8-6-2021

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Recommended Citation

Petroelje, Tyler R., "Patterns of carnivore competition, time-to-kill, and predation risk on white-tailed deer fawns in a multi-predator landscape" (2021). *Theses and Dissertations*. 5283.
https://scholarsjunction.msstate.edu/td/5283

Patterns of carnivore competition, time-to-kill, and predation risk on white-tailed deer fawns in a multi-predator landscape

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A Dissertation
Submitted to the Faculty of
Mississippi State University
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy
in Forest Resources
in the Department of Wildlife, Fisheries & Aquaculture

Mississippi State, Mississippi

August 2021

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Date of Degree: August 6, 2021

Institution: Mississippi State University

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Title of Study: Patterns of carnivore competition, time-to-kill, and predation risk on white-tailed deer fawns in a multi-predator landscape

Pages in Study: 124

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Identifying factors influencing kill rates or predation risk is crucial to relate predator effects on prey populations. In multi-predator landscapes, some predators may also perceive predation risk which may not only influence their distributions but also their effects on prey populations across landscapes. In the Upper Peninsula of Michigan, USA white-tailed deer (*Odocoileus virginianus*) exist in a multi-predator landscape which includes black bears (*Ursus americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and gray wolves (*C. lupus*). The objectives of this research were to examine spatial relationships among predators and their prey by identifying: 1) competition between wolves and coyotes, 2) factors influencing kill rates of predators, and 3) predator-specific predation risk for white-tailed deer fawns. We quantified the degree of temporal, dietary, and spatial overlap of wolves and coyotes at the population level to estimate the potential for interference competition and identify the mechanisms for how these sympatric canids coexist. We observed significant overlap across resource attributes yet the mechanisms through which wolves and coyotes coexist appear to be driven largely by how coyotes exploit differences in resource availability in heterogenous landscapes. We examined how heterogeneity in landscapes, search rate, and prey availability influence the time between kills for black bears, bobcats, coyotes, and wolves. Spatial heterogeneity in prey availability appeared to be a unifying extrinsic factor mediating time-to-kill across predators, potentially a consequence of more frequent reassessments of patch quality, which can reduce kill rates. We used white-tailed deer fawn predation sites to identify predator-specific predation risk with consideration for active predator occurrence, adult female white-tailed deer occurrence, linear features which may influence prey vulnerability, and habitat characteristics including horizontal cover and deer forage availability. Predator occurrence alone was a poor metric for predation risk. We identified differing landscapes of risk among ambush and cursorial foraging strategies which were more important for defining spatial variation in predation risk than predator density. These findings suggest that in a multi-predator landscape some predators may benefit from greater landscape heterogeneity due to availability of niche space, even though resource heterogeneity reduced predator efficacy and habitat complexity reduced predation risk for prey.

DEDICATION

To Caitlin. For all your love, support, and encouragement throughout this journey.

ACKNOWLEDGEMENTS

I thank Drs. Jerrold Belant and Dean Beyer, Jr. for their mentorship and dedication to my education and research; and Drs. Bronson Strickland, Kevin Hunt, and Andrew Kouba for reviewing this dissertation and for their advice, support, and suggestions throughout my research. I am grateful for the funding provided by the Safari Club International (SCI) Foundation as well as the SCI Michigan Involvement Committee; without their financial support, this project would not have been possible. I also thank the Michigan Department of Natural Resources for providing funding, administrative support, and staff who invested their time in the field or laboratory including Erin Largent, Jeff Lukowski, Gordy Zuehlke, Neil Harri, Brian Roell, Tom Cooley, Caitlin Ott-Conn, Julie Melotti, Monica Joseph, Chuck Sartori, and many more.

This dissertation was born out of data collected on the Michigan Predator-Prey Project which was in no part a single person effort. Of those people, Todd Kautz, Nick Fowler, Ashley Lutto, and Cody Norton invested significant time and energy, and provided great friendship throughout the adventures of field work in Crystal Falls and across the Upper Peninsula of Michigan, thank you. I thank the technicians and support staff of the Michigan Predator-Prey project who collected data year-round, day and night, on four carnivore species and five prey species which made this dissertation possible, including Conner Almond, Jake Boone, Chris Boyce, Polly Chen, Kelly Deweesee, Caleb Eckloff, Zack Farley, Ty Frank, Jen Grauer, Kaitlin Haase, Kris Harmon, Sara Harrington, Kyle Hines, Abbi Hirschy, Jackie Jeffery, Brian Kidder, Carrie Kyle, Tom Lacerda, Joe LaRose, Nate Libal, Mollie Liskiewicz, Jason Lombardi, Ashley

Lutto, Phillip Lyons, Deb Martell, Ben Matykiewicz, Casey Maynard, Emily Moberg, Olivia Montgomery, Peter Mumford, Mac Nichols, Morgan Oberly, Anne Patterson, Erica Perez, Matthew Peterson, Steffen Peterson, Monique Picon, Garret Price, Elizabeth Robbe, Alyssa Roddy, David Rogers, Jessie Roughgarden, Greta Schmidt, Evan Shields, Brett Skelly, Kyle Smith, Missy Stallard, Savanna Summers, Logan Thompson, Daniel Tomasetti, Katie Torreano, Kyle Travis, Wes Tucker, Annie Washakowski, Sara Wendt, Tanya Wolf, Chloe Wright, and Chantel Wright. I thank Greg Davidson with Find It Detection Dogs and his staff Jen Blum and Nicole Cook for their many days afield conducting carnivore cluster investigations. I thank the many landowners and public of Crystal Falls, Michigan that assisted this research through land access and hospitality. I thank my wife, Caitlin, and my family for their continued support throughout my research and education. I thank Clay Wilton, Jared Duquette, Nate Svoboda, Chris Ayers, Zac Loman, Florent Bled, the members of the Carnivore Ecology Laboratory, and more who provided friendship, discussion, and support while at Mississippi State. Finally, I thank the faculty and staff of Mississippi State University Department of Wildlife, Fisheries and Aquaculture, and the Forest and Wildlife Research Center, including, but not limited to Laura Andrews, Annice Hill, Angela Hill, and Diane Weeks who guided me through the day-to-day operations.

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CHAPTER I

INTERFERENCE COMPETITON BETWEEN WOLVES AND COYOTES DURING VARIABLE PREY ABUNDANCE

Abstract

Interference competition occurs when two species have similar resource requirements and one species is dominant and can suppress or exclude the subordinate species. Wolves (*Canis lupus*) and coyotes (*C. latrans*) are sympatric across much of their range in North America where white-tailed deer (*Odocoileus virginianus*) can be an important prey species. We assessed the extent of niche overlap between wolves and coyotes using activity, diet, and space use as evidence for interference competition during 3 periods related to the availability of white-tailed deer fawns in the Upper Great Lakes region of the USA. We assessed activity overlap (Δ) with data from accelerometers onboard global positioning system (GPS) collars worn by wolves (n = 11) and coyotes (n = 13). We analyzed wolf and coyote scat to estimate dietary breadth (B) and food niche overlap (α). We used resource utilization functions (RUFs) with canid GPS location data, white-tailed deer RUFs, ruffed grouse (*Bonasa umbellus*) and snowshoe hare (*Lepus americanus*) densities, and landscape covariates to compare population-level space use. Wolves and coyotes exhibited considerable overlap in activity (Δ = 0.86–0.92), diet (B = 3.1–4.9; α = 0.76–1.0), and space use of active and inactive RUFs across time periods. Coyotes relied less on deer as prey compared to wolves and consumed greater amounts of smaller prey items. Coyotes exhibited greater population-level variation in space use compared to wolves. Additionally, while active and inactive, coyotes exhibited greater selection of some land covers as compared to wolves. Our findings lend support for interference competition between wolves and coyotes with significant overlap across resource attributes examined. The mechanisms through which wolves and coyotes coexist appear to be driven largely by how coyotes, a generalist species, exploit narrow differences in resource availability and display greater population-level plasticity in resource use.

Introduction

The competitive exclusion principle posits that co-occurring species with high resource use overlap will compete resulting in exclusion when resources are limited (Gause 1934, Hardin 1960). Intermediate to exclusion, resource competition can reduce fitness of individuals and result in a reduction of species abundance (Fedriani et al. 2000). Interference competition occurs where two species have similar resource requirements that are concentrated or limited and one species is dominant (e.g., kleptoparasitism, territory displacement; Case and Gilpin 1974). Described as an active form of competition, interactions between individuals often result in the subordinate species realizing some cost (Schoener 1983) such as loss of space (Tannerfeldt et al. 2002), reduction in time active (Hayward et al. 2009), or loss of life (e.g., intraguild predation; Polis et al. 1989, Sunde et al. 1999).

Reducing interactions or competition may improve fitness for one or both species experiencing interference, as seen with cape foxes (*Vulpes chama*) avoiding black-backed jackals (*Canis mesomelas*) to reduce interspecific killing (Kamler et al. 2012). Limiting competition also may be possible through niche partitioning (Schoener 1974). Niche partitioning can occur through natural selection where differences in morphology arise and allow adaptation of two otherwise competing species to fill niches that are functionally different (Wilson 1975). Ecologically, altering foraging time or effort can facilitate niche partitioning and reduce interspecific contact (Toweill 1986). Several species of bats, similar in body size and prey selection, coexist using temporal segregation (Swift and Racey 1983). In addition to temporal segregation, two species occupying a similar niche may exhibit spatial or dietary differentiation, or specialization, that can reduce competition and allow coexistence (Schoener 1974). However, as prey availability varies temporally, degree of competition may also vary, changing the intensity of resource partitioning (Major and Sherburne 1987). In field studies, interference competition is often inferred spatially (e.g., arctic fox (*Alopex lagopus*) that are excluded from red fox (*Vulpes vulpes*) territories; Tannerfeldt et al. 2002) and by measuring resource use overlap (e.g., dietary overlap among bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and gray fox (*Urocyon cinereoargenteus*); Fedriani et al. 2000).

Wolves (*Canis lupus*) and coyotes are sympatric across most of their ranges in North America (Arjo and Pletscher 2004) but differ in body size (wolves 18.0–55.0 kg [Mech 1974]; coyotes 9.1–14.7 kg [Bekoff and Gese 2003]). Where wolves occur, coyotes may modify their distribution, behavior, and pack size to limit interspecific competition or wolf aggression (Fuller and Keith 1981, Thurber and Peterson 1992, Arjo and Pletscher 1999, Berger and Gese 2007) and coyote abundance may be suppressed as compared to wolf free areas (Smith et al. 2003, Levi and Wilmers 2012). However, co-occurring wolves and coyotes can exhibit high spatial overlap when comparing home ranges and core areas (Arjo and Plechster 1999, Atwood 2006, Berger and Gese 2007); yet previous studies have not provided a mechanism for coexistence where this spatial overlap occurs. Home range overlap does not equate to overlap in resource use, nor does use occur across a home range or core area simultaneously or homogenously. Consideration for activity and spatial segregation between these species at finer spatial and temporal scales than the home range may provide a mechanism for coexistence. In addition, diet may be important to consider as across much of eastern North America, white-tailed deer (*Odocoileus virginianus*) are an important prey of wolves and coyotes (Ballard et al. 1999, Arjo et al. 2002), though deer age classes selected may differ between species (Patterson et al. 1998, Arjo et al. 2002, Mech and Boitani 2003, Kautz et al. 2019). The onset of white-tailed deer parturition provides a large influx of vulnerable prey (Petroelje et al. 2014) that exhibits immobility and hiding behavior for about 5 weeks post parturition, followed by increased mobility and social behavior (Ozoga et al 1982). This temporal variability in deer fawn size and mobility provides a resource within both wolves and coyotes optimal prey size range (Carbone et al. 1999) and may reduce interference competition.

We quantified the degree of temporal, dietary, and spatial overlap of wolves and coyotes at the population level to estimate the potential for interference competition and identify the mechanism for how these sympatric canids coexist using accelerometer-enabled GPS collars, scat analysis, and resource utilization functions during May–August. We hypothesized that coyotes, as the subordinate carnivore, avoid wolves through temporal differentiation. We predicted coyotes would shift activity peaks and would exhibit reduced activity as compared to wolves. We hypothesized that wolf and coyote diets differ due to body size and optimal prey size (Carbone et al. 1999, Thurber and Peterson 1992), where coyotes select smaller prey as compared to wolves. We predicted that wolves' diet would be mostly white-tailed deer as they are considered ungulate specialists. We predicted coyotes, as generalist omnivores, would exhibit a more variable diet due to avoidance of wolves and exclusion from prey resources by wolves.

We hypothesized that wolves, as the dominant carnivore, exclude coyotes from areas with greatest probability of occurrence by white-tailed deer, and use those areas disproportionately more as compared to availability. Specifically, we predicted wolves, while active, would select for areas with greater adult white-tailed deer probabilities. We predicted that coyotes, while active, would select for areas of greater snowshoe hare and ruffed grouse densities during all time periods and greater fawn probabilities shortly after deer parturition as compared to wolves. Finally, we predicted coyote resting sites (i.e., inactive sites) would be in areas of lesser probability of wolf occurrence.

Methods

Study area

This study was conducted in portions of North America's northern hardwood/boreal ecosystem in Michigan's Upper Peninsula, USA (46.27º, -88.23º) and comprised about 1000 km^2 (Figure 1.1). Property ownership consisted of commercial forest association lands (49%), privately owned lands (33%), and state forest lands (18%). Most of the study area was forested (86%) with dominant land cover types including deciduous hardwood forests, woody wetlands, and mixed forests (Table 1.1 [2011 National Land Cover Data, Jin el al. 2013]). Coyote densities were about 10 times greater (23.8 individuals/100 km^2) than wolf densities (2.8 individuals/100 km^2) during 2013–2015 (Kautz et al. 2019). Densities or abundance indices for other predator and prey species in the study area include American black bears (*Ursus americanus*, 25.9/100 km^2), bobcats (*Lynx rufus*, 3.8/100 km^2), white-tailed deer (571/100 km^2 [Kautz et al. 2019]), and beaver (*Castor canadensis*, 0.11 colonies/km of river [J. Belant, unpublished data]). Elevations ranged from 401 to 550 m. Monthly average May–August temperatures ranged from highs of 24.5º C during July to lows of 2.0º C during May and average rainfall during May–August was 34.4 cm (National Oceanic and Atmospheric Administration 1981–2010 Climate Normals).

Capture and telemetry

We captured coyotes and wolves each spring (May–June) using No. 3 padded foothold traps (Oneida Victor, Cleveland, Ohio, USA) and modified MB-750 foothold traps (modified off-set jaws, additional swivels, and altered drag; D. Beyer, unpublished data), respectively. Additionally, we captured coyotes with relaxed locking cable restraints (Wegan et al. 2014) during February–March each year. We anesthetized coyotes and wolves with a ketamine hydrochloride (4 mg/kg and 10 mg/kg, respectfully; Ketaset®, Fort Dodge Laboratories, Inc., Fort Dodge, Iowa, USA) and xylazine hydrochloride (2 mg/kg; 2 mg/kg; X-Ject E™, Butler Schein Animal Health, Dublin, Ohio, USA) mixture (Kreeger and Arnemo 2007). We fitted coyotes and wolves with a global positioning system (GPS) collar with a very high frequency (VHF) transmitter and an on-board tri-axial accelerometer to record activity (Model GPS7000SU, Lotek Wireless, Newmarket, Ontario, Canada). We programed GPS collars to acquire and store locations every 15 minutes from 1 May to 31 August 2013–2015. Before individuals were released at the capture site, we administered yohimbine hydrochloride (0.15 mg/kg; Hospira©, Forest Lake, Illinois, USA) to reverse the effects of xylazine hydrochloride. We uploaded data weekly using ultra high frequency communication and a handheld command unit (Lotek Wireless Inc., Newmarket, Ontario, Canada) from a fixed-wing aircraft. Approval for all capturing and handling procedures was through Mississippi State University's Institutional Animal Care and Use Committee (protocol 12-012).

Time periods

We selected 3 time periods related to white-tailed deer fawn availability to wolves and coyotes. The pre-parturition period (PPP, 1 May–26 May) is before the annual birth pulse of fawns occurs and only adult deer are on the landscape. The limited mobility period (LMP, 27 May–30 June) occurs when fawns are young, immobile, and within the predicted optimal prey size for coyotes beginning at fawn parturition to 35 days post-parturition (Ozoga et al. 1982, Carbone et al. 1999, Petroelje et al. 2014). The social mobility period (SMP, 1 July–31 August) occurs when fawns exceed the predicted optimal prey size of coyotes (Carbone et al. 1999) and when fawn behavior switches from hiding to running with associated family groups (Nelson and Woolf 1987). Fawns in Michigan gain on average 0.2 kg/day during their first month weighing about 9 kg by the end of LMP (Verme and Ullrey 1984) and would reach optimal prey size for wolves during SMP. After 31 August the fall molt begins, making it difficult to distinguish adult and fawn hair in scat samples (Adorjan and Kolenosky 1969).

Estimates of prey availability

We identified white-tailed deer, ruffed grouse (*Bonasa umbellus*), and snowshoe hare (*Lepus americanus*), *a priori*, as prey that may be important in wolf and coyote diets as they appeared to be dominant available prey in the study area (D. Beyer, unpublished data) and within the optimal prey size range (Carbone et al. 1999).

Snowshoe hare

Following recommendations of Hodges and Mills (2008), we estimated snowshoe hare abundance from mid-April to early May 2013–2015, following snowmelt, by counting pellet groups within 1 m^2 plots. Within each land cover class (Jin et al 2013, Table 1.1), we randomly generated 200 plot locations separated by $\geq$50 m using ArcMap 10.3 (Environmental Systems Research Institute, Redlands, CA, USA) and haphazardly selected sites to visit and attempted to sample ≥80 plots in each dominant land cover (>5%) and aspen (12%; *Populus tremuloides* or *P. grandidentata*; Ellenwood et al. 2015), as it is preferred winter forage for snowshoe hares (Bookhout 1965) and differs from the dominant deciduous cover (i.e., sugar maple [*Acer saccharum*]). We sampled remaining land cover types, with ≥30 pellet plot sites in each, to identify if any were of importance for snowshoe hare ("open water" and "developed" were not sampled). At each site, we compared the land cover layer designation to the actual vegetation observed using the designations provided by Jin et al. (2013) to correctly assign each plot for land cover classification. Each plot was a 10-cm × 10-m rectangle and we counted all pellets greater than 50% contained by the rectangle. We used plots that were uncleared of hare pellets prior to surveying as they do not require waiting a year before estimating hare density. These estimates may be greater than when using cleared plots if previous years pellets have not degraded (Murray et al. 2002, Murray et al. 2005, Berg and Gese 2010) though uncleared plots have provided similar estimates of hare density as cleared plots (Hodges and Mills 2008) and any bias from using uncleared plots should remain constant across years as new sites were sampled each year. Following Murray et al. (2002) we related pellet density (mean pellets/m^2 [x]) to hare density (hares/19 ha [y]), where $y = \exp(1.112 + 1.047*(\ln x + 1/6))$. For comparison to other prey densities and to apply densities to the landscape scale we converted hares/ha to hares/km^2 and applied a correction factor of 1.41 to account for natural log bias produced from the transformation (Murray et al. 2002). In addition, we calculated a study area density using the weighted mean by proportion of land cover to examine trends in the hare population over time.

Ruffed grouse

We used 65 roadside male grouse drumming survey sites and 5 visits to estimate density of grouse. Surveys were conducted when wind speeds were <8 mph and there was no precipitation, as these conditions may inhibit bird activity or detection (Zimmerman and Gutierrez 2007). We established survey sites >1.6 km apart to ensure site independence and assumed grouse have a maximum detection radius of 550 m from each survey point (Hansen et al. 2011). We conducted surveys from late April to early May 2013–2015 at the peak of ruffed grouse drumming in the upper Great Lakes region (Michigan Department of Natural Resources 2012). We conducted surveys from 0.5 hour before sunrise to 5 hours after sunrise and listened for grouse drumming for 5 minutes at each site to assess presence/absence of grouse (Hansen et al. 2011). We used an N-mixture model framework (Royle 2004, Kery et al. 2005) which estimates detection probability and site abundance using function 'pcount' within package unmarked (Fiske and Chandler 2011) for program R (version 3.01, R Development Core Team 2018) to estimate drumming grouse density. We used number of drumming grouse at each site, during each of the 5 visits, as the response data modeled as a Poisson distribution. We expected the timing of survey visits would influence detection of drumming grouse, given the seasonality of this behavior, and included survey date as a covariate of detection. We included proportion of aspen landcover (Ellenwood et al. 2015) within each site detection radius as a covariate of abundance. We used Akaike Information Criterion for small sample sizes (AICc) to rank models for best fit (Burnham and Anderson 2002) to estimate grouse abundance. We considered all combinations of covariates of detection and abundance, a total of 4 models each year, and we considered the model with the least AICc score as the best supported model for each year. We assumed the grouse population had a 1:1 sex ratio (Gullion 1981) and estimated the population density by doubling the estimated drumming (i.e., male) grouse abundance from the best supported N-mixture model and converted this number to a density by dividing it by the total area surveyed.

White-tailed deer

We estimated probability of occurrence by adult female and fawn deer across the landscape using a resource utilization function (RUF; Marzluff et al. 2004) to regress the occurrence distribution (OD; Figure 1.1) of individual deer on landscape covariates thought to influence their use. To estimate ODs, we used VHF relocation data from radio-collared adult female white-tailed deer (n = 113) captured using Clover traps (Clover 1956) and neonate fawn deer (n = 100) captured using vaginal implant transmitter guided searches or opportunistically during 2013–2015 (Kautz et al. 2019, Kautz et al. 2020). We used Brownian bridge movement models (BBMM) in package 'BBMM' (Nielson et al. 2013) for program R (version 3.01, R Development Core Team 2018) to produce a 99% OD for each deer/time period (i.e., PPP, LMP, SMP) combination. We included adult female deer with ≥20 VHF locations or fawn deer with ≥5 VHF locations, as neonates were subject to greater predation during the first 16 weeks after birth (Kautz et al. 2019) and including only fawns with ≥20 locations would bias the average RUF toward individuals that survived. A total of 87, 89, and 94 adult female deer during PPP, LMP, and SMP, respectively and 39 and 37 fawns during LMP, and SMP, respectively had adequate locations for analyses. The BBMM includes a term for a location error vector for estimated error of each VHF triangulation (estimated from average error triangulating known collar locations [LOAS, Ecological Software Solutions LLC., Hegymagas, Hungary]). The BBMM also allowed specification of the maximum time step (max.lag) for motion variance to be estimated between two locations which we set to 48 hours to meet the assumption that the movement between locations were related and not random. We regressed magnitude of the OD on 6 landscape variables (distance to water, distance to roads, distance to edge, patch size, and land cover) thought to influence deer resource selection (Duquette et al. 2014). Because the scale of deer movement data was coarser and lacked activity data as compared to wolf and coyote data, we did not include carnivore presence to predict occurrence. We used the 2011 National Land Cover Database (NLCD, Jin et al. 2013) as a categorical assignment of land cover across the 30 × 30 m grid. We combined land covers into the following 7 major classes: deciduous forest, mixed forest, evergreen forest, woody wetlands/emergent herbaceous wetlands, open water, grassland/shrub, and developed which included categories containing less than 1% of land cover (e.g., urban, agriculture, and barren; Table 1.1). We calculated landscape metrics for each cell including patch size and distance to edge (NLCD, Jin et al. 2013), distance to road (Michigan Geographic Framework, all roads v17a), and distance to water (Michigan Geographic Framework, hydrography lines v17a) in ArcMap 10.3 (Environmental Systems Research Institute, Redmond, California, USA) and Geospatial Modeling Environment (Beyer 2012). Before fitting models, we used Pearson's correlation to determine any covariates that were related (i.e., $|r| > 0.7$) and selected and retained the one that was more ecologically relevant for further analyses.

