites where wolves were present relative to sites wolves were absent (Fig. 3). Edge density did not influence first-order occupancy parameters for any species but had the largest positive effect on coyote-wolf co-occurrence and a negative effect on coyote–fox co-occurrence (Table 2). Human presence did not influence occupancy dynamics (Table 1).

Lower Peninsula occupancy model results

Across the 58 camera sites in the LP where wolves were absent, coyotes were detected at least once at 57% of sites, and foxes were detected at least once at 19% of sites. Both coyote and fox were detected at least once at 10% of sites. The top-ranked coyote and fox interaction model in the LP included edge density effects on first-order occupancy parameters, but not on the pairwise coyote–fox interaction (Table 3). Edge density had a

TABLE 1. Ranking of candidate gray wolf (*Canis lupus*), coyote (*C. latrans*), and red fox (*Vulpes vulpes*) multi-species occupancy models by AIC, Upper Peninsula of Michigan, USA, 1 August–5 September 2019.

Model	*K*	AIC	ΔAIC	Weight
EDGE + INTERACTION	21	8,985.00	0.00	0.53
EDGE + HUMAN + INTERACTION	27	8,987.13	2.13	0.18
EDGE + HUMAN	21	8,987.63	2.63	0.14
EDGE	18	8,987.85	2.85	0.13
NULL	15	8,993.43	8.43	0.01
HUMAN	18	8,994.22	9.22	0.01
HUMAN + INTERACTIONS	21	8,997.06	12.05	0.00

Notes: Models included the effect of edge density (EDGE), human presence (housing density; HUMANS), both, or neither (NULL) on first-order occupancy terms. We also considered models where EDGE and HUMANS affected two-species interaction terms (INTERACTION) in addition to first-order terms. *K* represents the number of model parameters, AIC is the Akaike information criterion, and Weight is the AIC model weight.

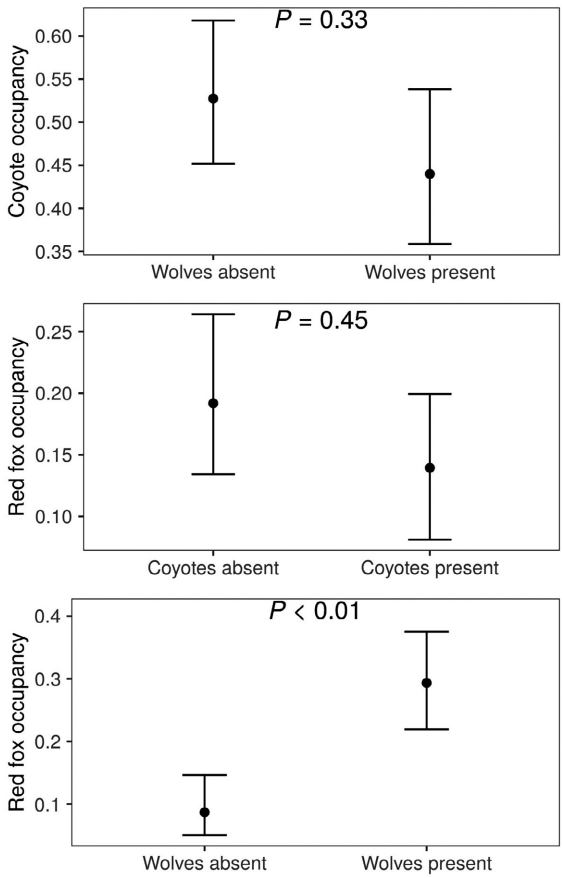

FIG. 3. Marginal occupancy probabilities for coyote (*Canis latrans*) based on gray wolf (*C. lupus*) presence, and for red foxes (*Vulpes vulpes*) based on coyote and wolf presence in study areas in the Upper Peninsula, Michigan, USA, 1 August–5 September 2019. Estimates derived from the top-ranked multi-species occupancy model.

negative effect on coyote occupancy, and a marginally significant positive effect on fox occupancy (Table 4). There was no effect of coyote presence at a site on red fox occupancy.

TABLE 2. Selected parameter estimates, standard errors, and associated *P* values from the top-ranked multi-species occupancy model for gray wolf (*Canis lupus*), coyote (*C. latrans*), and red fox (*Vulpes vulpes*), Upper Peninsula of Michigan, USA, 1 August–5 September 2019.

Parameter	Estimate	SE	*P*
Coyote			
Intercept	0.13	0.17	0.44
Edge density	0.23	0.17	0.18
Red fox			
Intercept	−2.21	0.34	<0.01
Edge density	0.03	0.26	0.91
Wolf			
Intercept	−0.59	0.21	0.01
Edge density	−0.12	0.20	0.57
Coyote × red fox interaction			
Intercept (interaction only)	−0.28	0.37	0.45
Edge density	−0.56	0.34	0.10
Wolf × coyote interaction			
Intercept (interaction only)	−0.29	0.30	0.33
Edge density	0.72	0.27	0.01
Wolf × red fox interaction			
Intercept (interaction only)	1.45	0.38	<0.01
Edge density	−0.10	0.32	0.74

Notes: The top-ranked model included edge density effects on both first-order and species interaction terms in the occupancy model. Intercepts for pairwise species interaction terms that were significantly different from 0 ($\alpha < 0.15$) indicate occupancies of the two species were correlated. Complete estimates from this model can be found in Appendix S1: Table S1.

Temporal results

In the UP where wolves were present, overlap of diel activity between wolves and foxes was lowest of all species pairs and overlap of diel activity was greatest between coyotes and foxes (Table 3, Fig. 4). In the LP where wolves were absent, diel activity overlap between coyotes and foxes was reduced and confidence intervals were 85% greater compared to the UP. Coyotes in areas where wolves were present vs. absent had 57% less intraspecific diel activity overlap than foxes (Table 5).

Table 3. Ranking of candidate coyote (*Canis latrans*) and red fox (*Vulpes vulpes*) multi-species occupancy models by AIC, Lower Peninsula of Michigan, USA, 1 August–5 September 2019.

Model	*K*	AIC	ΔAIC	Weight
EDGE	11	971.62	0.00	0.41
NULL	9	972.82	1.20	0.22
EDGE + HUMAN + INTERACTION	15	973.42	1.79	0.17
EDGE + HUMAN	13	974.60	2.98	0.09
EDGE + INTERACTION	12	974.67	3.05	0.09
HUMAN	11	978.07	6.45	0.02
HUMAN + INTERACTION	12	979.52	7.90	0.01

Notes: Models and terms are as in Table 1.

Table 4. Selected parameter estimates, standard errors, and associated *P* values from the top-ranked multi-species occupancy model for coyote (*Canis latrans*) and red fox (*Vulpes vulpes*), Lower Peninsula of Michigan, USA, 1 August–5 September 2019.

Parameter	Estimate	SE	*P*
Coyote			
Intercept	0.40	0.38	0.29
Edge density	−0.62	0.38	0.10
Red fox			
Intercept	−1.26	0.67	0.06
Edge density	0.57	0.41	0.16
Coyote – red fox interaction			
Intercept (interaction only)	0.15	0.87	0.86

Notes: The top-ranked model included edge density effects on first-order terms in the occupancy model. Intercepts for pairwise species interaction terms that were significantly different from 0 ($\alpha < 0.15$) indicate occupancies of the two species were correlated. Complete estimates from this model can be found in Appendix S1: Table S2.

Discussion

Our results provide marginal support for the fine-scale release of foxes from competition with coyotes by the occurrence of wolves. Further, these results are consistent with dampened effects of top-down control near the edge of current wolf range in North America (Newsome et al. 2017). Observed interactions appeared mediated by cumulative competition for foxes, which may employ spatial and temporal strategies to limit competition with dominant canids.

Spatial interactions

Fox occupancy probability was greater at sites where wolves were present, supporting our prediction. Reduced occupancy of coyotes due to wolf occurrence, and of foxes due to coyote occurrence, also supported our prediction in directionality though effects were not significant. Patterns of decreased co-occurrence of similarly sized canids supports three possible explanations; that we detected spatial avoidance as a mechanism supporting a trophic cascade among canid species with insufficient power, that we detected reduced effects of top-down control on coyotes by wolves near the edge of current wolf distribution (Newsome and Ripple 2015), or that co-occurrence of wolves and foxes is positively related regardless of coyote occurrence. We are unaware of evidence supporting the later. Avoidance of wolves by coyotes and coyotes by foxes is supported by the proposed mechanisms of asymmetrical interference competition and size-based dominance among canids (Peterson 1996, Levi and Wilmers 2012). Wolves and coyotes and coyotes and foxes are likely in direct competition; however, wolves may not perceive foxes as direct competitors due to differences in body size driving divergent prey selection (Carbone et al. 1999, Flagel et al. 2016) and foxes may also benefit from scavenging wolf kills (Ballard et al. 2003). Further, competition between foxes and coyotes may be reduced in the UP due to wolf presence, with spatial occurrence of foxes primarily driven by factors such as prey availability (Levi and Wilmers 2012) and secondarily due to risk from coyotes, which would make detection of avoidance more challenging. Future research may include interaction effects of predators and prey species though detecting small prey species (e.g. snowshoe hare [*Lepus americanus*]) with remote cameras can be more challenging (Glen et al. 2013).