We estimated the population-level RUF for adult female and fawn deer from the individual RUF averaged coefficients for each age class during each time period using the equation

$$\hat{\hat{\beta}}_i = \frac{1}{n}\sum_{j=1}^{n}\hat{\beta}_{ij} \tag{1.1}$$

where n is the number of individuals and $\hat{\beta}_{ij}$ is the estimate of coefficient i for individual j. We estimated the variance of the population-level coefficients using the equation

$$Var\left(\hat{\hat{\beta}}_i\right) = \frac{1}{n-1}\sum_{j=1}^{n}(\hat{\beta}_{ij} - \hat{\hat{\beta}}_i)^2 \tag{1.2}$$

to include intra-individual and inter-individual variation (Marzluff et al. 2004, Millspaugh et al. 2006). We then predicted probability of occurrence by adult female and fawn deer across the landscape for each period by using the scaled coefficients from each population-level RUF and spatially derived a relative value for resource suitability for all model covariates layered over a 30 × 30 m cell grid which corresponds to the resolution of NLCD (Jin et al. 2013), the coarsest resource attribute.

We used k-fold cross-validation as a measure of model fit for the RUFs of adult female and fawn deer. Following Long et al. (2014), for each fold of the cross-validation we withheld one individual to compare model fit against, then used the remaining individuals to build a population-level RUF. We then used that RUF to predict the probability of occurrence for each 30 x 30 m cell in the study area grid. We spatially matched and extracted the OD values from the withheld individual and the predicted values from the RUF where they overlapped on the grid. We then sorted the paired OD and RUF values based on the RUF predicted values and binned them into 8 groups with equal numbers of cells in each bin. For each bin, we regressed the sum of the OD values against the sum of the RUF predicted values then calculated the coefficient of determination (R^2) and slope of the relationship. To estimate overall model fit we averaged R^2 and slope values across all folds (individuals) for adult female deer and fawn deer separately, where a high R^2 and a positive slope indicate good predictive power or model fit (Johnson et al. 2000, Anderson et al. 2005, Long et al. 2009).

Activity pattern

To assess daily activity patterns of coyotes and wolves and examine how each species partitions times of activity we used accelerometers on board GPS collars. Accelerometers measured gravitational acceleration 4 times per second along 2 axes (x and y). We programed GPS collars to store activity data on the collar averaged across 5-minute intervals. We considered a collared individual active when summed accelerometer readings were ≥ 30.7 (Petroelje et al. 2020) and subset the 5-minute intervals to observations of active intervals only. We used a one-tailed t-test with unequal variances to assess if coyotes, the subordinate species, were active less of the time as compared to wolves, the dominate competitor (Hayward and Slotow 2009). We estimated the measure of mean daily (24-hr) overlap of activity between coyotes and wolves using the active 5-minute intervals and the R package Overlap (Ridout and Linkie 2009) for each time period (i.e., PPP, LMP, and SMP). We used the coefficient of overlapping (Δ) where 0 is no overlap and 1 is complete overlap as a measure of activity pattern overlap (Ridout and Linkie 2009, Linkie and Ridout 2011). We used the nonparametric estimator that works with circular data recommended for small sample sizes (Ridout and Linkie 2009). This coefficient uses minimum probability density functions, from the kernel density estimation, for both species at each time interval to estimate the area under the curve as a measure of overlap (Linkie and Ridout 2011).

Scat collection and diet analysis

We collected wolf and coyote scats opportunistically throughout the study area while driving along roads or performing other field activities during 1 May–31 August 2013–2015. We collected scats in plastic bags and labeled each with sample location, date collected, associated tracks present, and species. We used scat size and shape, and associated tracks to identify species of the deposited scat (Thompson 1952, Mech 1970, Green and Flinders 1981, Prugh and Ritland 2005). We excluded scats without associated tracks that were > 28.1 mm and < 29.0 mm as these were above the 3rd quantile for coyotes and below the 1st quantile for wolves and could therefore not be identified to species (Petroelje et al. 2019). We washed collected scats in double layered nylons and oven dried contents so all that remained was feathers, hair, bone fragments, seeds, and vegetation (Johnson and Hansen 1979). Once contents were dried, we identified prey items including white-tailed deer (adult or fawn; Adorjan and Kolenosky 1969), snowshoe hare, ruffed grouse, Rodentia, seeds, and other (which included other avian species, unknown species, vegetation, and invertebrates) based on hair coloration, scale pattern, and length (Mathiak 1938, Adorjan and Kolensky 1969, Spiers 1973, Wallis 1993). We recorded the proportion of each prey item in each scat using a 1 x 1 cm grid to estimate the percent volume of each item.

We assessed if coyote's diet contained greater volumes of deer fawns, grouse, and snowshoe hare compared to wolves using an analysis of variance. We calculated dietary breadth (B) and food niche overlap (α) for each species during each time period using Pianka's (1973) formulas:

$$B = 1/\left(\sum p_i^2\right) \tag{1.3}$$

$$\alpha = \sum (p_i q_i) \Big/ \sqrt{\sum p_i^2 \sum q_i^2} \tag{1.4}$$

where p_i is the proportion of food item i in the diet of predator p, and q_i is the proportion of food item i in the diet of predator q.

Space-use

Population-level resource selection assumes that individuals select habitats similarly (Thomas and Taylor 2006). However, Alldredge et al. (1998) suggested this assumption is rarely met and individual variation is important for population-level inference, especially if exclusion is occurring. Thus, we analyzed coyote and wolf location data with a Design III approach using individuals as replicates, accounting for individual-level variation, to assess population-level use (Thomas and Taylor 2006). We used RUFs to relate the OD of individual wolves and coyotes to covariates thought to influence resource use.

To generate each OD, we used 15-minute GPS relocations ($\bar{x}$ = 1,595.7/OD) from collared wolves and coyotes collected during 1 May–31 August 2013–2015. To identify the activity state of an individual at each GPS location we used activity data collected from accelerometers and assigned each 15-minute location as active if the nearest 5-minute activity interval was ≥ 30.7 (gravitational acceleration, unit-less), otherwise we considered the location as inactive (Petroelje et al. 2020). For each collared individual, we used a dynamic Brownian bridge movement model (dBBMM; Kranstauber et al. 2017) within the package 'move' for program R (version 3.01, R Development Core Team 2018) to generate a 99% OD across a 30 × 30 m grid for all inactive (i.e., sleeping, resting) and all active (i.e., traveling, foraging) GPS relocations for each time period (i.e., PPP, LMP, and SMP). The dBBMM offers improvements over traditional utilization distribution estimators (e.g., fixed-kernel estimators) as it accounts for temporal autocorrelation by using the time and distance between locations and assumes movement between locations is random, modeled as a conditional random walk, which is likely given 15-minute GPS relocations. The dBBMM model estimates Brownian motion variance (σ_m^2) which varies along the GPS path via a sliding window to account for changes in movement behavior (Kranstauber et al. 2017). We selected a window of 23 locations (5.75 hours) and a margin of 5 locations to estimate σ_m^2 as wolves and coyotes displayed similar crepuscular activity patterns during each time period (Figure 1.2). We generated ODs for each individual wolf or coyote during each time period (i.e., PPP, LMP, SMP) and each activity level (active or inactive), resulting in 6 ODs per individual (Figure 1.3), and considered the 99% OD as the outer boundary of area available to each wolf and coyote (Thomas et al. 2006).

We used linear models (Marzluff et al. 2004) to regress the occurrence probability within each grid cell (i.e., height of the OD) on 9 prey or landscape covariates to estimate the relative importance of each covariate for wolves and coyotes as a measure of space use to compare overlap. We included probability of occurrence for both adult female and fawn white-tailed deer as well as ruffed grouse and snowshoe hare densities within each grid cell as prey that may influence coyote and wolf use. Additionally, we included the same 30 × 30 m grid of landscape covariates calculated for white-tailed deer RUFs which included land cover, patch size, distances to nearest road, water, and land cover edge. For each coyote RUF, we also included the population-level predicted probability of occurrence for wolves in each grid cell as a measure of avoidance. Before fitting models we used Person's correlation to determine any covariates that were related (i.e., $|r| > 0.7$) and selected and retained the one that was more ecologically relevant for further analyses.

To estimate a population-level RUF, we calculated standardized mean parameter estimates for each species during each activity level and time period using equation (1) and then calculated the conservative population-level variance using equation (2) assuming the individuals were selected randomly from the population (Marzluff et al. 2004, Millspaugh et al. 2006). We set $\alpha = 0.05$ for all population-level RUFs for inference. This is conservative due to small sample size of fewer than 30 individual coyotes and wolves. To assess model fit we used k-fold cross validation of wolf and coyote RUFs following procedures used for white-tailed deer.

Results

Capture and telemetry

We captured and collared 19 coyotes (15 females, 4 males) and 12 wolves (5 females, 7 males). Coyotes and wolves wore collars for 102.9 (SD = 46.7) and 93.2 (SD = 24.1) days on average, respectively. Collars collected a total of 129,256 ($\bar{x} = 8{,}617.1$, SD = 2762.0) and 107,328 ($\bar{x} = 8{,}944.0$, SD = 2317.0) locations for coyotes and wolves, respectively. We recovered location and activity data from 13 coyotes (11 females, 2 males) and 11 wolves (5 females, 6 males) for analyses; no coyotes or wolves used in analyses were collared for > 1 year. Social status of individual wolves was unknown as the forested environment limited our inferences, though all individuals used in analyses were resident adults. Collared wolves represented each of the 4 packs within the study area. Two wolves collared from each of two packs were analyzed separately.

Estimates of prey availability

Snowshoe hare

We sampled 316, 413, and 448 pellet plots during 2013, 2014, and 2015, respectively. Mean pellets detected per plot ranged from 0.0 (CI = 0.0–0.7) in deciduous (excluding aspen) land covers to 5.6 (CI = 0.0–45.9) in woody wetlands (Table 1.2). Hare density was greatest during 2013 in aspen land cover (33.1/km^2) and least during 2015 in deciduous hardwoods (3.5/km^2). Hare density generally declined across years (2013–2015) when examined by all land cover types.

Ruffed grouse

We detected an average of 0.7, 0.4, and 0.6 drumming grouse at each site during 2013–2015, respectively. Timing of survey visit (i.e., date) influenced detection of drumming grouse during all 3 survey years (Table 1.3). N-mixture models estimated detection (15.8%–33.4%) and abundance (137–178) as relatively stable across years with confidence intervals overlapping each year (Table 1.3). Drumming male grouse abundance estimates were doubled to estimate a population density of 5.8, 4.9, and 4.4 grouse/km^2 during 2013–2015, respectively. In 2013 the top model included a positive relationship with proportion of aspen. No covariates of abundance were important to predicting grouse density in 2014 and 2015.

White-tailed deer

We used the unstandardized population-level RUF for each deer age class and time period to develop a spatial reference for predicted deer occurrence across the 30 × 30 m grid. Adult female deer occurrence during PPP was negatively related to distance to road ($\beta = -0.701$, CI = -1.357– -0.045, $P < 0.036$; Figure 1.4). During LMP adult female deer occurrence was negatively related with distance to roads (β = -0.746, CI = -1.012– -0.481, $P < 0.001$) and distance to edge (β = -0.062, CI = -0.121– -0.004, $P = 0.037$). During LMP fawn deer occurrence was also negatively related to distance to roads (β = -1.204, CI = -1.753– -0.654, $P < 0.001$). During SMP adult female and fawn deer occurrence was negatively related with distance to roads (β = -0.487, CI = -0.743– -0.230, $P < 0.001$ and β = -0.763, CI = -1.249– -0.277, $P = 0.003$, respectively). Model fit was generally good for fawns with a positive slope and $R^2 > 0.45$, but model fit for adult female deer was more variable with positive slopes during LMP and SMP and only during LMP was $R^2 > 0.45$ (Table 1.4).

Activity pattern

Mean proportion of time spent active generally increased for both species across time periods (Figure 1.5). During PPP, LMP, and SMP proportion of time spent active was 0.32 (SD = 0.09), 0.39 (SD = 0.09), and 0.49 (SD = 0.06) for coyotes and 0.22 (SD = 0.09), 0.36 (SD = 0.06), and 0.34 (SD = 0.05) for wolves, respectively. Proportion of time active between wolves and coyotes did not differ during PPP or LMP, however during SMP coyotes were more active than wolves ($P < 0.01$). Mean daily activity overlap for coyotes and wolves was greater than 0.86 across time periods (Table 1.5) though it was greatest during PPP ($\Delta = 0.92$). Two activity peaks, one near dawn and one near dusk, were detected for both canids though wolves lacked an activity peak during dawn hours in PPP and were often more active several hours following sunrise compared to coyotes (Figure 1.2).

Scat collection and diet analysis

We collected 522 and 518 scats initially classified as coyote or wolf, respectively. Diameter of scats with confirmed coyote tracks ($\bar{x} = 25.2$ mm, SD = 4.4 mm) were smaller

(Welch two sample t-test [$H_a < 0$], $P < 0.01$) than those from wolves ($\bar{x} = 33.3$ mm, SD = 6.1 mm). We determined 377 and 305 scats to be coyote or wolf, respectively, identified by tracks or scat diameter and contained associated collection date which were used in diet analyses. Coyote scats contained 3.1 times and 1.5 times greater volumes of hare ($\bar{x}$ = 5.31%, SD = 3.95%, $P < 0.01$) and rodents ($\bar{x}$ = 23.4%, SD = 3.54%, $P = 0.02$), respectively and 1.5 times lesser volumes of adult deer ($\bar{x}$ = 27.7%, SD = 4.54%, $P < 0.01$) compared to wolf scats. Volumes of grouse ($P = 0.25$) and fawns ($P = 0.41$) did not differ in wolf and coyote scats. Though food niche overlap varied among time periods (Table 1.5), it exceeded 0.85 each season and was greatest during PPP ($\alpha = 0.94$). Dietary breadth (*B*) varied for coyotes and wolves by time period (Figure 1.6) but in general coyotes (*B* = 3.44–4.90) had a wider dietary breadth than wolves (*B* = 3.09–3.91). Dietary breadth was greatest for coyotes during LMP (*B* = 4.90) the same season it was least for wolves (*B* = 3.09).

Space-use

Resource utilization functions for each species, activity level, and time period contained considerable variation among individuals, however, population-level RUFs consistently showed greater variation in selection of resource attributes by coyotes compared to wolves (Figure 1.7; 1.8). Though some individual wolves and coyotes selected for resource attributes similarly (Table 1.6), at the population-level, few resources were selected for by all individuals. Greater variability in resource-use was observed in coyotes during all time periods and activity levels except during PPP while inactive where selection for some resource attributes had greater variability for wolves. Model fit was inconsistent for wolves, all but one slope was positive and

R^2 values ranged from 0.14 to 0.62. Model fit was more consistent for coyotes with all slopes positive except for one and R^2 values ranged from 0.29 to 0.53 (Table 1.4).

At the population-level, wolf occurrence was not influenced by adult female deer occurrence during any time period while active or inactive. However, active wolf occurrence was positively related to hare densities ($\beta = 0.028$, CI = 0.003–0.054, $P = 0.03$) during LMP and negatively related to grouse densities ($\beta = -0.035$, CI = -0.058– -0.012, $P = 0.01$) during PPP. During LMP, while active and inactive, wolf occurrence was negatively related to distance to edge ($\beta = -0.023$, CI = -0.039– -0.008, $P < 0.01$ and $\beta = -0.005$, CI = -0.009– -0.001, $P = 0.02$, respectively) similar to white-tailed deer RUFs. During SMP, active wolf occurrence was inversely related to distance to roads and RUFs included a greater number of wolves with a positive relationship with adult female deer occurrence.

Population-level coyote occurrence was not associated with hare or grouse densities while active or inactive. Probability of occurrence by adult female deer (which was highly correlated to occurrence of fawn deer, > 0.89) also did not influence coyote occurrence at the population-level during any time period or activity level (Figure 1.7; 1.8). Population-level coyote occurrence was not influenced by probability of wolf occurrence during any time period while active or inactive.

Discussion

Wolves and coyotes exhibited considerable overlap in all metrics of resource use examined (Table 1.4). The greatest divergence was identified within diel activity patterns, then diet, followed by spatial partitioning during periods of activity and inactivity. Given the considerable overlap in all resource metrics, coyotes may experience interference competition by wolves, however, the combination of greater plasticity in activity, diet, and space use by coyotes likely allowed coexistence with wolves in this system.

Our prediction that coyotes may avoid wolves by altering timing of their active periods and decrease activity within those periods was not supported across time periods as activity overlap was high and coyotes were not less active than wolves (Figure 1.5). Wolf and coyote activity was predominantly crepuscular, with substantial overlap during all time periods as found previously (Arjo and Pletscher 1999), however, wolves lacked a dawn activity peak during PPP when coyotes did not. The proportion of time spent active for both species generally increased across time periods, but during SMP coyotes were more active than wolves. Temporal partitioning can be used to reduce aggression when interference competition exists (Litvaitis 1992), though, other canids exhibiting interference competition also lacked temporal partitioning (e.g., coyotes and kit fox [*Vulpes macrotis*; Kozlowski et al. 2008], coyotes and swift fox [*Vulpes velox*; Kitchen et al 1999]). Predators are often thought to follow activity patterns of their prey (Curio 1976) and though both canids were most active during crepuscular periods coyotes may not need to avoid wolves through temporal partitioning if spatial partitioning is sufficient to limit interference competition. It also is possible that temporal partitioning does not occur during summer with reduced wolf space use due to denning and pup rearing (Arjo and Pletscher 1999). We only examined activity during summer (i.e., May–August) and greater overlap between wolves and coyotes may occur during winter months when prey is more limited (Arjo et al. 2002) and may result in temporal partitioning to reduce interference competition not identified here.

Though wolves and coyotes differ in body size, and thus predicted optimal prey size (Carbone et al. 1999), dietary overlap was high during all periods (Figure 1.6). However, coyotes consumed greater volumes of smaller prey items than wolves. These patterns are similar to what was observed in Northwestern Montana, USA (Arjo et al. 2002) and Ontario, Canada (Benson et al. 2017) where wolf diets consistently included larger prey items as compared to coyotes. During LMP when wolves had the narrowest dietary breadth ($B = 3.0$) coyotes exhibited the greatest dietary breadth ($B = 4.9$), apparently a result of coyotes selecting for a greater diversity of prey items not selected for by wolves. Further, wolves consistently had greater amounts of deer in their diet compared to coyotes which is expected for an obligate carnivore and ungulate specialist (Paquet and Carbyn 2003), though deer (adult and fawns) still represented the greatest proportion of any prey for coyotes across time periods. We predicted that coyotes would select for smaller prey items based on their predicted optimal prey size (Carbone et al. 1999), and rodents and hare were found in greater volumes in coyote scat as compared to wolves. However, deer fawns and grouse found in diets of coyotes and wolves did not differ by volume in scats. Though rodents consistently represented a greater proportion of the coyote diet compared to wolves, greater differentiation would likely have been observed if prey remains of Rodentia in scat were identified to genus as beaver can be an important food resource for wolves (Mech and Peterson 2003) and coyotes are reported to consume a variety of small mammals (Bekoff 1977).

We found limited evidence for spatial segregation between wolves and coyotes (Figure 1.7; 1.8). Similarly, Berger and Gese (2007) found no evidence of spatial segregation between wolves and coyotes and Arjo and Pletscher (2004) found similar habitats were selected for by wolves and coyotes. During LMP coyotes exhibited the widest dietary breadth and wolves the narrowest dietary breadth, suggesting that though spatial segregation was not occurring, selection for differing prey may mediate the importance of spatial segregation seasonally. In addition, the population-level RUFs showed greater variation in selection by coyotes as compared to wolves when active and inactive. The greater variation observed in coyotes was likely due to more generalist behavior and their subordinate responses to wolves as seen in other populations (Arjo et al. 2002, Arjo and Pletscher 2004). Resource utilization functions for individual coyotes demonstrated selection for divergent resources suggesting coyotes can employ multiple strategies to coexist with wolves at fine spatial scales (Table 1.6). This is important to consider when characterizing population-level resource selection as individual variation may be greater (Marzluff et al. 2004), and potentially important, especially in the context of interference competition. In addition to individual variation, in complex landscapes selection of single resource attributes may not provide good estimates of species presence (as indicated by many of the individual models with multiple resource attributes influencing occurrence). Although coyotes and wolves did not select for similar attributes at the population-level, individual RUFs of each species included the same significant resource attributes (Table 1.6). Given our small sample size we did not include interaction terms for resource attributes to reduce over parameterization, though further investigation of landscape complexity and resource interactions may improve our understanding of coyote avoidance of wolves especially with respect to multiple prey species interactions. However, even at the population-level examining use of resource attributes with separate RUFs for active and inactive behaviors demonstrates the complexity of resource partitioning for a coyote population coexisting with wolves and how use may differ among activities (i.e., foraging, loafing). High individual variation in resource use among coyotes as manifested at the population-level likely facilitates coexistence between coyotes and wolves.

Our prediction that active wolf occurrence would be positively related to adult female deer occurrence was not supported. However, during LMP adult female and fawn deer and wolf active and inactive occurrence was negatively related to distance to edge at the population-level. In addition, adult female and fawn deer and active wolf occurrence during SMP was inversely related to distance to roads. Fawn white-tailed deer use has also been found to be greater near roads in other areas of Michigan's Upper Peninsula, USA (Duquette et al. 2014) and has been suggested as a refuge by decreasing probability of encountering wolves (Theuerkauf and Rouys 2008, Gurarie et al. 2011, Muhly et al. 2011). However, wolves sometimes use roads and trails for travel (Thurber et al. 1994, Whittington et al. 2005) and may hunt along these features as seen in Banff and Jasper National Parks, Canada where wolves encounter rates with caribou (*Rangifer tarandus*) increased near anthropogenic linear features (Whittington et al. 2011).

We predicted active coyotes would select areas of greater probability of occurrence for fawns, snowshoe hares, and ruffed grouse. Though fawns were a large proportion of the diet of coyotes during LMP (Figure 1.6), we did not see increasing coyote occurrence with greater deer probability (Figures 1.7; 1.8). Coyotes can respond functionally with respect to fawn consumption (Petroelje et al. 2014) and may not shift their space use to select for areas of high fawn use (Svoboda et al. 2019). Coyote occurrence was not positively related to hare density (Figure 1.7; 1.8), and though hare represented a smaller proportion of the coyote diet, the lack of a spatial response suggests coyotes may have also responded functionally as hare densities declined significantly over the study period (Table 1.2). Coyote occurrence was not influenced by grouse density though we would not expect a large spatial response as grouse represented a small proportion of the diet of coyotes across time periods (Figure 1.6).

We predicted inactive coyote occurrence would be inversely related to wolf occurrence to avoid encounters during vulnerable activities such as loafing or sleeping, but at the population-level RUF this prediction was not supported (Figure 1.7). Coyote avoidance of areas with greater wolf use has been observed in Michigan's Upper Peninsula, USA (Svoboda et al. 2019), though these areas of wolf use were reduced and intensity of use greater due to smaller home ranges resulting from scavenging on livestock carcass dumps which were not present in our study area (Petroelje et al. 2019). This variation in spatial response to wolves regionally may be explained by risk of aggressive interactions. Merkle et al. (2009) found that 79% of wolf-coyote interactions occurred at wolf-killed carcasses and 7% of those interactions resulted in a coyote mortality; thus avoidance of wolves may be less important where scavenging wolf kills is less common.

Predation on coyotes by wolves is often used to confirm interference competition (Thurber and Peterson 1992, Arjo and Pletscher 1999, Berger and Gese 2007, Merkle et al. 2009) and can account for up to 50% of mortality for transient coyotes (Berger and Gese 2007). Interference competition between wolves and coyotes occurs in the greater Yellowstone ecosystem where coyote densities in areas with wolves (coyotes, 0.19–0.48/km^2; wolves, 0.01–0.06/km^2) are reduced or limited compared to coyote densities in wolf-free areas (0.35–0.73/km^2; Berger and Gese 2007). In our study area, wolf (0.03/km^2) and coyote (0.19–0.24/km^2) populations occur at similar densities to the greater Yellowstone ecosystem, and wolf densities appear to have been stable since 2010 (O'Neil 2017). Individual coyotes were only collared for a single summer and fall and we did not record any wolf predation of collared coyotes; the only documented causes of mortality were human caused and only one uncollared coyote was found killed by wolves at a deer predation site during the study (J. Belant, unpublished data). However, aggressive interactions of wolves and coyotes likely decrease over time when wolves recolonize (Merkle et al. 2009), and wolves have been reestablished at moderate densities in the western Upper Peninsula of Michigan since the late 1990's (Beyer et al. 2009). Additionally, our study area was mostly forested, in contrast to more open habitats of the western United States, which is likely to influence visible distance, scent dispersion, and spatial overlap between wolves and coyotes. Greater habitat complexity can result in lesser competition by reducing niche overlap (Levins 1979) and reductions in scent dispersion in complex habitats increases search times for detection dogs (Leigh and Dominick 2015) and likely reflect conditions experienced by wolves and coyotes.