Where wolves were absent in the LP, use of an attractant likely increased canid detections (Holinda et al. 2020) but there is no evidence of altered detection probability due to a scent lure between species. Therefore, if competition with coyotes is a primary driver of spatial occurrence of foxes we would still have expected an inverse relationship between coyote and fox marginal occupancy probabilities. Proportions of human-altered land covers were greatest in the LP study area (Data S1: Study Area Means.csv), which may partially explain the lack of apparent spatial segregation between species as observed in other areas (Litvaitis 1992, Gosselink et al. 2003) and our estimate of risk to humans for canids may have been insufficient (see anthropogenic effects). We cannot disregard that a latent variable not tested in this study may mediate these species interactions.

Edge effects

In the UP, where wolves were present, probability of wolf and coyote co-occurrence increased with increased

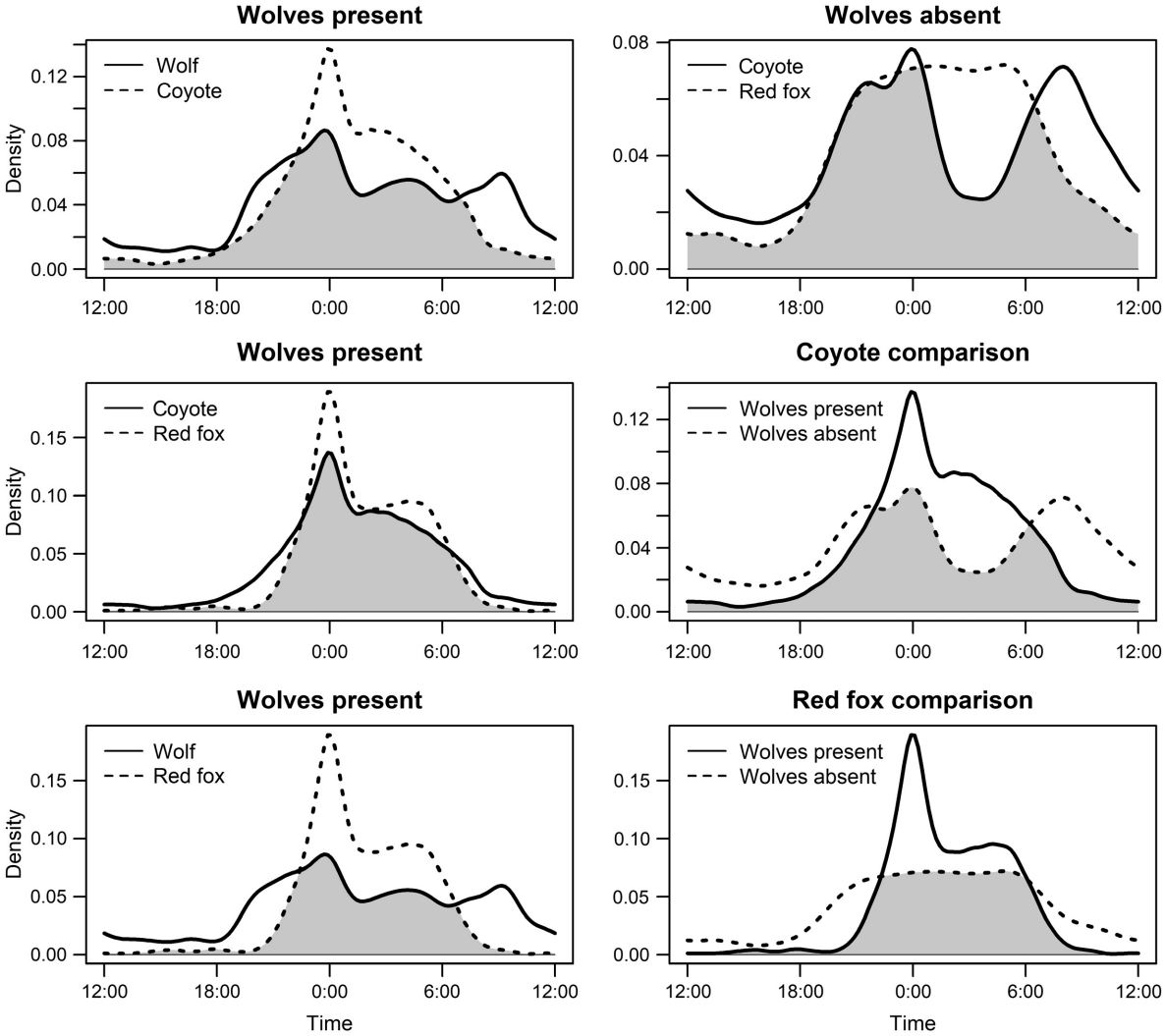

FIG. 4. Density estimates of diel activity of wolves (*Canis lupus*), coyotes (*C. latrans*), and red foxes (*Vulpes vulpes*), in Michigan, USA, 1 August–5 September 2019. Shaded areas represent areas of overlap between species and comparisons.

TABLE 5. Overlap in diel activity of gray wolves (*Canis lupus*), coyotes (*C. latrans*), and red foxes (*Vulpes vulpes*), Michigan, USA, 1 August–5 September 2019.

			95% confidence interval	
Wolves	Species comparison	Δ_4	Lower	Upper
Present	wolf–coyote	0.76	0.73	0.77
Present	coyote–red fox	0.85	0.83	0.86
Present	wolf–red fox	0.61	0.60	0.61
Absent	coyote–red fox	0.79	0.71	0.91
Present–absent	coyote–coyote	0.66	0.61	0.70
Present–absent	red fox–red fox	0.71	0.61	0.82

Notes: Δ_4 = estimated overlap. Confidence intervals estimated with 1,000 bootstrap iterations.

edge density consistent with our prediction. Increased habitat complexity may reduce competition and promote coexistence of intraguild predators (Janssen et al. 2007). Increased edge density (forested vs. open) is also correlated with increased risk of human caused mortality for wolves in the UP (O'Neil 2017), which may reduce competition for coyotes. Greater variability in habitat selection of coyotes (Arjo and Peltscher 2004) may reflect greater variation in prey selection (Petroelje et al. 2021) or human tolerance (O'Neil 2017) compared to wolves and may also reduce competition between species. Occupancy of foxes where wolves were present was unrelated to edge density. Less so than for coyotes, foxes are still at risk to wolves (Mech 1966, Peterson 1977) and all three species may also overlap in prey selection, particularly

for small- to medium-sized prey (Major and Sherburne 1987). It may be that with greater edge density, cumulative competition due to increased co-occurrence of wolves and coyotes limited spatial occurrence of foxes through increased overall risk and decreased prey availability.

In the LP study area, where wolves were absent, coyote occupancy probability was negatively correlated with increased edge density, whereas fox occupancy probability was directionally associated with increased edge density but lacked significance. The top-ranked model did not include an effect of edge density on co-occurrence of coyotes and foxes. Habitat edges are commonly associated with increased prey availability for coyotes (Theberge and Wedeles 1989, Ellington et al. 2020) and increased edge density can reduce competition among intraguild competitors (Janssen et al. 2007). It may be that decreased occurrence of coyotes and the directional effect of increased occurrence of foxes with increasing edge density spatially segregates these species, reducing competition. However, reduced cover due to increased pasture and agricultural lands in the LP study area may represent increased risk for coyotes (Van Deelen and Gosselink 2006). Edge habitat (forested vs. open) is associated with increased human mortality of wolves (O'Neil 2017) and as coyotes could be legally harvested during our study, avoidance of edge habitat may represent a risk minimizing strategy for coyotes, which would reduce competition with foxes.

Anthropogenic effects

We did not detect an effect of housing density on occupancy of species or interspecific interactions. Though associated with perceived risk to humans for pumas (*Puma concolor*) (Moss et al. 2016), wolves (Fowler et al. 2019), coyotes, and grey foxes (*Urocyon cinereoargenteus*) (Lesmeister et al. 2015), housing density may have been a poor estimator of perceived human risk in our study. Humans were attributed to 66% of wolf mortality in the UP during 1994–2013 (O'Neil 2017) and it was legal to harvest coyotes, but not foxes during our study. Further, foxes are less likely to come in conflict with humans than are wolves and coyotes (MDNR, *unpublished data*). Berger (2007) described a spatial "human shield" effect wherein human related factors would limit larger carnivores, which may indirectly benefit subordinate carnivores as reported between coyotes and foxes (Moll et al. 2018, Kellner et al. 2020). Also, expansion of coyotes presumably occurred in response to extirpation of wolves during European colonization of North America (Prugh et al. 2009). Therefore, we expected greater human risk to wolves and coyotes would decrease occurrence of both species, resulting in increased occurrence of foxes. However, low overall human density and heavily forested study areas providing refugia may have reduced risk for wolves (Oakleaf et al. 2006) and coyotes (Mueller et al. 2018) thereby reducing competitive effects on fox occupancy. We also suspect the number of interactions among species and risk variables may have been too complex to be detected by our models. A direct estimate of human risk at our camera sites was not possible, but future studies could consider pairwise species–human interactions.

Temporal partitioning

Wolves and foxes had the least overlap in diel activity where wolves were present. Though reports of despotic behavior by wolves on foxes are rare, wolves do kill foxes (Mech 1966, Peterson 1977). In our study, foxes co-occurred in close spatial proximity to wolves, and we suspect low diel activity overlap represented fine-scale temporal avoidance of wolves by foxes. Coyotes kill foxes more commonly than wolves (Sargeant and Allen 1989, Gosselink et al. 2007) and these species exhibited the greatest temporal overlap where wolves were present but where they were apparently also more spatially segregated. Therefore, it appears foxes limited interactions and likely competition with wolves temporally and with coyotes spatially through increased spatial co-occurrence with wolves. Similarly, dholes (*Cuon alpinus*) exhibited variable spatial and temporal avoidance strategies presumably reducing competition with tigers (*P. tigris*) and leopards (*P. pardus*; Karanth et al. 2017).