Alternatively, Crimmins and Van Deelen (2019) suggest that in areas where white-tailed deer are a main prey source, as in this study, coyotes are less likely to scavenge wolf kills as they are capable of killing adult deer, potentially reducing conflict in systems without large bodied ungulate resources. They found no evidence that increasing wolf populations were limiting coyote abundance in Wisconsin, USA which shares many similarities with our study area in Michigan’s Upper Peninsula, USA, though lesser wolf densities may also be important in facilitating coexistence in that region. Though deer were the greatest shared prey for wolves and coyotes in this study, based on the generalist nature of deer as supported by the adult female and fawn RUFs, it seems unlikely that deer present a concentrated prey source during the study period. Further, during this time fawns are of size to be consumed in a single meal or easily transported which reduces likelihood of scavenging and adult deer are difficult to capture.

Interference competition suggests that dominant species can suppress or exclude subordinate competitors where resource use overlap is high (Case and Gilpin 1974). Diet, space-use, and activity of coyotes overlapped substantially with wolves, and thus coyotes may experience interference competition from dominant wolves. However, exclusion of coyotes by wolves appeared to be mediated through greater generalist behavior by coyote’s selection of smaller prey, greater variation in prey selection and spatial partitioning when active and inactive, and greater time spent active during some time periods. This fine scale resource partitioning may be the mechanism for coexistence in other areas where coyote abundance is not suppressed by wolves. We suggest that though coyotes may experience interference competition by wolves, a stable population of coyotes, and the ability to coexist in a heavily forested environment occurred through ecological plasticity of coyotes' diet, space use, and activity. Where interference competition occurs, the subordinate species may be able to avoid exclusion through greater generalist behavior and facilitate coexistence. Thus, communities may support greater densities or numbers of species of competitors than expected if flexibility in resource use is sufficient to allow coexistence.

Table 1.1 Land cover designations modified from the national land cover data base with percent land cover within study area.

Land cover class	Definition of designation	Cover (%)
Deciduous forest	Areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. More than 75% of the tree species shed foliage simultaneously in response to seasonal change. Aspen (*Populus tremuloides* or *P. grandidentata*) represents dominant cover for 12% of deciduous forests within the study area (Ellenwood et al. 2015).	43
Woody or emergent herbaceous wetland	Areas where forest or shrub land vegetation accounts for greater than 20% of vegetative cover and the soil or substrate is periodically saturated with or covered with water. Areas where perennial herbaceous vegetation accounts for greater than 80% of vegetative cover and the soil or substrate is periodically saturated with or covered with water.	29
Mixed forest	Areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. Neither deciduous nor evergreen species are greater than 75% of cover.	10
Evergreen forest	Areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. More than 75% of the tree species maintain their leaves all year. Canopy is never without green foliage.	6
Grassland/herbaceous/ shrub/scrub	Areas dominated by grammanoid or herbaceous vegetation, generally greater than 80% of total vegetation. Not subject to intensive management such as tilling but can be utilized for grazing. Areas dominated by shrubs; less than 5 meters tall with shrub canopy typically greater than 20% of total vegetation. Includes true shrubs, young trees in an early successional stage or trees stunted from environmental conditions.	5
Open water	Areas of open water, generally with less than 25% cover or vegetation or soil.	4
Developed	All other areas modified by agriculture or developed land use practices such as farmed row crops, pastures, roads, and structures.	3

Extracted from Jin et al. (2013), Upper Peninsula of Michigan, USA, 2011.

Table 1.2 Mean pellet counts for snowshoe hare pellet plots by dominant land cover or species (i.e., aspen; *Populus tremuloides* or *P. grandidentata*) classification

Year	Land cover	n	$\bar{x}$	2.5% CI	97.5% CI	Density by land cover	Study area density[b]
2013	Aspen	34	4.0	0.0	18.7	33.1	15.4
	Deciduous[a]	52	0.2	0.0	0.7	3.9	
	Evergreen	80	4.0	0.0	16.4	20.2	
	Mixed	81	5.1	0.0	30.0	24.2	
	Woody wetland	69	3.7	0.0	19.3	22.9	
2014	Aspen	80	2.7	0.0	12.8	9.8	9.5
	Deciduous[a]	87	0.3	0.0	0.0	3.8	
	Evergreen	86	3.0	0.0	18.3	12.6	
	Mixed	81	2.3	0.0	19.0	10.3	
	Woody wetland	79	5.6	0.0	45.9	18.6	
2015	Aspen	90	0.6	0.0	6.8	5.6	6.5
	Deciduous[a]	88	0.0	0.0	0.0	3.5	
	Evergreen	83	2.3	0.0	15.0	10.5	
	Mixed	110	2.1	0.0	25.9	7.9	
	Woody wetland	77	2.6	0.0	21.2	11.5	

[a] Excluding aspen

[b] Weighted mean by proportion of each landcover within the study area

Included are the means ($\bar{x}$) and 95% confidence intervals (CI) with number of sites (n) and estimated density (hare/km^2) by landcover and overall study area for each year, Upper Peninsula of Michigan, USA, 2013–2015.

Table 1.3 Top N-mixture model for ruffed grouse drumming surveys each year as determined by AICc selection including estimates of detection and abundance

Year	Model[a]	Detection estimate (%)	Abundance estimate[b]	95% CI
2013	~date ~asp	24.5	178	93–346
2014	~date ~1	15.8	151	79–1246
2015	~date ~1	33.4	137	92–239

Also shown are 95% confidence intervals (CI) for estimates of abundance, Upper Peninsula of Michigan, USA, 2013–2015

Table 1.4 K-fold cross-validation results for resource utilization functions of wolves, coyotes, and adult female and fawn white-tailed deer

Species	Activity	Period	Slope	R^2	Positive slope	Negative slope	Significant positive	Significant negative
Wolves	Active	PPP	-2.02E-03	0.42	2	3	1	1
		LMP	9.17E-03	0.62	10	1	8	0
		SMP	1.16E-02	0.39	8	3	4	0
	Inactive	PPP	4.93E-03	0.14	4	2	0	0
		LMP	8.86E-03	0.53	11	0	7	0
		SMP	7.30E-03	0.28	9	2	1	0
Coyotes	Active	PPP	5.15E-02	0.35	5	2	3	0
		LMP	1.43E-03	0.54	7	6	5	2
		SMP	-7.41E-05	0.32	4	9	2	1
	Inactive	PPP	6.20E-02	0.25	5	2	2	0
		LMP	5.17E-04	0.38	8	5	4	1
		SMP	6.84E-04	0.29	7	6	2	1
Adult female deer	-	PPP	-3.14E-05	0.12	54	33	0	1
		LMP	4.39E-03	0.49	72	17	41	6
		SMP	1.54E-05	0.15	52	42	4	1
Fawn deer	-	LMP	4.95E-03	0.45	28	9	15	2
		SMP	3.94E-03	0.54	34	3	20	0

Validation results are shown for resource utilization functions estimated for two activity levels and 3 time periods related to white-tailed deer: pre-parturition (PPP, 1–26 May), fawn limited mobility period (LMP, 27 May–30 June), and fawn social mobility period (SMP, 1 July–31 August), Upper Peninsula of Michigan, USA, 2013–2015

Table 1.5 Overlap of wolf and coyote activity, diet, and space-use resource metrics

Resource metric		Time period			
		PPP	LMP	SMP	All time periods
Activity pattern[a]		0.92	0.86	0.86	0.88
Diet[b]		0.94	0.89	0.85	0.89
Spatial[c]	Active	1.00	1.00	1.00	1.00
	Inactive	1.00	1.00	1.00	1.00

[a] Activity overlap ($\Delta = 0$–1; Ridout and Linkie 2009)

[b] Food niche overlap ($\alpha = 0$–1; Pianka 1973)

[c] Proportion of the 14 resource coefficients from resource utilization functions where use was not divergent in the direction (+/-) of occurrence between wolves and coyotes at the population-level.

Though not directly comparable between resource metrics, all measures of overlap examined were high between wolves and coyotes across time periods related to white-tailed deer: pre-parturition period (1–26 May), fawn limited mobility period (27 May–30 June), and fawn social mobility period (1 July–31 August), Upper Peninsula of Michigan, USA, 2013–2015.

Table 1.6 Significant resource attributes from population-level resource utilization functions for wolves and coyotes

Species	Resource attribute	Active						Inactive					
		PPP		LMP		SMP		PPP		LMP		SMP	
		+	-	+	-	+	-	+	-	+	-	+	-
Coyote	Intercept	1	4	4	6	3	8	0	3	1	4	0	6
	Edge distance	0	5	2	8	4	7	1	2	2	3	1	5
	Road distance	NA	NA	NA	NA	6	5	1	2	1	4	3	3
	Water distance	3	2	4	6	2	3	NA	NA	2	1	NA	NA
	Doe occurrence	2	3	5	5	6	5	NA	NA	NA	NA	2	4
	Grouse density	2	3	6	4	4	7	2	1	2	3	4	2
	Hare density	2	3	5	5	6	5	0	3	2	3	4	2
	Patch size	NA	NA	NA	NA	5	6	NA	NA	2	3	1	5
	Wolf occurrence	3	2	6	4	6	5	1	2	2	3	2	4
Wolf	Intercept	1	3	3	4	7	4	0	0	2	2	2	3
	Edge distance	2	2	0	7	3	8	0	0	0	4	0	5
	Road distance	1	3	3	4	3	8	0	0	1	3	0	5
	Water distance	1	3	1	6	2	9	0	0	0	4	0	5
	Doe occurrence	1	3	3	4	3	8	0	0	2	2	2	3
	Grouse density	0	4	5	2	6	5	0	0	2	2	2	3
	Hare density	4	0	5	2	6	5	0	0	4	0	2	3
	Patch size	NA	NA	1	6	NA	NA	NA	NA	NA	NA	NA	NA

Number of individuals that had significant ($\alpha < 0.05$, confidence intervals do not include 0) positive (+) or negative (-) modeled relationship with each resource attribute from population-level resource utilization functions for wolves and coyotes (excluding land cover covariates). Resource utilization functions were estimated for active and inactive GPS locations during 3 time periods related to white-tailed deer: pre-parturition (PPP, 1–26 May), fawn limited mobility period (LMP, 27 May–30 June), and fawn social mobility period (SMP, 1 July–31 August), Upper Peninsula of Michigan, USA, 2013–2015

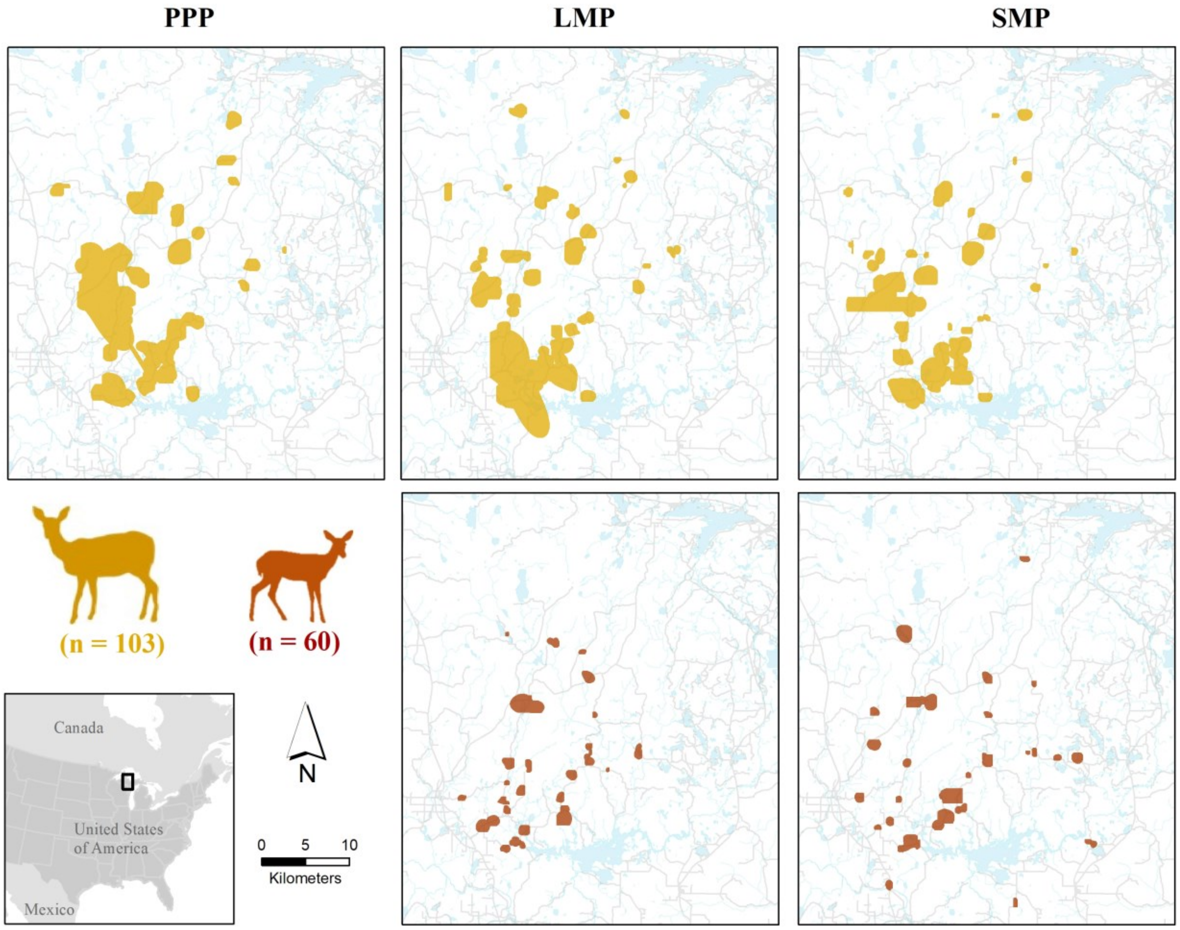

Figure 1.1 Adult female and fawn white-tailed deer occurrence distributions

Study area showing collared adult female (dark yellow) and fawn (dark red) white-tailed deer occurrence as semi-transparent 99% occurrence distributions estimated using Brownian Bridge movement models during each time period. Also shown are roads (grey lines) and water bodies (light blue lines and polygons), Upper Peninsula of Michigan, USA, 2013–2015. Inset shows study area location (black rectangle) relative to North America.

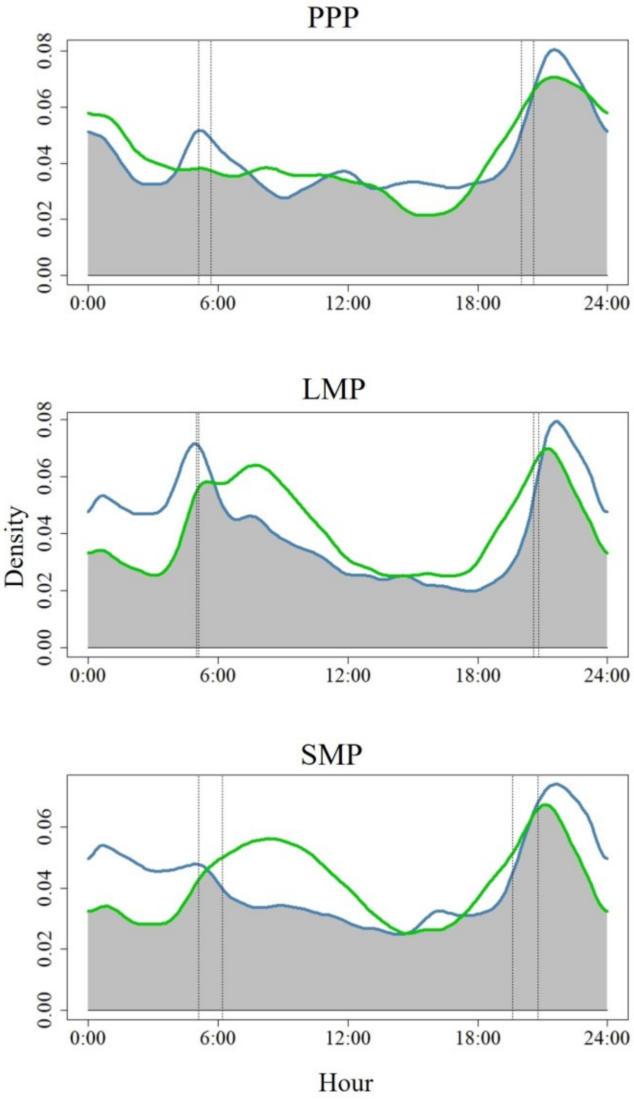

Figure 1.2 Wolf and coyote activity patterns

Activity patterns of wolves (green line) and coyotes (blue line) fitted with a kernel density plot showing earliest and latest sunrise and sunset (vertical dashed lines) and overlap (shaded grey) used to calculate activity overlap (Δ) during three time periods related to white-tailed deer: pre-parturition period (A, 1–26 May; Δ = 0.92), fawn limited mobility period (B, 27 May–30 June; Δ = 0.86), and fawn social mobility period (C, 1 July–31 August; Δ = 0.86), Upper Peninsula of Michigan, USA, 2013–2015.

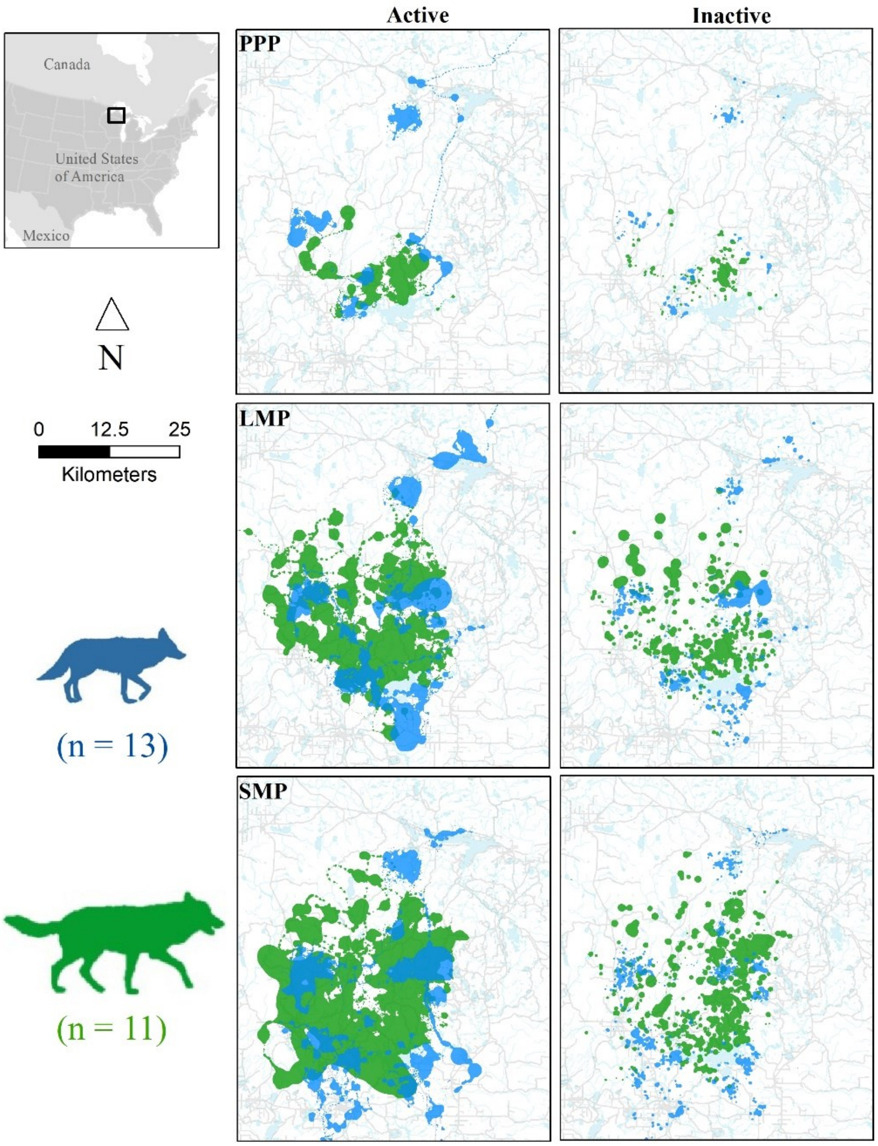

Figure 1.3 Wolf and coyote occurrence distributions

Study area showing collared wolf (green) and coyote (blue) occurrence as semi-transparent 99% occurrence distributions (OD) estimated using dynamic Brownian Bridge movement models. Dark regions of OD show where occurrence overlapped with collared wolves and coyotes. Also shown are roads (grey line) and water bodies (light blue), Upper Peninsula of Michigan, USA, 2013–2015. Inset shows study area location (black rectangle) relative to North America.

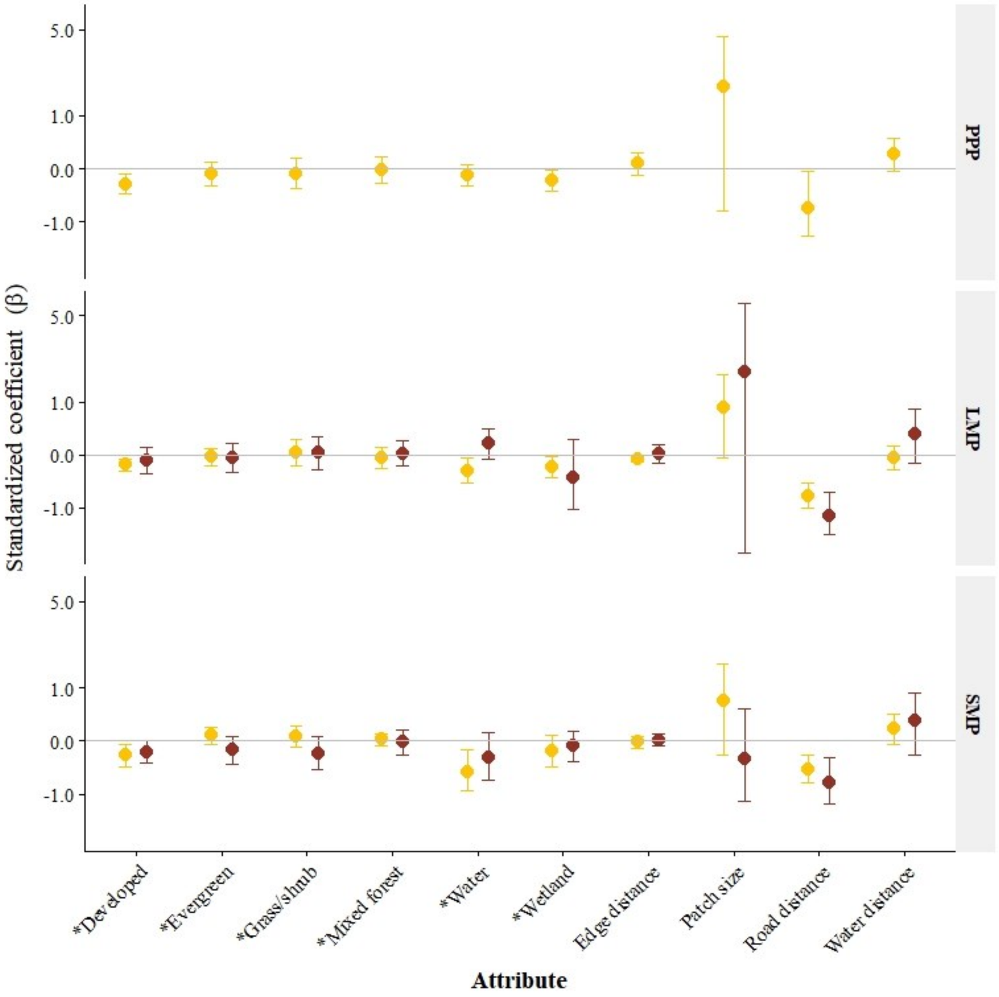

Figure 1.4 Adult female and fawn white-tailed deer population-level resource utilization functions

Population-level resource utilization functions standardized coefficients (β) with 95% confidence intervals, for adult female (yellow) and fawn (dark red) white-tailed deer. Landcover covariates (*) indicate selection relative to the reference value of deciduous landcover, the most common landcover on the landscape. The three time periods related to white-tailed deer availability include: pre-parturition period (PPP, 1–26 May), fawn limited mobility period (LMP, 27 May–30 June), and fawn social mobility period (SMP, 1 July–31 August), Upper Peninsula of Michigan, USA, 2013–2015.