Temporal overlap of coyotes and foxes where wolves were absent was reduced compared to where wolves were present through increased nocturnality of foxes relative to more crepuscular activity of coyotes. Variability in temporal overlap between coyotes and foxes was also 6.7-fold greater where wolves were absent than present. In areas with comparatively reduced wolf densities coyotes exhibit increased variability in diel activity (N. L. Fowler, T. R. Petroelje, T. M. Kautz, N. J. Svoboda, J. F. Duquette, K. F. Kellner, D. E. Beyer Jr., and J. L. Belant, *in review*), which may reduce opportunities for temporal segregation by foxes. Lacking the opportunity to spatially segregate from coyotes through co-occurrence with wolves, reduced overlap and increased temporal variability of foxes may facilitate their avoidance of coyotes (Mueller et al. 2018). Further research is needed to characterize these complex spatial and temporal occurrence relationships.

Conclusion

We provide partial support for the reported trophic cascade among wolves, coyotes, and foxes by demonstrating a fine-scale positive association between wolf and fox occurrence. Wolf–coyote and coyote–fox relationships were as expected though not significant and appeared to be mediated by factors related to edge density and human presence. Our results support potentially reduced top-down effects near the edge of wolf distributions owing to high dispersal and establishment capabilities of coyotes (Newsome and Ripple 2015). Dampened

top-down effects within this transition zone may extend 200 km or further (Newsome et al. 2017) from the edge of wolf distributions (Newsome and Ripple 2015), which included all but one of the wolf present study areas (LGP; $\bar{x}$ = 153 km). Though unable to fully explore this reported phenomenon future research may consider similar fine-scale studies stratified along a wider gradient of distances from current wolf distributions.

Results of this study suggest variable spatial and temporal occurrence patterns of subordinate canids consistent with perceptions of competition and risk supported by broad patterns in distribution and abundance (Levi and Wilmers 2012, Newsome and Ripple 2015). We also found support for the mediation of species interactions due to bottom-up forces related to edge density influencing suspected prey availability (Hunter and Price 1992). This is contrary to Ripple et al.'s (2016) definition of a trophic cascade solely driven by top-down forces. Interpretation of increased co-occurrence of wolves and coyotes with increased edge density and relationships of marginal occupancy between species could be debated, but we cannot discount potential bottom-up effects in our study. Detection of small prey is limited using remote cameras (Burton et al. 2015) and prohibited our direct evaluation of the effect of increased co-occurrence of wolves and coyotes on prey availability for foxes. Discerning top vs. bottom force control in multi-species interactions will require simultaneous estimation of both.

Statistical advancements have improved our ability to detect multi-species interactions though further research is needed to guide selection of covariates influencing species occurrence and detection and appropriate spatial and temporal scales (Rota et al. 2016, Devarajan et al. 2020). Our covariates were selected based on their reported effects on canid distributions and abundance indexing increased niche space and prey availability (edge density) and perceptions of human risk (housing density). However, other covariates are likely suitable for indexing similar effects depending on spatial or temporal scale. For example, increased road density in the Great Lakes Region is associated with reduced wolf occurrence (Mladenoff et al. 1995, Potvin et al. 2005), though ancillary analyses in our study indicated a positive association between road density and wolf occurrence, perhaps due to our fine spatial scale (Zimmerman et al. 2014). Though we used ecologically relevant detection scales in our study, seasonal variation in resource availability, perceived risk, and species life history traits (e.g., breeding and neonate rearing) also likely influence intraguild interactions. Future works may consider spatial and temporal stratification of scale in sampling design to discern these effects along with a framework to evaluate multiple covariates indexing similar ecological effects. As with all models, care must be taken to avoid over parameterization and selective reporting, which can degrade interpretability (Burnham et al. 2011, Head et al. 2015).

The number of studies evaluating trophic cascades in terrestrial systems has increased exponentially since the 1990s (Ripple et al. 2016) with much attention paid to the role of wolf recolonization in shaping ecological communities (Berger et al. 2008, Ripple and Beschta 2012). Though widely accepted in popular media (Mech 2017), evidence of wolf-induced trophic cascades is debated (Mech 2012, Peterson et al. 2014, Smith et al. 2016, Allen et al. 2017). Our results provide fine scale evidence for the role wolves may play in mediating intraguild competition between subordinate species. Broadly, our results are also consistent with the mesopredator release hypothesis (Prugh et al. 2009), the principles of despotic distribution of subordinate species, and the parity of competitive species chain length determining strength of competition (Levi and Wilmers 2012). Wolves will likely continue to recolonize areas sympatric with subordinate competitors, and prey species, which historically occurred at lesser densities or were absent altogether (Mech 1995, Arjo and Pletscher 2000, Gompper et al. 2015). Knowledge of the effects of lengthened trophic chains in ecological communities has heuristic value to our understanding of evolutionary processes and practical value in predicting responses of subordinate carnivores and prey species to recolonization and reintroductions of dominant carnivores.