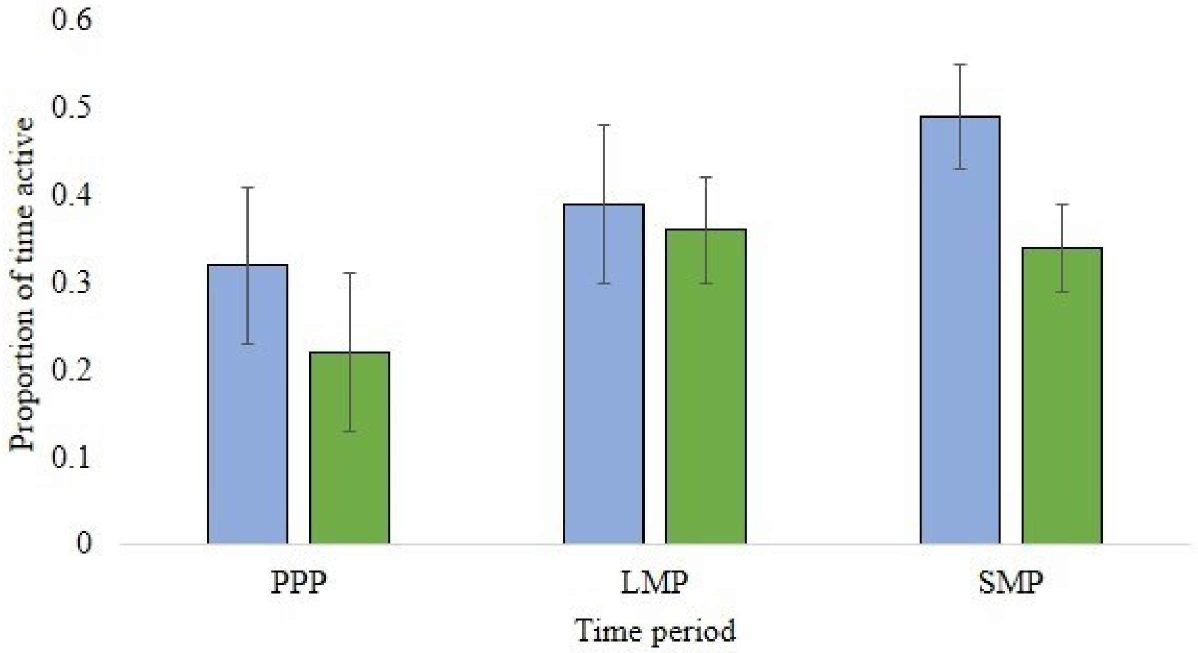

Figure 1.5 Wolf and coyote time spent active

Proportion of time spent active by wolves (green) and coyotes (blue) with standard deviation shown as error bars during 3 time periods related to white-tailed deer: pre-parturition (PPP, 1–26 May), fawn limited mobility period (LMP, 27 May–30 June), and fawn social mobility period (SMP, 1 July–31 August), Upper Peninsula of Michigan, USA, 2013–2015.

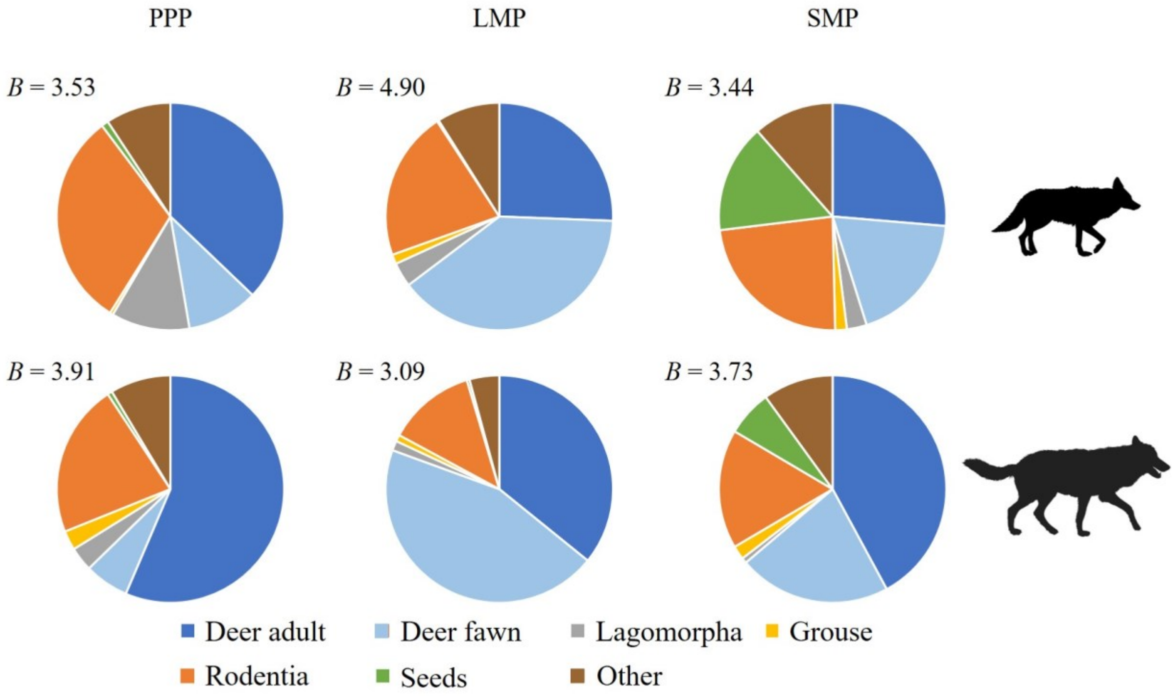

Figure 1.6 Wolf and coyote diet

Percent of prey items identified in wolf and coyote scats during three time periods related to white-tailed deer: pre-parturition (PPP, 1–26 May), fawn limited mobility period (LMP, 27 May–30 June), and fawn social mobility period (SMP, 1 July–31 August). Dietary breadth is shown for each time period and species (*B*; Pianka 1973), Upper Peninsula of Michigan, USA, 2013–2015.

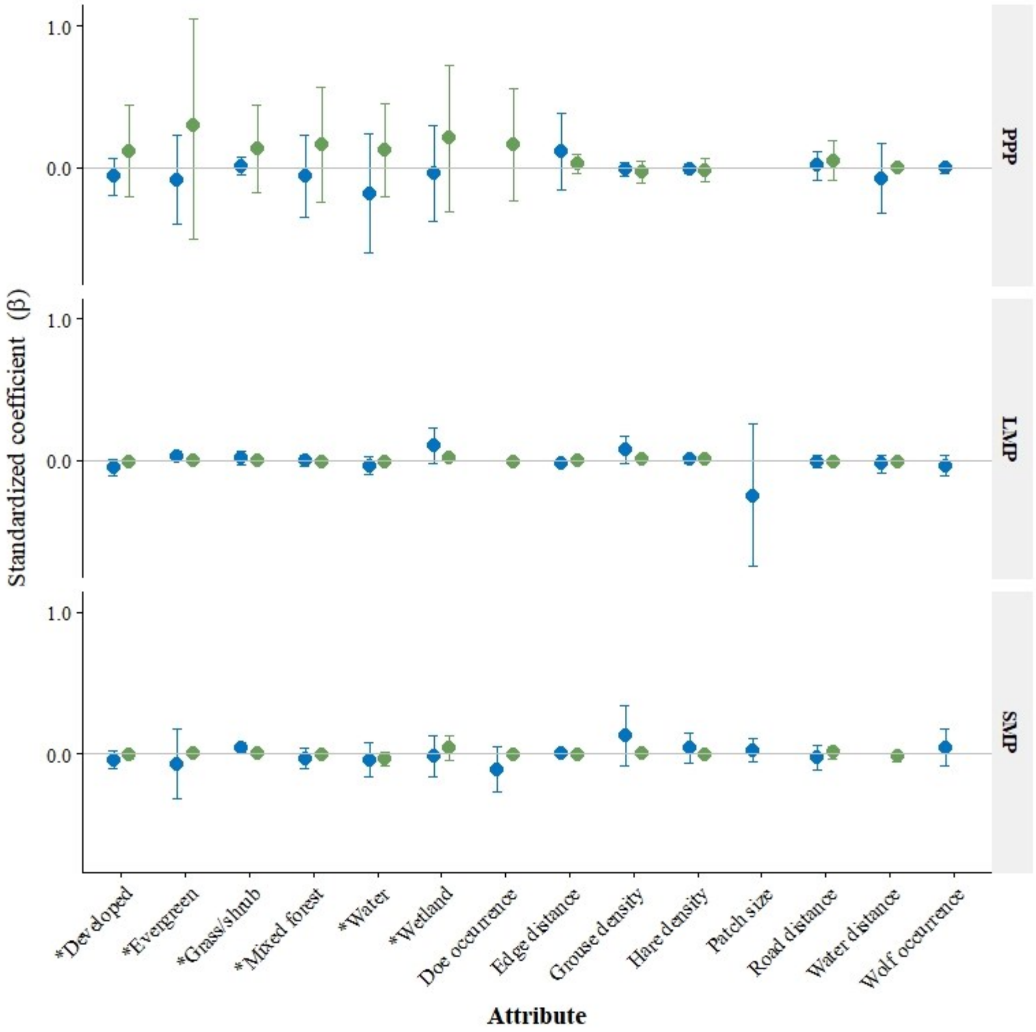

Figure 1.7 Inactive wolf and coyote population-level resource utilization functions

Population-level resource utilization functions standardized coefficients (β) with 95% confidence intervals, for inactive wolves (green) and coyotes (blue). Landcover covariates (*) indicate selection relative to the reference value of deciduous landcover, the most common landcover on the landscape. The three time periods related to white-tailed deer availability include: pre-parturition (PPP, 1–26 May), fawn limited mobility period (LMP, 27 May–30 June), and fawn social mobility period (SMP, 1 July–31 August), Upper Peninsula of Michigan, USA, 2013–2015.

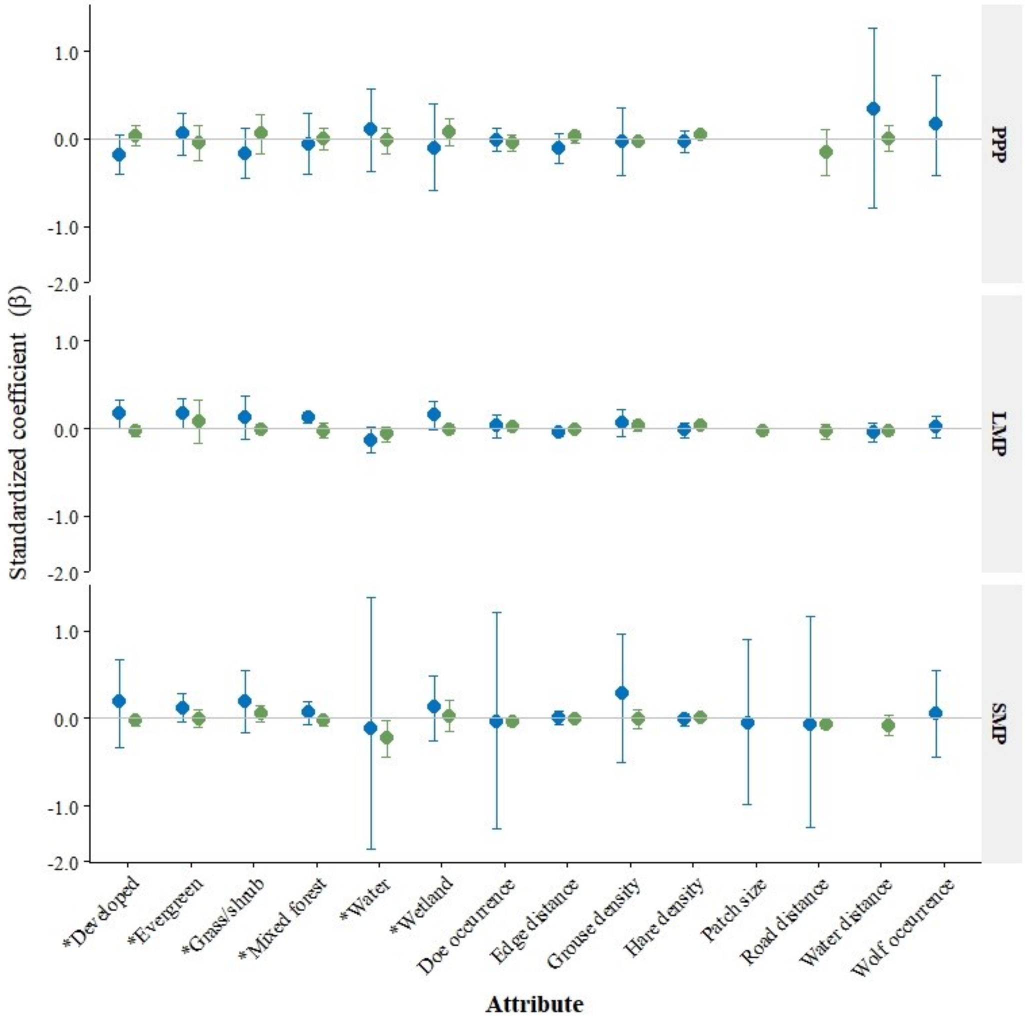

Figure 1.8 Active wolf and coyote population-level resource utilization functions

Population-level resource utilization functions standardized coefficients (β) with 95% confidence intervals, for active wolves (green) and coyotes (blue). Landcover covariates (*) indicate selection relative to the reference value of deciduous landcover, the most common landcover on the landscape. The three time periods related to white-tailed deer availability include: pre-parturition (PPP, 1–26 May), fawn limited mobility period (LMP, 27 May–30 June), and fawn social mobility period (SMP, 1 July–31 August), Upper Peninsula of Michigan, USA, 2013–2015.

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CHAPTER II

RESOURCE HETEROGENEITY MEDIATES TIME-TO-KILL ACROSS DIET AND FORAGING STRATEGIES IN CARNIVORES

Abstract

Foraging strategies should allow individuals to acquire resources that maximize caloric intake per unit time spent foraging, but there is limited understanding of the effects of heterogeneous environments on foraging habits and functional responses. Examining attack rates in heterogeneous environments can provide insights into how extrinsic factors influence time spent foraging per prey item. We used time-to-kill models developed from global positioning system collar defined hunt paths of carnivores (black bears [*Ursus americanus*], bobcats [*Lynx rufus*], coyotes [*Canis latrans*], and wolves [*C. lupus*]) with diverse dietary and foraging strategies to test 12 competing hypotheses of the influence of landscape heterogeneity, search rate, and prey densities on attack rates. We used GPS collar data from 15 black bears, 6 bobcats, 13 coyotes, and 11 wolves in Michigan, USA. We identified 1,180 (524 black bear, 258 bobcat, 245 coyote, and 153 wolf) hunt paths ending in a kill (*n* = 1,116) or censored (*n* = 64) during 27 May–30 June 2013–2015. Time-to-kill was greatest for cursorial carnivores and least for an ambush carnivore. Prey patchiness was the most influential variable on time-to-kill where greater patchiness reduced the likelihood of a kill by 37–54% for all carnivore species. Incorporating landscape characteristics improved our model describing time-to-kill for cursorial carnivores. Resource heterogeneity including prey availability and landscape characteristics appears a unifying extrinsic factor mediating time-to-kill across carnivores with diverse dietary and foraging strategies. Variation in resource heterogeneity should be considered when describing species' functional responses and demonstrates the importance for carnivores to continually reassess patch quality to achieve sustaining attack rates.

Introduction

Identifying factors influencing foraging strategies is crucial to understand acquisition of resources and relate predator effects on prey populations (Sih and Christensen 2001). As a prediction of foraging theory, foraging strategies should allow individuals to acquire resources that maximize caloric intake per unit time spent foraging (MacAurthur and Pianka 1966). Predators also should specialize on one prey type when resources are abundant and expand their dietary breadth to become generalists when resources are scarce (MacAurthur and Pianka 1966). However, this prediction contradicts competition-based foraging as competition favors specialization when resources become scarce (Robinson and Wilson 1998). Thus, we must consider the environment as variable when foraging in, and travelling between, patches (Abrams 1988). It is challenging to link population-level foraging strategies to predictions of predator responses to changes in prey abundance (i.e., functional response pattern; Solomon 1949, Holling 1959), because it often is not obvious how to distinguish predator choice (unequal attack probabilities) from diet selection (unequal consumption based on availability) with limited diet data (Sih and Christensen 2001).

Attack rates can be examined to better understand population-level effects of predators on populations of their prey (Sand et al. 2005, Franke et al. 2006, Merrill et al. 2010, Vucetich et al.

2012, Cristescu et al. 2020). Although attack rates provide an estimate of resource use, it is difficult to acquire these rates for individuals and relate them to populations due to limited sampling frequency and duration, and cost of identifying kill sites (Merrill et al. 2010, Vucetich et al. 2012). However, global positioning system (GPS) technology can be used to identify fine-scale predator movements without direct observation or intensive monitoring (Franke et al. 2006, Merrill et al. 2010, McPhee et al. 2012, Svoboda et al. 2013). These GPS data can facilitate identification of kill sites of predators (Sand et al. 2005), and in turn be used to relate kill sites to landscape characteristics (Rayl et al. 2018) and estimate predator attack rates under varying prey densities (McPhee et al. 2012).

All species may not respond similarly to variable prey densities or presence of competitors as species have differing dietary breadth ranging from specialized to opportunistic (Terraube et al. 2011, Peers et al. 2012). Variable prey density and competition also likely influence species attack rates differently as they are directly related to foraging decisions (Bastille-Rousseau et al. 2011), and prey densities and search rate influence attack rates (Merrill et al. 2010, McPhee et al. 2012). Determining the role of prey and predator numbers (ratio-dependence; Merrill et al. 2010, Sand et al. 2012) on attack rates may also be important for identifying functional responses of predators (Boutin 1992). Spatial heterogeneity in landscape features can result in prey patchiness which may influence attack rates as travel time and search rates vary among habitats and can incur a cost as with interspecific competition (Abrams 1988, Schoener 1974, Kauffman et al. 2007, Gorini et al. 2012, Gervasi et al. 2013). Other landscape attributes including road density, water features, edge, and patch size also can affect predator attack rates (McPhee et al. 2012, Fortin et al. 2015).

The western Great Lakes region of North America spans the northern deciduous and boreal ecosystems where carnivores including American black bears (*Urus americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and wolves (*C. lupus* spp.) are sympatric and have varied diets and foraging strategies. Black bears are omnivorous (Bull et al. 2001, Belant et al. 2006, Fortin et al. 2007) and can switch among plant-based prey efficiently but opportunistically feed on ungulate fawns when abundant (Bastille-Rousseau et al. 2011). Coyotes also are omnivores (Gese et al. 1988, Boutin and Cluff 1989) and quickly respond to increases in prey populations (Petroelje et al. 2014), likely due to their ability to exploit a wide breadth of small mammal species, amphibians, and fruits (Bekoff 1977). In contrast, bobcats are more specialized and exclusively carnivorous (Litvaitis and Harrison 1989, Peers et al. 2012). Bobcats have a narrow dietary breadth in the northern extent of their range (Newbury 2013) and may exhibit strong functional response patterns when a single prey species is common (Baker et al. 2001). Similarly, wolves are ungulate specialists with strong functional response patterns (Dale et al. 1994) but can be generalists during periods of variable prey availability (Mech 1970).

We assessed support for each of 12 competing models (Table 2.1; McPhee et al. 2012) to examine the influence of landscape characteristics, search rate, and prey densities on attack rates for carnivores with varying dietary breadth (i.e., generalist–specialist) and hunting strategies (i.e., cursorial–ambush). We predicted that carnivores with a narrower dietary breadth and strong functional responses (i.e., bobcats and wolves) and ambush hunting strategies (i.e., bobcats) will have greater attack rates when search rate, prey density, and patch size are greater, and prey patchiness is lesser (Schoener 1974, Abrams 1988) and would be influenced more by landscape heterogeneity due to specialization (McPhee et al. 2012, Fortin et al. 2015). Conversely, we predicted carnivores with a wide dietary niche and ability to prey switch quickly (i.e., black bears and coyotes) would follow a Type III functional response (Hollings 1959), where greater prey density and greater search rate alone influence greater attack rates.

Methods

Study area

The study area comprised about 1000 km^2 of the Upper Peninsula of Michigan, USA (46.27º, 88.23º; Figure 2.1). Land ownership consisted of State of Michigan, commercial forests, and private. Most of the area was forested (86%) with dominant land covers including deciduous forests, mixed forests, and woody wetlands (Figure 2.2 [2011 National Land Cover Database; NLCD Jin et al. 2013]). Road density was about 9.98 km/100 km^2 for primary roads (state highways) and 57.21 km/100 km^2 for secondary roads (i.e., unimproved roads, logging roads, and off-road vehicle trails; Michigan geographic framework - transportation v14a, Michigan Geographic Data Library 2002). Carnivore densities were 25.9/100 km^2 for black bears, 3.8/100 km^2 for bobcats, 23.8/100 km^2 for coyotes, and 2.8/100 km^2 for wolves (Kautz et al. 2019). Densities of primary prey species were 571/100 km^2 for white-tailed deer (*Odocoileus virginianus*; Kautz et al. 2019), 1,050/100 km^2 for snowshoe hare (*Lepus americanus*), and 503/100 km^2 for ruffed grouse (*Bonasa umbellus*; Petroelje et al. 2021). Elevations ranged from 401 to 550 m. Monthly May–August temperatures ranged from average highs of 24.5º C in July to average lows of 2.0º C in May. Average rainfall during May–August was 34.4 cm (National Oceanic and Atmospheric Administration 1981–2010 Climate Normals).

Identifying kill sites

We used previously reported data from GPS collared black bears, bobcats, coyotes, and wolves during 2013–2015 (see Petroelje et al. 2020). Collars attempted a GPS location every 15-

min during May–August of each year and stored activity data from an on-board accelerometer every 300 sec. We subset carnivore GPS movement data to 27 May–30 June when white-tailed deer fawns are largely immobile and use hiding as a primary defense against predation (Ozoga et al. 1982) and can provide a large portion of these carnivores' diets (Duquette et al. 2014, Kautz et al. 2019). We identified potential kill sites using a rule-based algorithm developed in R (version 3.0.2; R Core Team 2018) that calculated geometric mean centers of clusters of four or more GPS locations within 50 m of each other and occurred within 24 h (Svoboda et al. 2013, Petroelje et al. 2019). We predicted which clusters were kill sites using species-specific models which included mean and summed activity of the cluster, time of day, land cover within 50 m of the cluster center, patch size, and distance to water, land cover edge, and secondary and primary roads as model covariates (Petroelje et al. 2020). We identified land cover and distance to edge for each cluster using 2011 NLCD (Jin et al. 2013) and combined classes into open water, forest, woody/herbaceous wetland, shrub/herbaceous, and developed (i.e., urban, barren, road, agriculture). We determined distance to nearest hydrologic feature (Michigan Geographic Framework, hydrography lines v16a), distance to nearest road (Michigan Geographic Framework, all roads v16a), and distance to nearest land cover edge (2011 NLCD) from each cluster center using ArcMap 10.3 (Environmental Systems Research Institute, Redmond, California, USA). We assigned a GPS location as active when averaged accelerometer readings were > 35.9, 36.8, and 30.7 for black bears, bobcats, and coyotes and wolves, respectively (Petroelje et al. 2020).