Acknowledgments

We received support from Safari Club International (SCI) Foundation, SCI Michigan Involvement Committee, Michigan Department of Natural Resources, Camp Fire Conservation Fund, and Federal Aid in Wildlife Restoration Act under Pittman-Robertson projects MI W-147-R and MI W-155-R Study 1.44. We thank A. L. Lutto, J. C. Magee, D. C. Norton, J. Lukowski, E. Largent, and R. McGillviray for assistance with data collection. We thank project technicians and staff for assistance with data collection and the State University of New York College of Environmental Science and Forestry, Little Traverse Bay Bands of Odawa Indians, and Michigan Natural Features Inventory for support.

Literature Cited

Allen, B. L., et al. 2017. Large carnivore science: non-experimental studies are useful, but experiments are better. Nature Ecology & Evolution 1:1511–1519.

Arjo, W. M., and D. H. Peltscher. 2004. Coyote and wolf habitat use in northwestern Montana. USDA National Wildlife Research Center - Staff Publications 71. https://digitalcommons.unl.edu/icwdm_usdanwrc/71

Arjo, W. M., and D. H. Pletscher. 2000. Behavioral responses of coyotes to wolf recolonization in northwestern Montana. Canadian Journal of Zoology 77:1919–1927.

Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. Journal of Wildlife Management 74:1175–1178.

Ballard, W. B., L. N. Carbyn, and D. W. Smith. 2003. Wolf interactions with non-prey. Pages 259–271 *In* L. D. Mech, and L. Boitani, editors. Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago, Illinois, USA.

Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. Biology Letters 3:620–623.

Berger, K. M., and E. M. Gese. 2007. Does interference competition with wolves limit the distribution and abundance of coyotes? Journal of Animal Ecology 76:1075–1085.

Berger, K. M., E. M. Gese, and J. Berger. 2008. Indirect effects and traditional trophic cascades: a test involving wolves, coyotes, and pronghorn. Ecology 89:818–828.

Boitani, L., M. Phillips & Y. Jhala 2018. Canis lupus (errata version published in 2020). The IUCN Red List of threatened species 2018: e.T3746A163508960.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: Some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65:23–35.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. M. Bayne, and S. Boutin. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. Journal of Applied Ecology 52:675–685.

Carbone, C., G. M. Mace, S. C. Roberts, and D. W. Macdonald. 1999. Energetic constraints on the diet of terrestrial carnivores. Nature 402:286–288.

Caro, T. M., and C. J. Stoner. 2003. The potential for interspecific competition among African carnivores. Biological Conservation 110:67–75.

Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences USA 71:3073–3077.

Crooks, K. R., and M. E. Soulé. 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400:563–566.

Devarajan, K., T. L. Morelli, and S. Tenan. 2020. Multi-species occupancy models: review, roadmap, and recommendations. Ecography 43:1–13.

Ellington, E. H., E. M. Muntz, and S. D. Gehrt. 2020. Seasonal and daily shifts in behavior and resource selection: how a carnivore navigates costly landscapes. Oecologia 194:87–100.

Estes, J. A., and J. F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science 185:1058–1060.

Fiske, I., and R. Chandler. 2011. unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software 43:1–23.

Flagel, D. G., G. E. Belovsky, M. J. Cramer, D. E. Beyer Jr, and K. E. Robertson. 2016. Fear and loathing in a Great Lakes forest: cascading effects of competition between wolves and coyotes. Journal of Mammalogy 98:77–84.

Fowler, N. L., J. L. Belant, and D. E. Beyer, Jr. 2019. Nonlinear relationships between human activities and wolf-livestock depredations. Biological Conservation 236:385–392.

Fretwell, S. D., and A. L. Barach. 1977. The regulation of plant communities by the food chains exploiting them. Perspectives in Biology and Medicine 20:169–185.

Glen, A. S., S. Cockburn, M. Nichols, J. Ekanayake, and B. Warburton. 2013. Optimising camera traps for monitoring small mammals. PLoS ONE 8:e67940.

Gompper, M. E., J. L. Belant, and R. Kays. 2015. Carnivore coexistence: America's recovery. Science 347:382–383.

Gosselink, T. E., T. R. Van Deelen, R. E. Warner, and M. G. Joselyn. 2003. Temporal habitat partitioning and spatial use of coyotes and red foxes in east-central Illinois. Journal of Wildlife Management 60:90–103.

Gosselink, T. E., T. R. Van Deelen, R. E. Warner, and P. C. Mankin. 2007. Survival and cause-specific mortality of red foxes in agricultural and urban areas of Illinois. Journal of Wildlife Management 76:1862–1873.