Path movement and analysis

We used time-to-kill to estimate time between consecutive kill sites (McPhee et al. 2012). We used the subset GPS and activity data (27 May–30 June) from collared black bears, bobcats, coyotes, and wolves and considered each hunting path as the first GPS relocation following a kill cluster until the last GPS relocation before the next kill cluster and calculated time-to-kill as time between these locations. We considered time at kill sites as handling times. We used only active locations to estimate hunting paths from which we extracted path covariates. We used the time between the last point at a kill cluster to identify the beginning of a discrete hunting path and the first point at the next kill cluster as the end of the discrete hunting path.

GPS error and step calculation

To estimate collar location error, we deployed a GPS7000MU and GPS7000SU collar (models matching that of the collared carnivores; Lotek Wireless, New Market, Ontario, Canada) at each of two geodetic markers (maintained by National Geodetic Survey, National Oceanic and Atmospheric Administration) with tree canopy cover of 100% and 0%. We programmed each collar to obtain a location every 15-min. We measured the distance between the true location of the geodetic marker and each location recorded by the GPS collars. We used linear models to regress distance of each relocation from the geodetic marker against all combinations of dilution of precision (DOP), number of satellites used, navigation, and validation. We ranked these models using Akaike Information Criterion adjusted for small sample size (AICc) to identify a best model to describe collar GPS error (Burnham and Anderson 2002). We used the top-ranked model to calculate GPS error of each carnivore relocation.

As the true path of an animal is unknown, we estimated potential carnivore movements between 15-min relocations by calculating a 50% utilization distribution contour using a dynamic Brownian bridge movement model (function ‘dBBMM’ in package ‘move’ for R, Kranstauber et al. 2012) looping across GPS locations to estimate each step (i.e., the estimated occurrence between two consecutive locations; function ‘move.forud’ in package ‘moveud’ for R, Byrne et al 2014). We combined and exported all steps into a single shapefile for each individual.

Time-to-kill model

We categorized each 15-min relocation as kill (1) or no kill (0) based on kill site cluster identification model results. Within each buffered step, we identified covariates including search rate, prey density, predator activity, patch size, prey patchiness, natural edges, hydrologic features, land cover type, and human disturbance (i.e., roads) that may influence prey acquisition along a hunt path (McPhee et al. 2012). We did not include prey size as a covariate as it was not practical to identify prey items smaller than adult white-tailed deer at kill sites (Svoboda et al. 2013). We used accelerometer readings for each step as a measure of predator activity along the hunt path. We used Brownian motion variance, calculated by dBBMM, as an estimate of search rate for each step.

We created a grid across the study area with non-overlapping cells (30 x 30 m) equal to the resolution of the 2011 NLCD. We calculated distance to land cover edges and patch size using the 2011 NLCD as measures of habitat patchiness for each grid cell. We extracted estimated prey densities for each grid cell for ruffed grouse, snowshoe hare, and probability of occurrence for adult female and fawn white-tailed deer (see Petroelje et al. 2021) as these prey are within the predicted optimal prey range for black bears, bobcats, coyotes, and wolves (Carbone et al. 1999), appeared to be dominant prey within the study area (D. Beyer, *unpublished data*), and prey densities may influence kill rates (Merrill et al. 2010, McPhee et al. 2012). We used the standard deviation of prey density, within the buffered hunt path, as a measure of prey patchiness (McPhee et al. 2012). We calculated distance from each grid cell to nearest hydrologic feature (i.e., stream, river, or lake) and secondary road (unimproved roads, logging roads, off-road vehicle trails) as these may influence hunt paths. We overlaid buffered hunt paths onto the covariate grid and extracted all covariate values for each step where averaged accelerometer readings were > 35.9, 36.8, 30.7, and 30.7 for black bear, bobcat, coyotes, and wolves, respectively (Petroelje et al. 2020). As more than one grid cell could occur within each buffered step, we used the mean covariate value proportionate to amount of each grid cell within each buffered hunt path (function 'isctpolyrst' in Geospatial Modeling Environment, Beyer 2015). Finally, we calculated the proportion of each land cover within each buffered step as determined by the 2011 NLCD.

We tested for multicollinearity of variables using Pearson correlations and excluded covariates that are strongly correlated (i.e., $|r| > 0.70$; Dormann et al. 2013) to reduce over-parameterization of analyses. We used Cox proportional hazards (Cox 1972) to assess which covariates had the greatest influence on time-to-kill (function 'coxme' in package 'coxme' for program R; Therneau 2020). Unlike McPhee et al. (2012), we did not include a data duplication method as we did not account for previous prey size as all prey were the size of adult white-tailed deer or smaller. We included search rate, prey densities, prey patchiness, predator activity, distance to edges, distance to water, and distance to road as explanatory model covariates. We included a random effect term to account for unobserved heterogeneity among individuals. We ranked models for each hypothesis and species using AICc and calculated Akaike weights to aid in model selection (Burnham and Anderson 2002). The standard deviation of the random effects for mixed effects Cox models is directly interpretable and allows for comparison of risk score for each individual (i.e., the random effect term; Therneau 2020) relative to the hazard of making a kill.

Results

During the study period (27 May–30 June), GPS location and activity data were available for 15 black bears, six bobcats, 13 coyotes, and 11 wolves and used for analyses. We obtained 212,040 carnivore GPS locations with a mean relocation success for collars > 91.9% for all carnivores (Table 2.2). Step lengths were right-skewed, median step lengths were greatest for black bears (23.3 m) and least for wolves (14.0 m), but mean step lengths were greatest for wolves (149.2 m) and least for bobcats (80.2 m). We identified 4,776 GPS clusters for carnivores of which the kill site model predicted 1,147 clusters (24.%) as predations. Mean GPS error for collars at geodetic markers was 7.2 m (*n* = 1,151, minimum = 0.1 m, 1st quantile = 3.0 m, 3rd quantile = 9.1 m, maximum = 184.3 m). The top-ranked model for step error calculations included DOP and number of satellites (SATS) as fixed effects where error = 1.26*DOP + -0.68*SATS + 7.22.

We used 1,180 hunt paths ending in a kill cluster (*n* = 1,116; Figure 2.1) or censored (*n* = 64) during 27 May–30 June from carnivores. Mean time-to-kill was greatest for wolves (26.3 h) and coyotes (21.4 h) and least for black bears (16.4 h) and bobcats (7.6 h; Table 2.2, Figure 2.3). The concepts that best described time-to-kill included landscape characteristics for wolves and coyotes and effective prey density for black bears and bobcats (Table 2.1, 2.3). Time-to-kill for wolves increased when proportion of developed landcover (hazard ratio [HR] = 0.27), grouse density (HR = 0.83), and prey patchiness (HR = 0.46) increased and decreased when distance to water (HR = 2.14) and hare density (HR = 1.67) increased (model 9). Time-to-kill for coyotes increased when distance to water (HR = 0.79), prey patchiness (HR = 0.54), and activity (HR = 0.73) increased and decreased when distance to road (HR = 9.15) and proportion of wetland (HR = 4.33), developed (HR = 1.53), herbaceous (HR = 1.98), and forest (HR = 3.66) landcovers increased (model 11). Time-to-kill for black bears increased as activity (HR = 0.77) and prey patchiness (HR = 0.64) increased and decreased when fawn occurrence (HR = 1.88) and hare density (HR = 1.23) increased (model 4; Figure 2.4). Time-to-kill for bobcats increased as prey patchiness (HR = 0.64) increased (model 5). Prey patchiness was the most influential variable on time-to-kill across carnivore species where greater patchiness reduced the hazard of a kill (HR = 0.46–0.64). The standard deviation of the random effects was 1.01 for wolves (i.e., a 1% increase or decrease in the hazard), 1.93 for coyote, 1.39 for black bears, and 2.02 for bobcats.

Discussion

Irrespective of foraging strategy or dietary breadth, heterogeneity in prey availability mediated time-to-kill of carnivore functional responses. Effective density (i.e., variable prey density or distribution) best described time-to-kill for black bears and bobcats, suggesting greater generalist responses compared to wolves and coyotes. This contradicted our predictions for bobcats given that specialist species have less diverse foraging behavior as compared to generalists with ability to switch among prey with changes in their density or availability (O’Donoghue et al. 1998, Owen-Smith and Mills 2008). Incorporating landscape characteristics that can alter prey accessibility or vulnerability better explained time-to-kill for wolves and coyotes, with coyotes responding as specialists (e.g., Sacks and Neale 2002) though they had wider dietary breadth than wolves during this period (Petroelje et al. 2021). Though the concepts of effective density and landscape characteristics were originally categorized as independent (McPhee et al. 2012), we recognize they are not mutually exclusive in that prey are influenced by landscape attributes which introduces heterogeneity in their spatial distribution and availability.

Greater prey patchiness increased time-to-kill across species. Even when a single prey species is abundant and easily captured, multispecies functional responses likely better reflect generalist responses (Smout et al. 2010) and may explain why observed species responses to resource heterogeneity were similar. In addition, prey patchiness is related to landscape complexity and heterogeneity which may reduce encounter rates (Stoner 2009) and thus prey availability regardless of foraging strategy. In the context of resource availability this heterogeneity is important as prey patchiness can stabilize predator-prey dynamics where predators lack an aggregated response to prey (Nachman 2006). This is supported by our observations of territorial carnivore species, which are unlikely to aggregate, that had reduced kill rates as prey patchiness increased. Though increasing evidence demonstrates the importance of spatio-temporal variability in single predator-single prey relationships (Rayl et al. 2018, Smith et al. 2020), we demonstrate the importance of resource heterogeneity across multiple carnivore species and their prey as more representative systems.

Effective density considers total prey density, patchiness, and search rate which best described time-to-kill for black bears and bobcats. Encounter rates of prey are likely important for both opportunistic (i.e., black bear) and ambush (i.e., bobcat) carnivores which may explain why effective prey density best described time-to-kill for these species. This is supported by the observed decrease in time-to-kill where white-tailed deer fawn occurrence is greater for black bears, as found with caribou (*Rangifer tarandus*) neonates (Rayl et al. 2018). Limited data exist on factors driving bobcat attack rates but kill rates of other felids, such as cougar (*Puma concolor*), increase with ungulate density (Knopff et al. 2010, Cristescu et al. 2020). Though individual prey densities did not influence attack rate for bobcats we recognize that other prey resources were likely present in wetland areas where bobcats disproportionally spent time (Figure 2.2) for which we had no density estimates available (e.g., shrews and moles [Soricomorpha], mice and voles [Cricetidae, Zapodidae], muskrats [*Ondatra zibethicus*], etc.). Search rate was inversely related to time-to-kill for black bears, yet they are considered an opportunistic predator (Bastille-Rousseau et al. 2011) and we expected increased search rate would result in increased probability of encountering prey. We also included carnivore activity as a correlate of search effort, yet greater activity reduced the attack rate for black bears and did not influence time-to-kill for bobcats. It may be that increased activity along the hunt path is related to travel and lesser searching behavior, and a quadratic term for activity may better describe the relationship of activity and search behavior along hunt paths. Alternatively, search rate may be unimportant, or movement activity could be inversely related to attack rate for a predator employing an ambush strategy (Avgar et al. 2008).

Landscape characteristics considered the mosaic of landcovers and linear features within hunt paths and best described time-to-kill for wolves and coyotes. Coyotes used land covers proportionately similar to wolves along hunt paths (Figure 2.2), yet the increased attack rate in developed land contrasted with wolves, potentially a result of coyotes avoiding wolves while traveling or selecting for different prey (Svoboda et al. 2019, Petroelje et al. 2021). For example, linear features such as roads did influence time-to-kill for coyotes where distance from roads increased the attack rate. The attack rate for wolves decreased with greater proportion of developed land along the hunt path, similar to McPhee et al. (2012), but wolves used these areas at a greater rate than available when active (Figure 2.2). One probable explanation is use of roads can be important for travel (Thurber et al. 1994, Whittington et al. 2005) and wolves may not have hunted along these features during our study. Greater variation in resource selection among coyotes compared to wolves (Petroelje et al. 2021) may have increased coyote model complexity; the effects of landscape characteristics on individual variation in attack rates can be substantial even for specialists (Cristescu et al. 2020). Indeed, the standard deviation for individual attack rates for coyotes represented a 93% change in the hazard of a kill. Landscape characteristics can also drive prey density which is important when describing functional response of coyotes during winter (O'Donoghue et al. 1998), yet no single prey type greatly influenced coyote attack rate during summer in our study. Prey density was inversely related to time-to-kill for wolves and though population-level prey density has little support for influencing kill rates (Vucetich et al. 2002, Mech and Peterson 2003), our measure of prey density or occurrence incorporated heterogeneity in prey availability among patches along the hunt path. Though greater hare densities increased the attack rate for wolves we caution that hares represented a small portion of the diet of wolves during this period (Petroelje et al. 2021) and the greater attack rate was likely unrelated to greater predation of hares. Habitat edges promote landscape heterogeneity and influence kill probability (Fortin et al. 2015) yet edge effects did not influence the attack rate for coyotes or wolves in our study. That search rate of wolves was not related to time-to-kill supports studies that found independence between search rate and attack rates (Messier and Crete 1985, Dale et al. 1995, Hayes et al. 1999; but see McPhee et al. 2012).

Time-to-kill for wolves and coyotes was similar which may be a result of their cursorial foraging strategy and ecological similarities, though the diet of coyotes contained greater proportion of smaller prey during this period (Petroelje et al. 2021). Wolf time-to-kill was much lesser for our study than reported for larger prey (Sand et al. 2008) or during winter (McPhee et al. 2012), as time-to-kill is likely related to ratio of carnivore-prey body size (McPhee et al. 2012) wolves and coyotes were likely consuming small prey relative to their body size. This difference in observed attack rate emphasizes the importance of comparing kill rates in kg/unit time when possible (Cristescu et al. 2020) and accounting for seasonality in annual kill rate estimates (Sand et al. 2008, Metz et al. 2011). Black bears had an intermediate time-to-kill which we suspect was in part a consequence of foraging on diverse prey (i.e., animal and plant species) and greater false positives in identifying kill sites (Petroelje et al. 2020). Bobcats had the shortest time-to-kill of species examined, and though body size is similar to coyotes (Feldhamer et al. 2003), as an obligate carnivore and ambush predator attack rates may vary with prey vulnerability and body size. Kill rates of cougars were greater in summer when neonatal ungulates were vulnerable, yet total ungulate biomass consumed was similar among seasons (Clark et al. 2014).

Our approach could over- or under-estimate predator attack rates compared to visiting all clusters (Elbroch et al. 2018); however, identifying kills at clusters is imperfect, especially when prey are small (Svoboda et al. 2013, Petroelje et al. 2020). Large variation in individual kill rates (Cristescu et al. 2020), coupled with few individuals monitored, can further bias population-level kill rate estimates. We recommend monitoring fewer clusters of more individuals than all clusters of few individuals to estimate population-level attack rates. Using hunt paths to estimate time-to-kill should also account for small prey transported by predators; some hunt paths we identified likely represented searching and carrying behavior (Windell et al. 2019). Our modeled kill sites likely included foraging (e.g., black bear feeding on berries) or scavenging (e.g., wolves returning to a deer predation) behavior and may be better termed ‘time-to-forage’ rather than ‘time-to-kill’. Incorporating sex, age, or sociality (e.g., wolf packs) may better explain individual variation in kill rates (Patterson and Messier 2000, Knopff et al. 2010, Mattisson et al. 2011, Metz et al. 2011).

Our results contradict predictions that predators with wide dietary breadth exhibit a functional response influenced only by search rate and prey density in heterogeneous environments. Irrespective of diet or foraging strategy, prey patchiness directly influenced time-to-kill across species. Heterogeneity relative to species distributions and prey availability varies temporally (e.g., parturition; Rayl et al. 2018) and should be integrated in estimates of species functional response. We offer empirical support for spatial heterogeneity in prey availability mediating attack rates and suggest that decreased foraging efficiency in more heterogeneous environments is a consequence of more frequent reassessments of patch quality, which can reduce attack rates (Gorini et al. 2012). Unless we consider resource heterogeneity and control for this spatial variation in estimates of kill rates, we cannot expect to accurately describe population-level responses of predators to their prey (Nachman 2006, Kauffman et al. 2007, Gorini et al. 2012, Fortin et al. 2015) which may ultimately affect prediction of oscillation dynamics among predators and their prey (Gorini et al. 2012).

Table 2.1 Competing concepts and models

Concept	Explanation	Model	Best supported
Null	Time-to-kill is not influenced by any variables.	1. No variables	
Traditional	Holling's (1959) prediction that search rate and prey density influence time-to-kill	2. Search rate and prey density	
Effective density	Prey density affects time-to-kill and patchiness of prey may further alter effective density	3. Prey Density	
		4. Search rate, prey density and patchiness	Black bear
		5. Search rate and prey patchiness	Bobcat
Compensatory	Predators compensate for low prey density or aggregation by faster search movement. Search rate alone, or an interaction of search rate with prey density may drive time-to-kill.	6. Search rate	
		7. Search rate, prey density, search rate × prey density	
Landscape characteristics	Landscape characteristics that alter prey accessibility or vulnerability act alone or in combination with search rate, prey density, and prey patchiness to influence time-to-kill.	8. Landscape	
		9. Landscape, prey density, prey patchiness	Wolf
		10. Landscape, search rate	
		11. Landscape, prey density, prey patchiness, search rate	Coyote
Full model	All factors influence the time-to-kill.	12. Prey density, prey patchiness, search rate, search rate × prey density, and landscape	

Competing hypotheses and associated models to examine the influence of several predictor variables (e.g., landscape, prey densities, etc.) on kill rates of prey by black bears, bobcats, coyotes, and wolves. Table modified from McPhee et al. (2012).

Table 2.2 Carnivore summary statistics used to characterize hunt paths

Attribute	Species			
	Black bears	Bobcats	Coyotes	Wolves
Collared females / males (*n*)	8 / 7	2 / 4	11 / 2	5 / 6
Total species years (*n*)[1]	26	7	13	12
Total GPS locations (*n*)	107,616	30,624	40,320	33,480
Mean GPS locations / individual (*n*)	2,909 [879]	3,062 [638]	2,688 [900]	2,748 [713]
Mean GPS fix success rate (%)	91.9 [15.7]	96.6 [3.8]	96.3 [5.3]	94.6 [4.8]
Median step length (m)	23.3	18.1	19.0	14.0
Mean step length (m)	88.1	80.2	108.6	149.2
Identified clusters (*n*)	2,345	599	1,059	773
Predicted kill clusters (*n*)	509	261	231	146
Mean kill clusters / individual (*n*)	24.2 [17.7]	43.5 [8.8]	23.8 [6.2]	18.3 [6.6]
Hunt paths (*n*)	524	258	245	153
Mean time-to-kill (h)	16.4 [27.8]	7.6 [8.0]	21.4 [23.8]	26.3 [31.7]

[1] Some individuals were collared for multiple years

Summary statistics of GPS collared black bears, bobcats, coyotes, and wolves used to characterize hunt paths, Upper Peninsula of Michigan, USA, 2013–2015. Standard deviation shown in brackets when applicable.

Table 2.3 Competing model results using Akaike Information Criterion

Species	Model	K	AICc	Δ AICc	Weight	Cumulative	LL
Black bear	4	8	5123.83	0.00	0.88	0.88	-2553.77
	11	15	5128.35	4.52	0.09	0.97	-2548.7
	12	16	5130.42	6.60	0.03	1.00	-2548.68
	9	13	5137.5	13.67	0.00	1.00	-2555.39
	10	10	5164.48	40.65	0.00	1.00	-2572.03
	2	6	5165.34	41.51	0.00	1.00	-2576.59
	7	7	5167.16	43.33	0.00	1.00	-2576.47
	8	8	5169.74	45.92	0.00	1.00	-2576.73
	3	4	5172.66	48.84	0.00	1.00	-2582.29
	5	5	5194.15	70.33	0.00	1.00	-2592.02
	6	3	5256	132.17	0.00	1.00	-2624.98
	1	1	5263.07	139.25	0.00	1.00	-2630.53
Bobcat	5	5	2358.68	0.00	0.52	0.52	-1174.22
	12	16	2360.49	1.81	0.21	0.73	-1163.15
	9	13	2361.63	2.95	0.12	0.85	-1167.09
	11	15	2362.16	3.48	0.09	0.94	-1165.11
	4	8	2363.27	4.59	0.05	0.99	-1173.35
	10	10	2367.83	9.15	0.01	1.00	-1173.48
	8	8	2372.44	13.75	0.00	1.00	-1177.94
	6	3	2373.75	15.07	0.00	1.00	-1183.83
	7	7	2379.11	20.43	0.00	1.00	-1182.34
	1	1	2379.30	20.62	0.00	1.00	-1188.64
	2	6	2379.75	21.07	0.00	1.00	-1183.71
	3	4	2384.59	25.91	0.00	1.00	-1188.22
Coyote	11	15	2100.35	0.00	0.49	0.49	-1034.13
	12	16	2101.55	1.20	0.27	0.76	-1033.58
	10	10	2103.74	3.39	0.09	0.85	-1041.40
	9	13	2104.21	3.86	0.07	0.92	-1038.32
	8	8	2104.22	3.87	0.07	0.99	-1043.80
	4	8	2107.68	7.33	0.01	1.00	-1045.54

Competing model results using Akaike Information Criterion for small sample sizes (AICc) for black bears, bobcats, coyotes, and wolves, Upper Peninsula of Michigan, USA, 2013–2015. Included are number of parameters (K), and log likelihood (LL). Models defined in Table 2.1.

Table 2.3 (continued)

Species	Model	K	AICc	Δ AICc	Weight	Cumulative	LL
Coyote	2	6	2120.03	19.68	0.00	1.00	-1053.84
	3	4	2120.23	19.88	0.00	1.00	-1056.03
	7	7	2121.96	21.61	0.00	1.00	-1053.74
	5	5	2143.84	43.49	0.00	1.00	-1066.80
	1	1	2150.51	50.16	0.00	1.00	-1074.25
	6	3	2153.69	53.34	0.00	1.00	-1073.80
Wolf	9	13	1144.98	0.00	0.84	0.84	-558.18
	11	15	1149.23	4.25	0.10	0.94	-557.86
	12	16	1151.62	6.64	0.03	0.97	-557.81
	8	8	1151.96	6.98	0.03	1.00	-567.48
	10	10	1156.33	11.35	0.00	1.00	-567.39
	5	5	1178.28	33.30	0.00	1.00	-583.94
	4	8	1179.00	34.02	0.00	1.00	-581.00
	1	1	1181.81	36.83	0.00	1.00	-589.89
	3	4	1184.31	39.33	0.00	1.00	-588.02
	6	3	1185.84	40.86	0.00	1.00	-589.84
	2	6	1188.51	43.53	0.00	1.00	-587.97
	7	7	1190.32	45.34	0.00	1.00	-587.77

Competing model results using Akaike Information Criterion for small sample sizes (AICc) for black bears, bobcats, coyotes, and wolves, Upper Peninsula of Michigan, USA, 2013–2015. Included are number of parameters (K), and log likelihood (LL). Models defined in Table 2.1.