Head, M. L., L. Holman, R. Lanfear, A. T. Kahn, and M. D. Jennions. 2015. The extent and consequences of P-hacking in science. PLoS Biology 13:e1002106.

Hesselbarth, M. H., M. Sciaini, K. A. With, K. Wiegand, and J. Nowosad. 2019. landscapemetrics: an open-source R tool to calculate landscape metrics. Ecography 42:1648–1657.

Holinda, D., J. M. Burgar, and A. C. Burton. 2020. Effects of scent lure on camera trap detections vary across mammalian predator and prey species. PLoS ONE 15:e0229055.

Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73:724–732.

Janssen, A., M. W. Sabelis, S. Magalhães, M. Montserrat, and T. Van der Hammen. 2007. Habitat structure affects intraguild predation. Ecology 88:2713–2719.

Jin, S., C. Homer, L. Yang, P. Danielson, J. Dewitz, C. Li, Z. Zhu, G. Xian, and D. Howard. 2019. Overall methodology design for the United States national land cover database 2016 products. Remote Sensing 11:2971.

Karanth, K. U., A. Srivathsa, D. Vasudev, M. Puri, R. Parameshwaran, and N. S. Kumar. 2017. Spatio-temporal interactions facilitate large carnivore sympatry across a resource gradient. Proceedings of the Royal Society B 284:20161860.

Kellner, K. F., J. E. Hill, M. G. Gantchoff, D. W. Kramer, A. M. Bailey, and J. L. Belant. 2020. Responses of sympatric canids to human development revealed through citizen science. Ecology and Evolution 10:8705–8714.

Kohn, B. E., R. Thiel, and J. L. Hansen. 2001. Road density as a factor in habitat selection by wolves and other carnivores in the Great Lakes Region. Carnivore Conservation in the Twenty-first Century 97:110.

Lesmeister, D. B., C. K. Nielsen, E. M. Schauber, and E. C. Hellgren. 2015. Spatial and temporal structure of a mesocarnivore guild in Midwestern North America. Wildlife Monographs 191:1–61.

Levi, T., and C. C. Wilmers. 2012. Wolves–coyotes–foxes: a cascade among carnivores. Ecology 93:921–929.

Linnell, J. D., and O. Strand. 2000. Interference interactions, co-existence and conservation of mammalian carnivores. Diversity and Distributions 6:169–176.

Litvaitis, J. A. 1992. Niche relations between coyotes and sympatric Carnivora. Pages 73–85 *In* A. H. Boer, editor. Ecology and management of the eastern coyote. University of New Brunswick, Fredericton, New Brunswick, USA.

Major, J. T., and J. A. Sherburne. 1987. Interspecific relationships of coyotes, bobcats, and red foxes in western Maine. Journal of Wildlife Management 51:606–616.

Mech, L. D. 1966. The wolves of Isle Royale. U.S. National Parks Service Fauna Series No. 7. U.S. Government Printing Office, Washington, D.C., USA.

Mech, L. D. 1995. The challenge and opportunity of recovering wolf populations. Conservation Biology 9:270–278.

Mech, L. D. 2012. Is science in danger of sanctifying the wolf? Biological Conservation 150:143–149.

Mech, L. D. 2017. Where can wolves live and how can we live with them? Biological Conservation 210:310–317.

Merkle, J. A., D. R. Stahler, and D. W. Smith. 2009. Interference competition between gray wolves and coyotes in Yellowstone National Park. Canadian Journal of Zoology 87:56–63.

Mladenoff, D. J., T. A. Sickley, R. B. Haight, and A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes Region. Conservation Biology 9:279–294.

Moll, R. J., J. D. Cepek, P. D. Lorch, P. M. Dennis, T. Robison, J. J. Millspaugh, and R. A. Montgomery. 2018. Humans and urban development mediate the sympatry of competing carnivores. Urban Ecosystems 21:765–778.

Moss, W. E., M. W. Alldredge, K. A. Logan, and J. N. Pauli. 2016. Human expansion precipitates niche expansion for an opportunistic apex predator (*Puma concolor*). Scientific Reports 6:39639.

Mueller, M. A., D. Drake, and M. L. Allen. 2018. Coexistence of coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) in an urban landscape. PLoS ONE 13:e0190971.

Newsome, T. M., et al. 2017. Top predators constrain mesopredator distributions. Nature Communications 8:15469.

Newsome, T. M., and W. J. Ripple. 2015. A continental scale trophic cascade from wolves through coyotes to foxes. Journal of Animal Ecology 84:49–59.

Oakleaf, J. K., D. L. Murray, J. R. Oakleaf, E. E. Bangs, C. M. Mack, D. W. Smith, J. A. Fontaine, M. D. Jimenez, T. J. Meier, and C. C. Niemeyer. 2006. Habitat selection by recolonizing wolves in the northern Rocky Mountains of the United States. Journal of Wildlife Management 70:554–563.