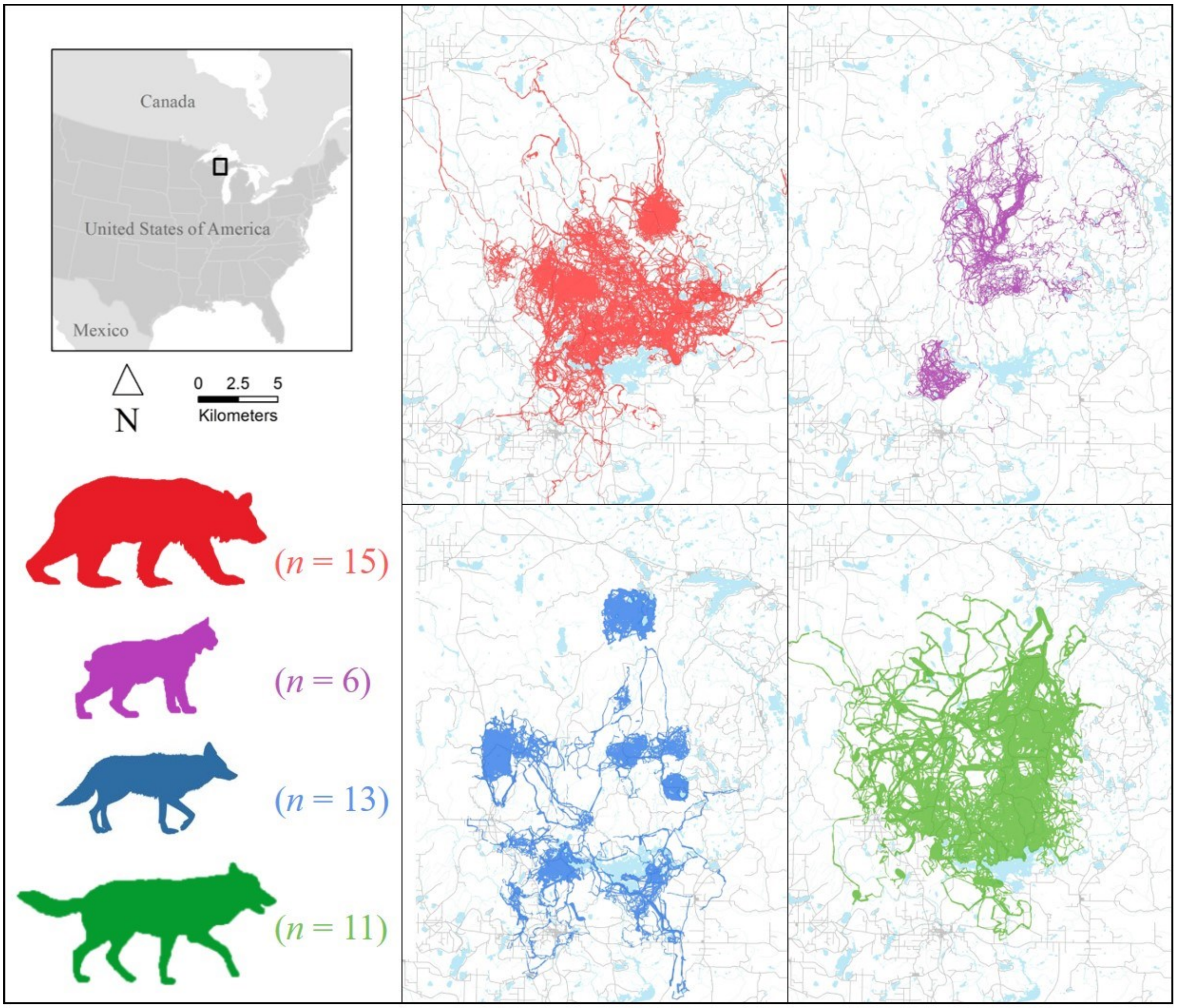

Figure 2.1 Hunt paths of black bears, bobcats, coyotes, and wolves

Study area showing local roads (grey lines), hydrologic features (light blue), and 15 min steps calculated using 50% dynamic Brownian Bridge models to estimate hunt paths of collared black bears, bobcats, coyotes, and wolves, Upper Peninsula of Michigan, USA, 2013–2015. Inset showing study area location (black polygon) in North America.

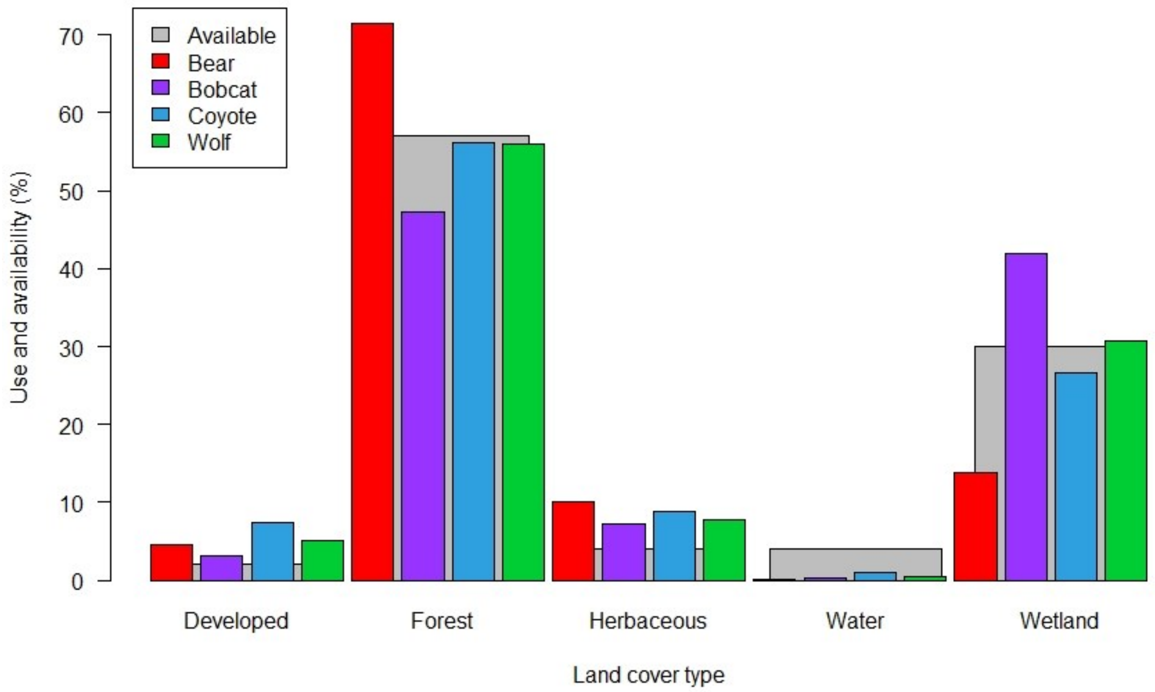

Figure 2.2 Landcover availability and use by active carnivores

Percent of active steps within each land cover by black bears, bobcats, coyotes, and wolves along hunt paths during the white-tailed deer fawn limited mobility period (27 May–30 June), Upper Peninsula of Michigan, USA, 2013–2015. Study area availability of landcovers included for comparison.

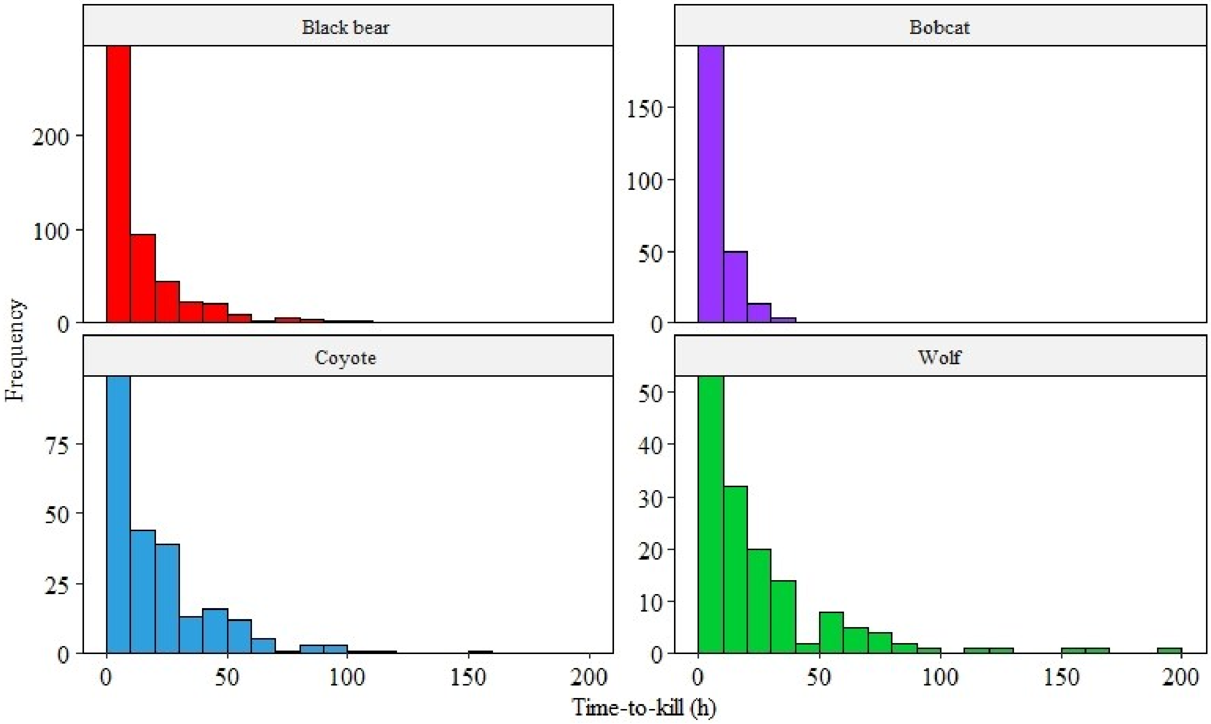

Figure 2.3 Frequency and duration of time-to-kill for carnivores

Frequency and duration of time-to-kill for hunt paths of black bears (*n* = 524), bobcats (*n* = 258), coyotes (*n* = 245), and wolves (*n* = 153) during the limited mobility period for white-tailed deer fawns (27 May–30 June), Upper Peninsula of Michigan, USA, 2013–2015.

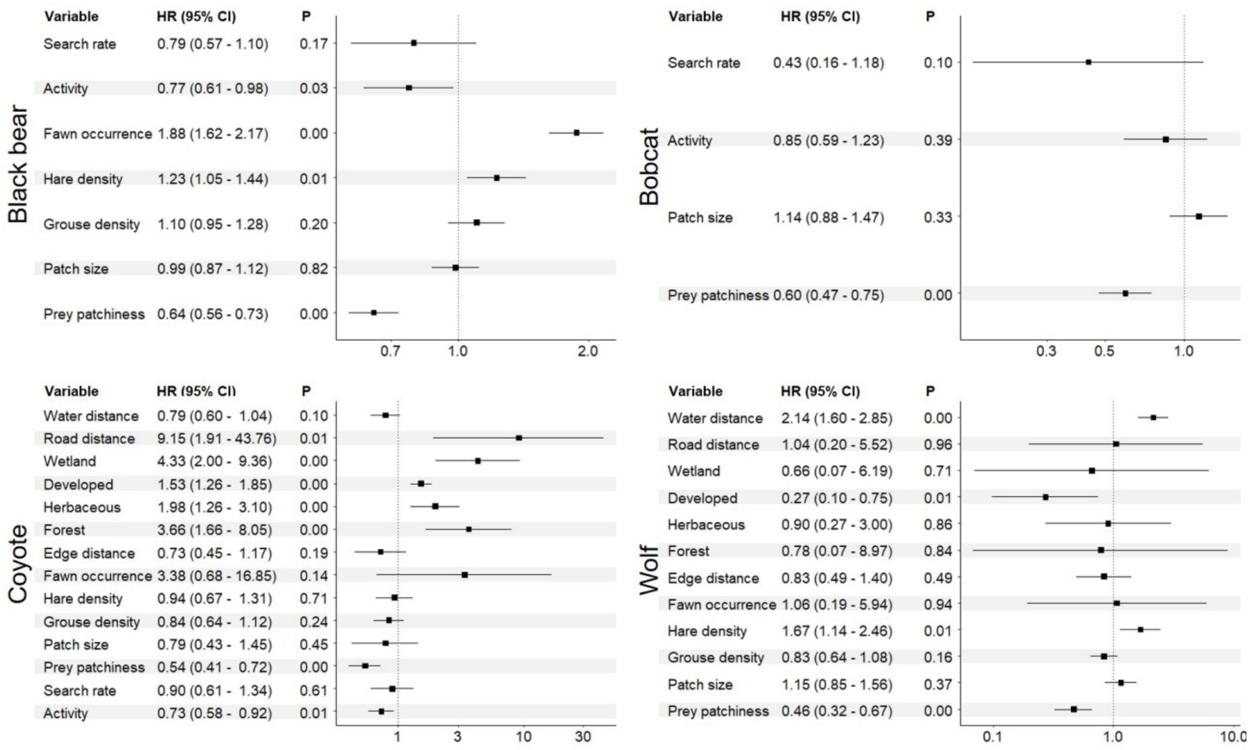

Figure 2.4 Model covariates best describing time-to-kill for carnivores

Top-ranked model results using AICc selection of mixed effects Cox models to identify variables influencing time-to-kill for black bears, bobcats, coyotes, and wolves, Upper Peninsula of Michigan, USA, 2013–2015. Hazard ratios (HR), 95% confidence intervals (CI) and P values are included.

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CHAPTER III

VARIABLE PREDATION RISK FOR A NEONATE UNGULATE IN A MULTI-PREDATOR LANDSCAPE

Abstract

Predation risk is central to understanding prey distributions and the effects of predators on their prey. Numerous spatio-temporal factors are suggested to influence predation risk but are more accurately correlates of true predation risk, represent risk effects, or do not reflect instantaneous risk. There is limited understanding of how these factors vary among species in multi-predator systems where avoidance of a single predator is not sufficient for survival and avoidance of all predators is unlikely. We used 100 white-tailed deer (*Odocoileus virginianus*) fawn predation sites from black bears (*Ursus americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and wolves (*C. lupus*) to identify predator-specific predation risk during 2013–2015 in Michigan, USA. We used a competing model framework which considered all combinations of occurrence of predator species when active, adult female deer occurrence, linear features as travel corridors, and habitat characteristics (e.g., horizontal cover, deer forage availability) to describe spatial variation in fawn kill sites. We then assessed how relative density of predators may contribute to spatial variation when considering composite risk from all four predators. Predation risk from bobcats, the only ambush predator, lacked inclusion of habitat characteristics in the best supported risk model which differed from black bears, coyotes, and wolves. Proportion of landscape predicted as risky was 47% for black bears, 5% for bobcats, 3% for coyotes, and 44% for wolves. The relationship between composite and density-weighted composite predation risk explained 69% of the spatial variation in risk. We demonstrated that diverse factors including foraging strategies influence predation risk among predator species which can markedly alter landscape-level distributions of these risks. Consideration of predator occurrence or habitat metrics alone is unlikely to adequately describe spatial variation in risk across foraging strategies in a multi-predator system. When possible, composite or density-weighted composite predation risk should be considered as risk across predator species is not homogenous.

Introduction

Predator-prey relationships are often evaluated by examining the response of prey to predation risk (Brown et al. 1999, Kauffman et al. 2007, Kohl et al. 2020). The response of prey to fear of predators has been co-opted with foraging theory (MacAurthur and Pianka 1966) to explain prey distributions (Brown et al. 1999, Laundré et al. 2001, Hernández and Laundré 2005). However, predation is a multi-step process consisting of a predator encountering, engaging, and attacking prey (Lima and Dill 1990); therefore, the probability of encountering prey may not be consistent with predation probability (Prugh et al. 2019). Further, predation risk (probability of being killed by a predator) is often not clearly distinguished from risk effects (fitness costs of antipredator behavior) which creates challenges when comparing risk across studies. Instead, estimating probabilistic kill occurrence may reflect ‘true’ predation risk and provide a mechanistic link to the predation process (Hebblewhite and Merrill 2007, Moll et al. 2017, Lendrum et al. 2018, Prugh et al. 2019).

Studies describing predation risk generally have involved a single predator which can oversimplify multi-predator systems where avoidance of predation risk is more complex (Sih et al. 1998, Atwood et al. 2007, Moll et al. 2017, Prugh et al. 2019). Multiple predators may impart contrasting patterns of risk across habitats, times of the day, or seasonally (Lone et al. 2017). For example, elk (*Cervus elaphus*) balance predation risk from wolves (*Canis lupus*) and cougars (*Puma concolor*), but cougars may have a greater effect on habitat selection and diel activity of elk than wolves, though are not often considered (Kohl et al. 2020). The few studies that have investigated predation risk from multiple predators typically use indices of predation risk or measure risk effects rather than estimate probabilistic predation risk from kill sites (Moll et al. 2017). Predator density is often unknown in multi-predator-ungulate studies and given that encounter rates are related to predator density (Prugh et al. 2019), composite predation risk is unlikely to accurately describe population-level risk without accounting for individual predator densities (Griffen 2006).

Though numerous spatio-temporal factors can influence predation risk there is limited understanding of the contribution or variation of these factors among species in a multi-predator system (Moll et al. 2017, Prugh et al. 2019). Predation risk varies across time and space and is influenced by prey occurrence, topography, and vegetation structure assumed to influence prey vulnerability (Ripple and Beschta 2006, Shrader et al. 2008, Tolon et al. 2009, Willems and Hill 2009, Laundré et al. 2010). Linear features such as roads also may increase predation risk (Lendrum et al. 2018). Additionally, selecting habitat structure to reduce efficiency of predator hunting strategies may mediate predation risk (Laundré et al. 2010, Lone et al. 2014). Forage availability or quality has been linked to survival where poor nutrition or selection of high-quality forage may result in greater mortality risk (Hernández and Laundré 2005, Shallow et al.

2015, Forrester and Wittmer 2019). Predator presence or probability of use is often used to identify areas of greatest risk of predation (Hernández and Laundré 2005, Kittle et al. 2008, Thaker et al. 2011) but has been suggested as a weak form of inference to true predation risk (Prugh et al. 2019). Predators will select areas for purposes other than foraging (i.e., resting sites [Zalewski 1997]) and some predators also may perceive predation risk (Berger and Gese 2007) which may influence predator distributions based on not only their prey but also their potential predators. Inactivity does not exclude predators from opportunistically consuming prey when not actively foraging (Bastille-Rousseau et al. 2011), but during activities such as sleeping all foraging ceases and those areas reflect a skewed representation of use or occurrence as related to predation risk. Identifying predation risk focused on active movements can account for spatial variability in risk and may better describe observed predation patterns (Fortin et al. 2005, Kohl et al. 2020).

Studies of adult ungulate predation risk are common (Moll et al. 2017), though consideration for neonate predation risk is often of interest as they typically experience greater mortality rates (DelGiudice et al. 2006, Carstensen et al. 2009, Duquette et al. 2014a). Much of that mortality occurs within 6 weeks of parturition for species such as white-tailed deer (*Odocoileous virginianus*), of which 80% may be attributed to predation and predator density can influence relative contribution of mortality (Kautz et al. 2019). The reliance on habitat structure for fawn hiding cover (Ozoga and Verme 1982, Pettorelli et al. 2005, Van Moorter et al. 2009) brings importance to vegetation phenology following parturition (Duquette et al. 2014b) which may influence the magnitude of predation risk for neonates. Additionally, since adult female white-tailed deer select areas for parturition and functionally fawn habitat within their home ranges, neonate deer are subject to selectivity of adult females balancing predation risk, quality hiding cover, and quality forage (Kittle et al. 2008, Van Moorter et al. 2009). Adult female deer also spend considerable time near fawns which can be an important risk factor for fawns (Panzacchi et al. 2009).

White-tailed deer (hereafter deer) in the western Upper Peninsula of Michigan, USA live in a multi-predator landscape including American black bears (*Ursus americanus*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), and wolves (Svoboda et al. 2013, Duquette et al. 2014b, Petroelje et al. 2014, Svoboda et al. 2019, Kautz et al. 2020) with diverse foraging strategies (e.g., ambush, cursorial, opportunistic) and differ 9-fold in abundance (Kautz et al. 2019). We estimated predator-specific and composite predation risk for fawn deer from black bears, bobcats, coyotes, and wolves by exploring the relative contributions of active predator-specific occurrence, adult female deer occurrence, linear features, and habitat characteristics on kill sites of fawn deer as a measure of predation risk. We then assessed the spatial difference in composite predation risk with and without consideration for predator-specific density. We hypothesized that factors describing predation risk would vary among predators given diverse foraging strategies and accounting for predator densities when considering composite predation risk would result in a markedly different risk landscape as some predators were much more abundant than others in our study area (Kautz et al. 2019). We predicted that cursorial and ambush predators would have differing risk landscapes. We also predicted composite predation risk from all four predators would be unrelated to density-weighted composite predation risk.

Methods

Study area

We conducted our study during May–August 2013–2015 in about 1000 km^2 of the western Upper Peninsula of Michigan, USA (46.27º, 88.23º) (Figure 3.1). Landownership was a mosaic of state forest, commercial forest, and private. Most of the study area was forested (86%) with dominant land covers including deciduous forests, woody wetlands, and mixed and evergreen forests (2011 National Land Cover Database [NLCD], Jin el al. 2013; Table 3.1). Fawn deer densities in the study area were 334 fawns/100 km^2 and peak parturition occurred about 7 June (Kautz et al. 2019). Predator densities were greatest for black bears (25.9/100 km^2) followed by coyotes (23.8/100 km^2), bobcats (3.8/100 km^2), and wolves (2.8/100 km^2; Kautz et al. 2019). Elevations ranged from 401 to 550 m. Monthly June–August temperatures ranged from average lows of 9.2º C during June to average highs of 25.7º C during July (National Oceanic and Atmospheric Administration 1981–2010, ncdc.noaa.gov/cdo-web/datatools/normals).

Landscape and habitat characteristics

Horizontal cover

We used land covers defined by the 2011 NLCD (30-m resolution; Table 3.1) and estimated horizontal cover within deciduous forest, woody wetlands, mixed forest, evergreen forest, grassland/herbaceous, and emergent herbaceous wetland land covers. We collected horizontal cover data during the limited mobility (LMP, 27 May–30 June) and social mobility (SMP, 1 July–31 August) periods of fawn behavior (Ozoga and Verme 1982, Duquette et al. 2014b, Petroelje et al. 2014). We identified and visited ≥ 20 random sites in each land cover during each period and year (2013–2015) to assess horizontal cover. We estimated horizontal cover at each site using the cover cylinder method, modified from Ordiz et al. (2009). At each site, we placed a fabric vegetation profile board (Nudds 1977; 120 cm high by 60 cm across) and measured the minimum sighting distance (*D*; the minimum distance at which the board can no longer be seen) at a height of 80 cm to better approximate eye height of black bear, bobcat, coyotes, and wolves (T.R. Petroelje, unpublished data) in the four cardinal directions (Ordiz et al. 2009). We calculated the mean horizontal cover value of the four cardinal direction values for each site, then averaged these values for each land cover class during each time period and generated a grid with 30 x 30 m cells equal in size to the NLCD to apply respective values.

Forage availability

To estimate available forage for deer we used the same sites sampled for horizontal cover analysis. We sampled plant species that deer in Wisconsin and Michigan select for forage (Table 3.2; McCaffery et al. 1974, Stormer and Bauer 1980) during spring and summer. At each site, we established a 2 x 2 m quadrat at the center and another 10 m away in each cardinal direction, for a total of 5 quadrats. Within each quadrat, we collected, dried, and weighed all current year's growth on select woody plants (Table 3.2) rooted within the quadrat and exhibiting browsing vegetation (leaves and fleshy shoots) below 2 m. Additionally, within each quadrat, we established a 0.5 x 1 m plot in a randomly selected corner and collected, dried, and weighed all green leaves and fleshy stems of select herbaceous plants (Table 3.2; Jones et al. 2010). We air dried samples in paper bags for one week, then dried samples in a forced-air oven at 60°C to remove remaining moisture before weighing 48 hours later. We used these weights as multipliers to estimate dry weight of available forage (from trees, shrubs, and herbaceous plants) per square meter for each land cover and applied respective values to the same 30 x 30 m grid used for horizontal cover.

Linear features

We used the 30 x 30 m grid generated for horizontal cover and forage estimates to measure the distance from the center of each grid cell to the nearest road (Michigan Geographic Framework, All roads dataset, http://gis.michigan.opendata.arcgis.com/datasets/d666111d1a7a4231b9bd410f1e7e883c_7) or hydrologic feature (Michigan Geographic Framework, National Hydrology Dataset, http://gis.michigan.opendata.arcgis.com/datasets?q=Hydro&sort_by=relevance).

Adult female and fawn deer occurrence

We used previously developed models of adult female white-tailed deer occurrence (see Petroelje et al. 2021) and applied the population-level predicted probability of occurrence to the grid of 30- x 30-m cells used for landscape and vegetation characteristics. We scaled adult female deer occurrence for each cell from 0 to 1, where greater values indicate greater likelihood of occurrence (Duquette et al. 2014b). Adult female deer occurrence was inversely related to distance to nearest road and to water and developed land covers relative to deciduous forests (Petroelje et al. 2021).

Predator occurrence

We used predator-specific spatial models to assess occurrence within the study area during LMP and SMP for black bears, bobcats, coyotes, and wolves. For each predator, we used a Design III approach to estimate population-level occurrence from individual occurrence distributions (Marzluff et al. 2004, Thomas and Taylor 2006, Svoboda et al. 2019). To define individual predator occurrence distributions (OD), we used previously collected global positioning system (GPS) and accelerometer data from predators (15 black bears, 6 bobcats, 13 coyotes, and 11 wolves) which were collared in our study area during May–August 2013–2015 with a 15-min relocation interval (see Petroelje et al. 2020). We subset all GPS data to include only active GPS locations as indicated by accelerometer values greater than 35.9, 36.8, 30.7, and 30.7 for black bear, bobcat, coyote, and wolf, respectively (Petroelje et al. 2020). We generated 99% ODs for each collared individual using dynamic Brownian bridge movement models (function dBBMM; Kranstauber et al. 2017) within the package ‘move’ for R (version 3.01, R Development Core Team 2018) across the same 30 x 30 m grid used for vegetation characteristics.

We estimated population-level occurrence for each predator species and time period (i.e., LMP or SMP) using resource utilization functions (RUF; Marzluff et al. 2004) to regress OD on nine covariates that describe prey availability, landscape heterogeneity, and linear features. For prey availability we included ruffed grouse density, snowshoe hare density, and adult female and fawn white-tailed deer occurrence (see Petroelje et al. 2021) within each grid cell. We used the 2011 NLCD as categorical assignment of land cover type for each grid cell and to calculate landscape metrics including distance to land cover edge and land cover patch size available to predators. We combined land covers into the same classes used to define vegetation characteristics (Table S1). We also included the landscape features distance to road and water for each grid cell. For each predator, we calculated standardized mean parameter estimates and population-level variance across individuals during each time period (Petroelje et al. 2021). We then used model parameter coefficients to develop a probability of occurrence map for each predator species for LMP and SMP. We scaled parameter coefficient values into the model equation for each grid cell, masked each predator grid to the extent used by adult female and fawn deer, and scaled the resulting probabilities from 0 to 1 (Svoboda et al. 2019).

We used k-fold cross validation to assess model fit of predator-specific occurrence from each species population-level RUF. For each fold, we withheld one individual (observed) from the population-level RUF (predicted) and binned spatially overlapping OD and RUF values into eight groups with equal numbers of cells in each bin. We then regressed the sum of the OD values against the sum of the RUF values for each bin and calculated the coefficient of determination (R^2) and the slope of the relationship (Petroelje et al. 2021). Finally, we averaged R^2 and slope across all individuals for each predator species to assess overall model fit as indicated by a high R^2 and a positive slope (Long et al. 2009).

Predation Risk

We used fawn predation sites (*n* = 100; Figure 3.1) identified by tracking radio-collared individuals (*n* = 32; see Kautz et al. 2019) or identified at predator GPS cluster sites (*n* = 68; see Petroelje et al. 2020) during 27 May–31 August 2013–2015. To limit the area of inference, we used a 100% fixed kernel estimator to calculate a polygon encompassing all fawn predation sites. For each predation site we generated 20 random locations within the fixed kernel polygon and used conditional logistic regression in R (R Core Team 2019) within package survival (Therneau 2013) to estimate the influence of covariates on fawn predation risk (Kauffman et al. 2007). Before fitting models, we tested all covariates for multicollinearity ($|r| > 0.70$) and excluded those highly related. We assessed all combinations of 4 model sets which included landscape features (roads and hydrography), vegetation characteristics (i.e., horizontal cover and forage availability), active predator-specific occurrence, or adult female deer occurrence to identify their influence on predator-specific predation risk. We used Akaike Information Criterion for small samples (AICc) to assess the relative influence of each model and selected the model with the lowest AICc as the best supported (Burnham and Anderson 2002). We evaluated the influence of individual covariates and their relationship at $\alpha = 0.1$ given our sample size was < 30 fawn predations for each predator. We used GME to create a grid of 30 x 30 m cells (equal to the spatial scale of the National Land Cover Database) with the same dimensions as used for identifying fawn kill sites and applied coefficients from the top-ranked model to the grid to assess species-specific predation risk. For each predator species we calculated the proportion of the landscape predicted as risky as defined by being above the relative mean predation risk (i.e., 1).

We then calculated two measures of composite predation risk (CPR) after applying a linear stretch for each predator-specific raster between 0 and 1. First, we summed all species-specific predation risk rasters and applied a linear stretch. Second, we summed density-weighted species-specific rasters and applied a linear stretch. To quantify the relationship between CPR and density-weighted CPR, we binned spatially overlapping values into eight groups with equal numbers of cells in each bin and regressed the sum of the CPR values against the sum of the density-weighted CPR values for each bin. We then calculated the R^2 and the slope of the relationship.

Results

We conducted 598 vegetation surveys, 262 during LMP and 336 during SMP. Horizontal cover was least (i.e., minimum sighting distance was the greatest) in deciduous forests (23.5 m, SD = 12.4 m) and herbaceous wetlands (23.3 m, SD = 18.8 m) during LMP and SMP and greatest in woody wetlands (16.6 m, SD = 6.9 m) in LMP and woody wetlands (15.5 m, SD = 7.5 m), mixed forests (14.9 m, SD = 9.1 m), and grassland/herbaceous (15.9 m, SD = 7.0 m) land covers during SMP (Table 3.3). Available forage was greatest in grassland/herbaceous land cover during LMP (14.2 ± 8.3 [SD] g/m^2) and SMP (27.0 ± 15.2 [SD] g/m^2) and least in evergreen forests (5.0 ± 4.4 [SD] g/m^2) during LMP and evergreen (7.0 ± 8.1 [SD] g/m^2) and mixed (7.0 ± 6.3 [SD] g/m^2) forests during SMP. Mean distance to nearest road and hydrography was 847.8 m (SD = 731.9 m) and 411.0 m (SD = 343.3 m), respectively.

Overall, black bear occurrence increased with shrub/herbaceous land cover relative to deciduous land cover (the most common land cover, 38% of the landscape) during LMP ($\bar{x}(\beta) = 0.16$, $P < 0.00$) and SMP ($\bar{x}(\beta) = 0.32$, $P < 0.00$; Table 3.4). Bobcat occurrence decreased with distance to water during LMP ($\bar{x}(\beta) = -0.07$, $P = 0.03$) and SMP ($\bar{x}(\beta) = -0.08$, $P = 0.04$). Coyote occurrence was greater in mixed forests ($\bar{x}(\beta) = 0.11$, $P < 0.00$) during LMP relative to deciduous land cover. Wolf occurrence increased with greater snowshoe hare densities ($\bar{x}(\beta) = 0.03$, $P = 0.03$) during LMP and decreased with distance to edge ($\bar{x}(\beta) = -0.02$, $P < 0.00$) in LMP and distance to roads ($\bar{x}(\beta) = -0.06$, $P = 0.01$) in SMP (Table 3.4). R^2 estimate using k-fold cross validation ranged from 0.32 to 0.64 and all but one population-level slope (coyote occurrence during SMP) had a positive relationship (Table 3.5).

Sixty fawn predation sites were identified during LMP and 40 during SMP, which included 22 bear, 21 bobcat, 28 coyote, and 29 wolf predations. Black bear, coyote, and wolf predation risk were best described by habitat characteristics with adult female and predator-specific occurrence also influencing predation risk of coyotes. Bobcat predation risk was best described by adult female deer and bobcat occurrence receiving 45% of the AICc weight with only one other competing model < 2 AICc from the top model (Table S6). The linear feature model (distance to roads and hydrography) received the least support across species (Table 3.6). Best supported model estimates of black bear predation risk indicated a trend of positive effects of habitat characteristics on risk though neither covariate had a significant relationship with risk (Table 3.7). Predation risk from bobcats increased with adult female occurrence ($\beta = 2.81$, SE = 0.30, $P < 0.00$) and bobcat occurrence ($\beta = 1.91$, SE = 0.31, $P = 0.04$). Predation risk from coyotes increased in areas with lesser horizontal cover (i.e., further sighting distance; $\beta = 1.63$, SE = 0.26, $P = 0.06$), and greater coyote occurrence ($\beta = 1.69$, SE = 0.26, $P = 0.04$) and adult female occurrence ($\beta = 1.44$, SE = 0.20, $P = 0.07$). Predation risk from wolves increased with greater deer forage availability ($\beta = 1.33$, SE = 0.15, $P = 0.05$). Proportion of landscape predicted as risky (i.e., having an estimated risk >1) was 47% for black bears, 5% for bobcats, 3% for coyotes, and 44% for wolves (Figure 3.2). Spatial patterns in CPR were similar for areas of greatest individual species risk though the magnitude varied when relative density was considered (Figure 3.3). However, the relationship explained 69% of the observed spatial variation between the predicted CPR and density-weighted CPR maps (Figure 3.4).

Discussion

No single factor best described predation risk across predator species; the number and type of metrics influencing risk varied considerably as found in other multi-predator systems (Thaker et al. 2011, Lone et al. 2014, Norum et al. 2015, Kohl et al. 2020). The observed spatial variation in predator-specific predation risk for fawns was most influenced by adult female deer and bobcat occurrence for bobcats which differed from the importance of habitat characteristics in describing predation risk for black bears, coyotes, and wolves. The contrast between predation risk from ambush and cursorial predators manifested as a 15-fold difference among these species in the proportion of area predicted as risky.

The importance of habitat characteristics in describing predation risk for black bears, coyotes, and wolves supports the role of greater horizontal cover providing concealment and greater habitat complexity providing refugia. For example, predation of white-tailed deer fawns by coyotes was greater in areas with fewer cover types and less edge habitat (Gulsby et al. 2017), and weak support has been found between fawn survival and available cover (Chitwood et al. 2015), which suggests that scale of habitat complexity may also be important. Though habitat characteristics best described predation risk for black bears, no significant trends were observed for either covariate though effect sizes were similar to coyotes and wolves. However, greater cover may not reduce predation risk from opportunistic predators of neonate ungulates (Bastille-Rousseau et al. 2011). Observed increased predation risk from wolves in areas with greater deer forage availability supports observations of female caribou (*Rangifer tarandus*) with calves that avoided increased risk from wolves in part through reduced selection of greater forage as compared to females without calves (Viejou et al. 2018). Interestingly, horizontal cover was not important for describing bobcat predation risk though more open habitats may reduce risk from ambush predators (Lone et al. 2014, Moll et al. 2016).

Adult female deer occurrence was the most influential factor describing bobcat predation risk in contrast with the other three predators, potentially due to bobcats using an ambush hunting strategy (Wikenros et al. 2015). In addition, predation risk from bobcats increased with their occurrence which may be why ambush hunting strategies can elicit greater risk effects from prey (Preisser et al 2007, Thaker et al. 2011). Though greater predator occurrence is often thought to increase predation risk, we observed mixed support of predator occurrence where bobcat and coyote occurrence increased predation risk but not black bear or wolf occurrence. The observed importance of predator occurrence in wolf-elk and multi-predator/prey systems

(Ripple et al. 2001, Thaker et al. 2011) may be explained by the interpretation of predation risk such that predator occurrence may influence risk effects but may not directly reflect true predation risk. Alternatively, predator-prey encounter rates and predation risk for prey exhibiting herding behavior (e.g., elk; Kauffman et al. 2007) may be more similar than encounter rates and predation risk for prey such as white-tailed deer, which are habitat generalists and maintain independent home ranges. However, predator occurrence may share no relationship or even a negative relationship with prey occurrence (Svoboda et al. 2019) and as others have suggested (Prugh et al. 2019) predator occurrence alone may not be an appropriate measure of risk. For example, though wolf and fawn deer occurrence were inversely associated with distance to roads (Petroelje et al. 2021), linear features were not important in describing predation risk from wolves and further, roads and developed land covers appeared to offer refuge to fawns relative to the mean predation risk. That predator occurrence was not included in all predators' top models and was never the only factor in any predators' top model, highlights the challenges with using predator occurrence as a proxy for true predation risk.

Distance to linear features were not supported for describing predation risk of any predator even though roads were important for describing adult female and fawn deer occurrence (Petroelje et al. 2021). Though linear features including roads may serve as refugia to some prey through decreased probability of encountering wolves (Theuerkauf and Rouys 2008, Gurarie et al. 2011, Muhly et al. 2011), we observed greater wolf occurrence near roads (Table S4) which may increase encounter rates with prey (Whittington et al. 2011) and result in greater mortality risk (Lendrum et al. 2018). However, roads may serve as both refugia for prey and travel corridors for predators if diel activity differs between deer and predators (Higdon et al. 2019, Crawford et al. 2021, Kautz 2021). Alternatively, the lack of effect of roads on predation despite greater encounter rates by wolves suggests encounter rates alone may be poor metrics for true predation risk. As bobcat predation risk was best described by adult female deer occurrence (which was greatly influenced by roads), probabilistic predation risk was greater near roads. However, when accounting for density in composite predation risk, roads might provide refuge for fawns given bobcats lesser density relative to black bears and coyotes (Kautz et al. 2019). Though bobcats use linear features including riparian habitats (Woolf et al. 2002, Koehler 2006), distance to hydrography was not influential for describing predation risk.

Much of our understanding of ungulate predation risk comes from wolf-ungulate studies (Moll et al. 2017) but if we had only used wolves to describe predation risk, their lesser density and contrasting spatial risk with bobcats would not have encompassed much of the composite predation risk. Despite lesser per-individual kill rates, coyotes and black bears in our study contributed most to fawn mortality due to their 9-fold greater abundance (Kautz et al. 2019) which contributed to their disproportionate influence on composite risk when considering density. Though bobcat and wolf densities were similar, we estimated a greater proportion of the landscape as risky (44% vs 5%) for wolves, yet both species contributed similar proportion of fawn mortality (Kautz et al. 2019). However, CPR explained 69% of the spatial variation of density-weighted composite predation risk likely due to habitat characteristics best describing predation risk and being similar in direction and magnitude for three of the four predators.

Though the limited number of fawn predations sites we identified likely reduced our ability to infer patterns, observed variation among covariates influencing predator-specific risk suggests use of a single predator to describe predation risk would be inappropriate for this multi-predator system. We considered activity of predators with respect to occurrence and predation risk but lacked information about the diel cycle or activity of adult female and fawn deer.

Investigating when prey are killed with respect to their spatial occurrence in concert with multi-predator risk (Kohl et al. 2020) may further elucidate spatio-temporal variation in predation risk. Identification of risky times also may clarify the role of linear features including roads serving as refugia (Kautz 2021) and may inform how risk effects and predation risk are associated, and if prey can accurately assess true predation risk for individual or multiple predators.

Predation risk for prey in multi-predator systems is complex and predator occurrence or habitat characteristics alone were not appropriate for describing risk across species. Instead of using measures of predator presence or habitat characteristics as assumed correlates of predation risk, we recommend defining predation risk using kill sites of prey where predator occurrence and habitat characteristics explain the observed spatial variability in kill sites. By accounting for predator-specific risk of predation, we identified differing landscapes of risk for the same prey, which suggests prey manage risks among predators simultaneously. Much of the variability in composite predation risk may be described without accounting for predator density, but when relative contribution of each predator to total mortality is unknown density may be important to consider. In addition, our results support previous studies that suggest ambush foraging strategies may impart divergent patterns of predation risk (Moll et al. 2016, Makin et al. 2017, Kohl et al. 2020) as compared to coursing or opportunistic predators and should be considered when present. In multi-predator systems, we suggest considering composite predation risk adjusted for predator-specific density to better describe true predation risk and the role it may play in shaping prey distributions.

Table 3.1 Land cover designations modified from the national land cover data base with percent land cover within study area

Land cover	Definition of designation	Cover (%)
Deciduous forest	Areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. More than 75% of the tree species shed foliage simultaneously in response to seasonal change. Aspen (*Populus tremuloides* or *P. grandidentata*) represents dominant cover for 12% of deciduous forests within the study area (Ellenwood et al. 2015).	43
Woody or emergent herbaceous wetland	Areas where forest or shrub land vegetation accounts for greater than 20% of vegetative cover and the soil or substrate is periodically saturated with or covered with water. Areas where perennial herbaceous vegetation accounts for greater than 80% of vegetative cover and the soil or substrate is periodically saturated with or covered with water.	29
Mixed forest	Areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. Neither deciduous nor evergreen species are greater than 75% of total tree cover.	10
Evergreen forest	Areas dominated by trees generally greater than 5 meters tall, and greater than 20% of total vegetation cover. More than 75% of the tree species maintain their leaves all year. Canopy is never without green foliage.	6
Grassland/herbaceous/shrub/scrub	Areas dominated by grammanoid or herbaceous vegetation, generally greater than 80% of total vegetation. Not subject to intensive management such as tilling but can be utilized for grazing. Areas dominated by shrubs; less than 5 meters tall with shrub canopy typically greater than 20% of total vegetation. Includes true shrubs, young trees in an early successional stage or trees stunted from environmental conditions.	5
Open water	Areas of open water, generally with less than 25% cover or vegetation or soil.	4
Developed (i.e., urban, pasture, agriculture)	All other areas modified by agriculture or developed land use practices such as farmed row crops, pastures, roads, and structures.	3

Extracted from Jin et al. (2013), Upper Peninsula of Michigan, USA, 2011

Table 3.2 List of plant species selected by white-tailed deer for forage and sampled or collected at vegetation survey sites

Taxa	Common names
Corylus cornuta	Beaked hazelnut
Poaceae	Grasses
Salix spp.	Willows
Betula papyrifera	Paper birch
Acer sp.	Maples
Diervilla sp.	Bush honeysuckles
Asteraceae	Asters
Populus spp.	Aspen
Prunus sp.	Cherries
Waldsteinia fragarioides	Barren strawberry
Rubus sp.	Blackberries/raspberries
Pteridium aquilinum	Bracken fern
Maianthemum canadense	False lily of the valley
Calystegia sepium	Hedge bindweed
Cyperaceae	Sedges
Gaultheria procumbens	Wintergreen
Trifolium sp.	Clovers

Preferred forage determined by McCaffery et al. (1974) and Stormer and Bauer (1980), Upper Peninsula of Michigan, USA, 2013–2015

Table 3.3 Mean horizontal cover and available forage for white-tailed deer

Land cover	Horizontal cover (*D*)				Forage (g)			
	LMP		SMP		LMP		SMP	
	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Deciduous forest	23.5	12.4	23.7	12.9	7.4	7.2	6.9	7.0
Evergreen forest	20.6	8.1	20.9	9.5	5.0	4.4	7.0	8.1
Grassland/ herbaceous	21.2	8.5	15.9	7.0	14.2	8.3	27.0	15.2
Herbaceous wetland	23.3	18.8	28.5	18.6	6.5	9.5	6.9	9.3
Mixed forest	19.1	6.7	14.9	9.1	6.1	4.9	7.0	6.3
Woody wetland	16.6	6.9	15.5	7.5	6.1	7.8	10.5	14.2

Horizontal cover estimated using minimum sighting distance (*D*) and available forage by dried vegetation weight with standard deviations (SD) by land cover class (Jin et al. 2013) during 27 May–30 June (LMP) and 1 July–31 August (SMP), Upper Peninsula of Michigan, USA, 2013–2015

Table 3.4 Mean standardized coefficients, $\bar{x}(\beta)$, of population-level resource utilization functions (RUF) for black bears, bobcats, coyotes, and wolves

Species	Covariate	Time period							
		LMP				SMP			
		n	$x(\beta)$	95% CI	P(β = 0)	*n*	$x(\beta)$	95% CI	P(β = 0)
Black bear	Intercept	29	-0.031	-0.243 – 0.182	0.771	28	0.017	-0.074 – 0.109	0.701
	Distance to edge	29	-0.036	-0.094 – 0.022	0.215	28	-0.060	-0.098 – -0.022	0.003*
	Hare density	29	-0.025	-0.052 – 0.002	0.071	28	-0.008	-0.040 – 0.025	0.627
	Grouse density	29	-0.079	-0.250 – 0.092	0.351	28	-0.030	-0.136 – 0.075	0.559
	Distance to water	29	-0.013	-0.087 – 0.060	0.712	28	-0.009	-0.104 – 0.087	0.857
	Patch size	29	0.076	-0.068 – 0.220	0.291	28	-0.037	-0.092 – 0.018	0.180
	Deer occurrence	29	-0.059	-0.165 – 0.046	0.260	28	0.032	-0.122 – 0.186	0.670
	Water	25	-0.199	-0.288 – -0.110	0.000*	28	-0.211	-0.405 – -0.016	0.035*
	Developed	29	0.124	-0.091 – 0.339	0.247	28	-0.110	-0.222 – 0.003	0.055
	Evergreen forest	29	-0.021	-0.113 – 0.071	0.643	28	-0.015	-0.142 – 0.111	0.806
	Mixed forest	29	0.052	-0.047 – 0.152	0.290	28	0.031	-0.028 – 0.090	0.296
	Shrub/herbaceous	29	0.162	0.061 – 0.263	0.003*	28	0.323	0.180 – 0.465	0.000*
	Wetland	29	-0.011	-0.124 – 0.103	0.851	28	0.041	-0.035 – 0.117	0.278

Number of individuals for each predator (*n*) with each respective coefficient in the individual RUF top model during two time periods related to white-tailed deer: fawn limited mobility period (LMP, 27 May–30 June), and fawn social mobility period (SMP, 1 July–31 August), Upper Peninsula of Michigan, USA, 2013–2015. Also included are 95% confidence intervals (CI), and probability of the null hypothesis $\beta = 0$ with significant effects (*)

Table 3.4 (continued)

Species	Covariate	Time period							
		LMP				SMP			
		n	x(*β*)	95% CI	P(*β* = 0)	*n*	x(*β*)	95% CI	P(*β* = 0)
Bobcat	Intercept	6	-0.027	-0.083 – 0.028	0.257	6	0.056	-0.092 – 0.205	0.374
	Distance to edge	6	-0.013	-0.045 – 0.019	0.347	6	-0.034	-0.075 – 0.006	0.080
	Hare density	6	0.008	-0.031 – 0.046	0.634	6	-0.011	-0.076 – 0.054	0.680
	Grouse density	6	0.003	-0.070 – 0.075	0.931	6	0.059	-0.105 – 0.222	0.399
	Distance to water	6	-0.069	-0.129 – -0.008	0.033*	6	-0.084	-0.165 – -0.003	0.044*
	Patch size	6	-0.008	-0.064 – 0.049	0.741	6	-0.056	-0.117 – 0.005	0.064
	Deer occurrence	6	-0.040	-0.151 – 0.071	0.398	6	-0.014	-0.080 – 0.052	0.616
	Water	6	-0.050	-0.196 – 0.096	0.419	6	-0.144	-0.220 – -0.068	0.005*
	Developed	6	-0.012	-0.049 – 0.025	0.443	6	-0.038	-0.118 – 0.041	0.270
	Evergreen forest	6	0.061	-0.010 – 0.133	0.079	6	0.055	-0.028 – 0.139	0.150
	Mixed forest	6	0.031	-0.001 – 0.064	0.055	6	0.087	-0.054 – 0.227	0.174
	Shrub/herbaceous	6	0.040	-0.086 – 0.167	0.452	6	0.081	-0.058 – 0.220	0.194
	Wetland	6	0.109	-0.028 – 0.245	0.097	6	0.112	-0.001 – 0.225	0.052

Number of individuals for each predator (*n*) with each respective coefficient in the individual RUF top model during two time periods related to white-tailed deer: fawn limited mobility period (LMP, 27 May–30 June), and fawn social mobility period (SMP, 1 July–31 August), Upper Peninsula of Michigan, USA, 2013–2015. Also included are 95% confidence intervals (CI), and probability of the null hypothesis *β* = 0 with significant effects (*)

Table 3.4 (continued)