O'Neil, S. 2017. The spatial ecology of gray wolves in the Upper Peninsula of Michigan, 1994–2013. Michigan Technical University, Houghton, Michigan, USA.

Pace, M. L., J. J. Cole, S. R. Carpenter, and J. F. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends in Ecology and Evolution 14:483–488.

Paine, R. T. 1980. Food webs: Linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49:666–685.

Palomares, F., and T. M. Caro. 1999. Interspecific killing among mammalian carnivores. American Naturalist 153:492–508.

Peterson, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. National Parks Service Scientific Monograph Series. No. 11. U.S. National Park Service, Washington, D.C., USA.

Peterson, R. O. 1996. Wolves as interspecific competitors in canid ecology. Pages 315–323 *in* L. N. Carbyn, S. H. Fritts, and D. Seip, editors. Wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton, Canada.

Peterson, R. O., J. A. Vucetich, J. M. Bump, and D. W. Smith. 2014. Trophic cascades in a multicausal world: Isle Royale and Yellowstone. Annual Review of Ecology, Evolution, and Systematics 45:325–345.

Petroelje, T. R., J. L. Belant, D. E. Beyer, Jr., and N. J. Svoboda. 2020. Identification of carnivore kill sites is improved by verified accelerometer data. Animal Biotelemetry 8:18.

Petroelje, T. R., T. M. Kautz, D. E. Beyer, Jr., and J. L. Belant. 2021. Interference competition between wolves and coyotes during variable prey abundance. Ecology and Evolution 11:1413–1431.

Potvin, M. J., T. D. Drummer, J. A. Vucetich, D. E. Beyer Jr, R. O. Peterson, and J. H. Hammill. 2005. Monitoring and habitat analysis for wolves in Upper Michigan. Journal of Wildlife Management 69:1660–1669.

Prugh, L. R., C. J. Stoner, C. W. Epps, W. T. Bean, W. J. Ripple, A. S. Laliberte, and J. S. Brashares. 2009. The rise of the mesopredator. BioScience 59:779–791.

R Core Team. 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Ridout, M. S., and M. Linkie. 2009. Estimating overlap of daily activity patterns from camera trap data. Journal of Agricultural, Biological, and Environmental Statistics 14:322–337.

Ripple, W. J., and R. L. Beschta. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. Biological Conservation 145:205–213.

Ripple, W. J., J. A. Estes, O. J. Schmitz, V. Constant, M. J. Kaylor, A. Lenz, J. L. Motley, K. E. Self, D. S. Taylor, and C. Wolf. 2016. What is a trophic cascade? Trends in Ecology & Evolution 31:842–849.

Rosenzweig, M. L. 1966. Community structure in sympatric Carnivora. Journal of Mammalogy 41:602–612.

Rota, C. T., M. A. R. Ferreira, R. W. Kays, T. D. Forrester, E. L. Kalies, W. J. McShea, A. W. Parsons, and J. J. Millspaugh. 2016. A multispecies occupancy model for two or more interacting species. Methods in Ecology and Evolution 7:1164–1173.

Sargeant, A. B., and S. H. Allen. 1989. Observed interactions between coyotes and red foxes. Journal of Mammalogy 70:631–633.

Smith, D. W., R. O. Peterson, D. R. MacNulty, and M. Kohl. 2016. The big scientific debate: trophic cascades. Yellowstone Science 24:70–71.

Stewart, S. I., V. C. Radeloff, R. B. Hammer, and T. J. Hawbaker. 2007. Defining the wildland–urban interface. Journal of Forestry 105:201–207.

Svoboda, N. J., J. L. Belant, D. E. Beyer, J. F. Duquette, and P. E. Lederle. 2019. Carnivore space use shifts in response to seasonal resource availability. Ecosphere 10:e02817.

Theberge, J. B., and C. H. Wedeles. 1989. Prey selection and habitat partitioning in sympatric coyote and red fox populations, southwest Yukon. Canadian Journal of Zoology 67:1285–1290.

Tucker, M. A., T. J. Ord, and T. L. Rogers. 2014. Evolutionary predictors of mammalian home range size: body mass, diet and the environment. Global Ecology and Biogeography 23:1105–1114.

United States Census Bureau. 2010. TIGER/line shapefiles 2010. http://www.census.gov

Van Deelen, T. R., and T. E. Gosselink. 2006. Coyote survival in a row-crop agricultural landscape. Canadian Journal of Zoology 84:1630–1636.

Zimmerman, B., L. Nelson, P. Wabakken, H. Sand, and O. Liberg. 2014. Behavioral response of wolves to roads: scale-dependent ambivalence. Behavioral Ecology 25:1353–1364.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3494/suppinfo