Species	Covariate	Time period							
		LMP				SMP			
		n	x(β)	95% CI	P(β = 0)	*n*	x(β)	95% CI	P(β = 0)
Coyote	Intercept	13	-0.036	-0.172 – 0.099	0.568	13	0.219	-0.472 – 0.910	0.502
	Distance to edge	13	-0.041	-0.082 – 0.001	0.053	13	0.008	-0.057 – 0.072	0.795
	Hare density	13	-0.018	-0.090 – 0.055	0.599	13	-0.015	-0.072 – 0.041	0.567
	Grouse density	13	0.060	-0.078 – 0.198	0.360	13	0.247	-0.455 – 0.949	0.458
	Wolf occurrence	13	0.019	-0.090 – 0.127	0.716	13	0.045	-0.405 – 0.495	0.831
	Deer occurrence	13	0.023	-0.091 – 0.136	0.672	13	-0.042	-1.358 – 1.274	0.946
	Distance to water	13	-0.037	-0.134 – 0.060	0.420	NA	NA	NA	NA
	Patch size	NA	NA	NA	NA	13	-0.047	-0.976 – 0.883	0.915
	Distance to road	NA	NA	NA	NA	13	-0.060	-1.327 – 1.206	0.919
	Water	13	-0.116	-0.245 – 0.013	0.073	13	-0.101	-1.737 – 1.535	0.895
	Developed	13	0.147	-0.001 – 0.295	0.051	13	0.163	-0.303 – 0.630	0.459
	Evergreen forest	13	0.154	-0.001 – 0.309	0.052	13	0.105	-0.040 – 0.249	0.140
	Mixed forest	13	0.106	0.051 – 0.161	0.001*	13	0.054	-0.063 – 0.171	0.336
	Shrub/herbaceous	13	0.113	-0.101 – 0.327	0.271	13	0.175	-0.151 – 0.500	0.264
	Wetland	13	0.134	-0.007 – 0.275	0.060	13	0.107	-0.224 – 0.438	0.494

Number of individuals for each predator (*n*) with each respective coefficient in the individual RUF top model during two time periods related to white-tailed deer: fawn limited mobility period (LMP, 27 May–30 June), and fawn social mobility period (SMP, 1 July–31 August), Upper Peninsula of Michigan, USA, 2013–2015. Also included are 95% confidence intervals (CI), and probability of the null hypothesis β = 0 with significant effects (*)

Table 3.4 (continued)

Species	Covariate	Time period							
		LMP				SMP			
		n	x(*β*)	95% CI	P(*β* = 0)	*n*	x(*β*)	95% CI	P(*β* = 0)
Wolf	Intercept	11	0.023	-0.056 – 0.101	0.530	11	0.083	-0.042 – 0.208	0.168
	Distance to road	11	-0.030	-0.101 – 0.042	0.383	11	-0.062	-0.107 – -0.017	0.012*
	Distance to water	11	-0.023	-0.062 – 0.016	0.219	11	-0.072	-0.175 – 0.032	0.155
	Distance to edge	11	-0.016	-0.025 – -0.007	0.003*	11	-0.004	-0.017 – 0.008	0.466
	Deer occurrence	11	0.011	-0.027 – 0.048	0.542	11	-0.034	-0.072 – 0.004	0.073
	Hare density	11	0.028	0.003 – 0.054	0.030*	11	0.003	-0.017 – 0.024	0.731
	Grouse density	11	0.026	-0.031 – 0.083	0.330	11	-0.006	-0.101 – 0.088	0.887
	Patch size	11	-0.024	-0.064 – 0.016	0.212	NA	NA	NA	NA
	Water	11	-0.059	-0.129 – 0.010	0.088	11	-0.205	-0.393 – -0.016	0.036*
	Developed	11	-0.026	-0.076 – 0.025	0.287	11	-0.029	-0.078 – 0.019	0.208
	Evergreen forest	11	0.076	-0.145 – 0.297	0.460	11	-0.004	-0.097 – 0.088	0.922
	Mixed forest	11	-0.021	-0.092 – 0.051	0.537	11	-0.028	-0.074 – 0.019	0.212
	Shrub/herbaceous	11	-0.008	-0.059 – 0.042	0.717	11	0.049	-0.035 – 0.133	0.224
	Wetland	11	-0.007	-0.053 – 0.039	0.730	11	0.022	-0.135 – 0.178	0.766

Number of individuals for each predator (*n*) with each respective coefficient in the individual RUF top model during two time periods related to white-tailed deer: fawn limited mobility period (LMP, 27 May–30 June), and fawn social mobility period (SMP, 1 July–31 August), Upper Peninsula of Michigan, USA, 2013–2015. Also included are 95% confidence intervals (CI), and probability of the null hypothesis *β* = 0 with significant effects (*)

Table 3.5 K-fold cross-validation results for resource utilization functions for black bears, bobcats, coyotes, and wolves

Species	Period	Slope	R^2	Positive slope	Negative slope	Significant positive	Significant negative
Black bears	LMP	9.86E-03	0.5	18	11	10	5
	SMP	7.80E-03	0.48	22	6	10	0
Bobcats	LMP	4.06E-03	0.61	5	1	4	1
	SMP	3.36E-03	0.64	6	0	5	0
Coyotes	LMP	1.43E−03	0.54	7	6	5	2
	SMP	−7.41E−05	0.32	4	9	2	1
Wolves	LMP	9.17E−03	0.62	10	1	8	0
	SMP	1.16E−02	0.39	8	3	4	0

Cross-validation results are shown during two time periods related to white-tailed deer: fawn limited mobility period (LMP, 27 May–30 June) and fawn social mobility period (SMP, 1 July–31 August), Upper Peninsula of Michigan, USA, 2013–2015

Table 3.6 Predator-specific model rankings for fawn predation risk

Species	Model	K	AICc	Δ AICc	AICc weight	LL
Black bear	Habitat characteristics	2	134.09	0.00	0.17	-65.03
	Adult female deer occurrence	1	134.76	0.67	0.12	-66.38
	Habitat characteristics + adult female deer occurrence	3	135.23	1.14	0.10	-64.59
	Linear features + adult female deer occurrence	3	135.28	1.19	0.09	-64.62
	Linear features + habitat characteristics + adult female deer occurrence	5	135.54	1.45	0.08	-62.71
	Predator occurrence	1	135.57	1.47	0.08	-66.78
	Habitat characteristics + predator occurrence	3	136.06	1.97	0.06	-65.00
	Adult female deer occurrence + predator occurrence	2	136.24	2.15	0.06	-66.11
	Linear features + habitat characteristics	4	136.54	2.45	0.05	-64.23
	Linear features	2	136.58	2.49	0.05	-66.28
	Habitat characteristics + adult female deer occurrence + predator occurrence	4	137.16	3.07	0.04	-64.54
	Linear features + adult female deer occurrence + predator occurrence	4	137.27	3.18	0.03	-64.59
	Linear features + habitat characteristics + adult female deer occurrence + predator occurrence	6	137.27	3.18	0.03	-62.54
	Linear features + habitat characteristics + predator occurrence	5	138.47	4.38	0.02	-64.17
	Linear features + predator occurrence	3	138.52	4.43	0.02	-66.23

Models were ranked using Akaike Information Criterion for small sample sizes (AICc), included are number of model parameters (K), the difference in model selection (Δ AICc) and log likelihood (LL) for each model. Upper Peninsula of Michigan, USA, 2013–2015

Table 3.6 (continued)

Species	Model	K	AICc	Δ AICc	AICc weight	LL
Bobcat	Adult female deer occurrence + predator occurrence	2	118.69	0.00	0.45	-57.33
	Linear features + adult female deer occurrence + predator occurrence	4	119.75	1.06	0.26	-55.83
	Adult female deer occurrence	1	121.69	3.00	0.10	-59.84
	Habitat characteristics + adult female deer occurrence + predator occurrence	4	122.32	3.63	0.07	-57.11
	Linear features + adult female deer occurrence	3	123.05	4.36	0.05	-58.50
	Linear features + habitat characteristics + adult female deer occurrence + predator occurrence	6	123.62	4.93	0.04	-55.71
	Habitat characteristics + adult female deer occurrence	3	125.65	6.96	0.01	-59.80
	Linear features + habitat characteristics + adult female deer occurrence	5	127.03	8.34	0.01	-58.45
	Predator occurrence	1	129.82	11.13	0.00	-63.91
	Habitat characteristics	2	130.77	12.08	0.00	-63.37
	Linear features	2	131.53	12.84	0.00	-63.75
	Habitat characteristics + predator occurrence	3	132.50	13.81	0.00	-63.22
	Linear features + predator occurrence	3	133.56	14.87	0.00	-63.75
	Linear features + habitat characteristics	4	134.27	15.58	0.00	-63.09
	Linear features + habitat characteristics + predator occurrence	5	136.27	17.58	0.00	-63.07

Models were ranked using Akaike Information Criterion for small sample sizes (AICc), included are number of model parameters (K), the difference in model selection (Δ AICc) and log likelihood (LL) for each model. Upper Peninsula of Michigan, USA, 2013–2015

Table 3.6 (continued)

Species	Model	K	AICc	Δ AICc	AICc weight	LL
Coyote	Habitat characteristics + adult female deer occurrence + predator occurrence	4	167.24	0.00	0.25	-79.59
	Habitat characteristics + predator occurrence	3	168.25	1.01	0.15	-81.10
	Habitat characteristics	2	169.04	1.79	0.10	-82.51
	Adult female deer occurrence + predator occurrence	2	169.15	1.91	0.10	-82.57
	Habitat characteristics + adult female deer occurrence	3	169.23	1.98	0.09	-81.59
	Adult female deer occurrence	1	170.30	3.06	0.05	-84.15
	Linear features + habitat characteristics	4	170.37	3.13	0.05	-81.15
	Predator occurrence	1	170.41	3.17	0.05	-84.20
	Linear features + habitat characteristics + predator occurrence	5	170.92	3.68	0.04	-80.41
	Linear features + habitat characteristics + adult female deer occurrence + predator occurrence	6	171.26	4.02	0.03	-79.56
	Linear features + habitat characteristics + adult female deer occurrence	5	171.93	4.69	0.02	-80.91
	Linear features	2	172.50	5.25	0.02	-84.24
	Linear features + adult female deer occurrence + predator occurrence	4	173.18	5.94	0.01	-82.56
	Linear features + predator occurrence	3	173.39	6.15	0.01	-83.68
	Linear features + adult female deer occurrence	3	173.65	6.41	0.01	-83.81

Models were ranked using Akaike Information Criterion for small sample sizes (AICc), included are number of model parameters (K), the difference in model selection (Δ AICc) and log likelihood (LL) for each model. Upper Peninsula of Michigan, USA, 2013–2015

Table 3.6 (continued)

Species	Model	K	AICc	Δ AICc	AICc weight	LL
Wolf	Habitat characteristics	2	176.81	0.00	0.20	-86.39
	Predator occurrence	1	178.02	1.21	0.11	-88.01
	Habitat characteristics + predator occurrence	3	178.13	1.32	0.10	-86.04
	Adult female deer occurrence	1	178.41	1.60	0.09	-88.20
	Habitat characteristics + adult female deer occurrence	3	178.75	1.95	0.08	-86.36
	Linear features + habitat characteristics	4	178.88	2.08	0.07	-85.41
	Linear features + habitat characteristics + adult female deer occurrence	5	178.90	2.09	0.07	-84.40
	Adult female deer occurrence + predator occurrence	2	179.60	2.80	0.05	-87.79
	Linear features	2	179.61	2.81	0.05	-87.80
	Habitat characteristics + adult female deer occurrence + predator occurrence	4	179.85	3.04	0.04	-85.89
	Linear features + adult female deer occurrence	3	179.88	3.07	0.04	-86.92
	Linear features + habitat characteristics + adult female deer occurrence + predator occurrence	6	180.91	4.11	0.03	-84.39
	Linear features + habitat characteristics + predator occurrence	5	180.92	4.11	0.03	-85.41
	Linear features + predator occurrence	3	181.56	4.75	0.02	-87.76
	Linear features + adult female deer occurrence + predator occurrence	4	181.73	4.92	0.02	-86.83

Models were ranked using Akaike Information Criterion for small sample sizes (AICc), included are number of model parameters (K), the difference in model selection (Δ AICc) and log likelihood (LL) for each model. Upper Peninsula of Michigan, USA, 2013–2015

Table 3.7 Top-model or model averaged covariate estimates of black bear, bobcat, coyote, and wolf predation risk for fawn white-tailed deer

Species	Covariate	Estimate	exp(Estimate)	Std. error	Z value	P
Black bear	Horizontal cover	0.47	1.60	0.31	1.52	0.13
	Forage	0.17	1.18	0.21	0.79	0.43
Bobcat	Bobcat occurrence	0.65	1.91	0.31	2.10	0.04
	Doe occurrence	1.03	2.81	0.30	3.45	0.00
Coyote	Horizontal cover	0.49	1.63	0.26	1.88	0.06
	Forage	0.20	1.22	0.17	1.14	0.25
	Coyote occurrence	0.53	1.69	0.26	2.01	0.04
	Doe occurrence	0.36	1.44	0.20	1.80	0.07
Wolf	Horizontal cover	0.15	1.16	0.21	0.71	0.48
	Forage	0.29	1.33	0.15	1.92	0.05

Impact of covariates were estimated using conditional logistic regression, Upper Peninsula of Michigan, USA, 2013–2015

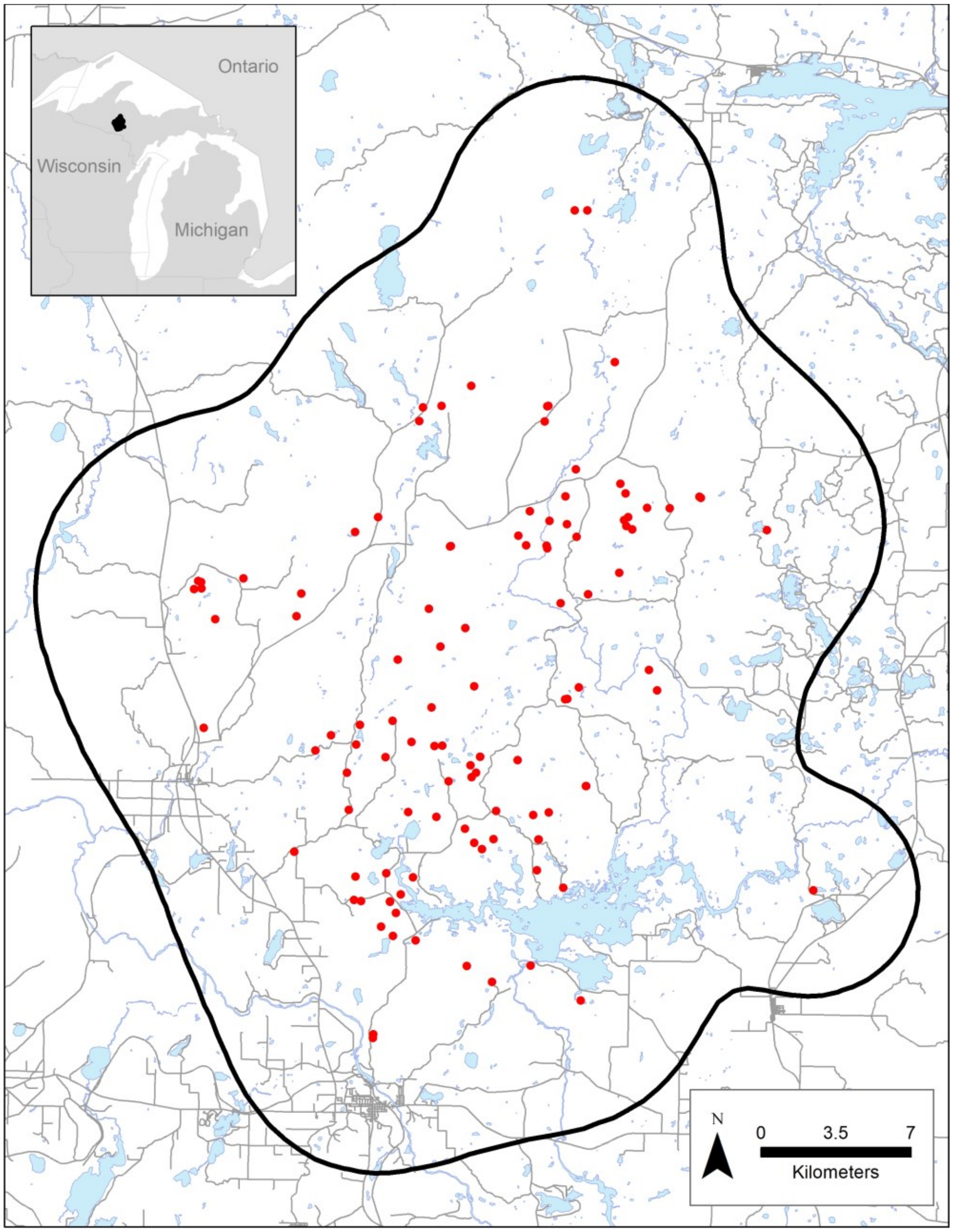

Figure 3.1 Locations of fawn white-tailed deer predations (*n* = 100) encompassed by a fixed kernel polygon defining the study area

Also shown are roads (gray lines) and water bodies (blue polygons) with inset showing study area location (black polygon) relative to Ontario, Canada and Wisconsin and Michigan, USA. Upper Peninsula of Michigan, USA, 2013–2015

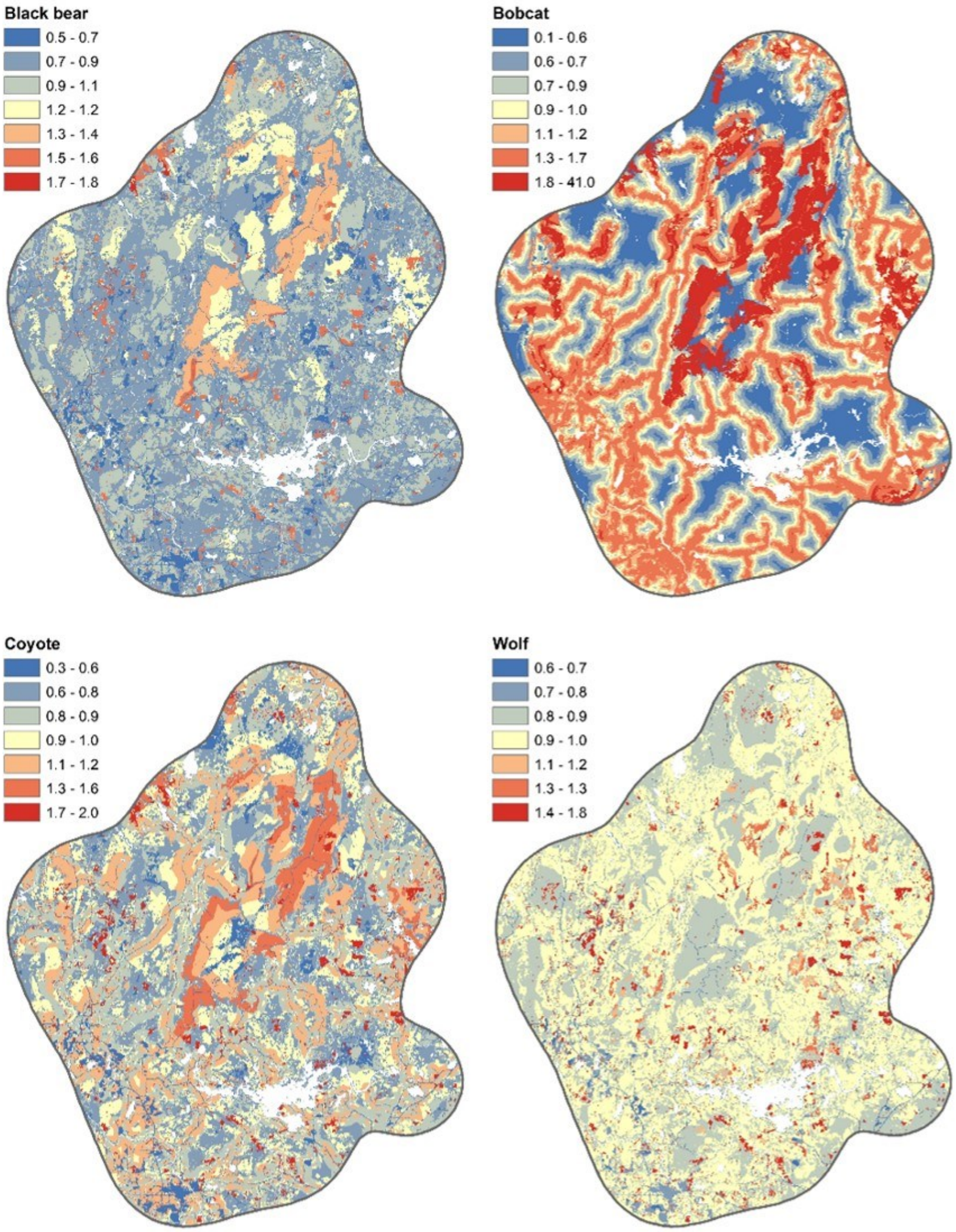

Figure 3.2 Predicted predator-specific predation risk using the top model or model averaged parameter estimates when appropriate

Values indicate relative predation risk as compared to mean predation risk (i.e., 1). Upper Peninsula of Michigan, USA, 2013–2015

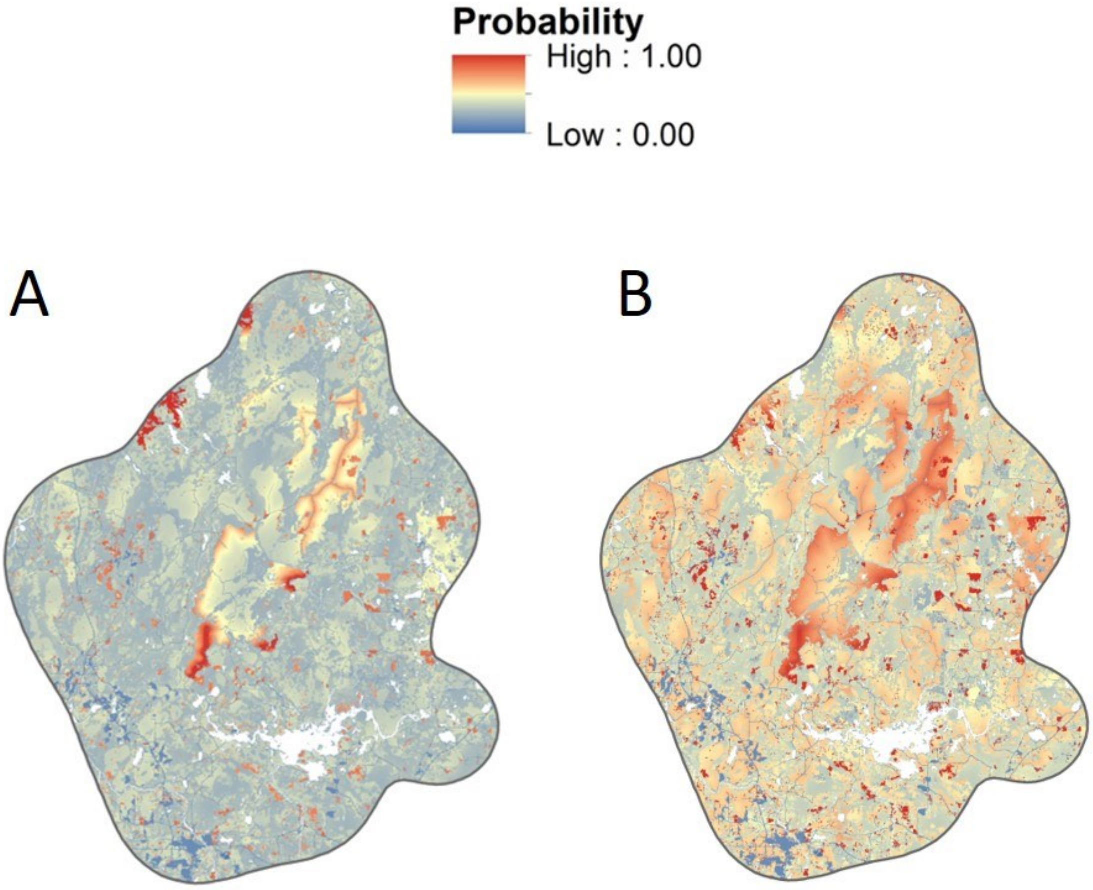

Figure 3.3 Composite predation risk with and without accounting for predator density

Scaled predictions of (i.e., summed risk of black bears, bobcats, coyotes, and wolves; A) and density-weighted composite predation risk (B). Upper Peninsula of Michigan, USA, 2013–2015

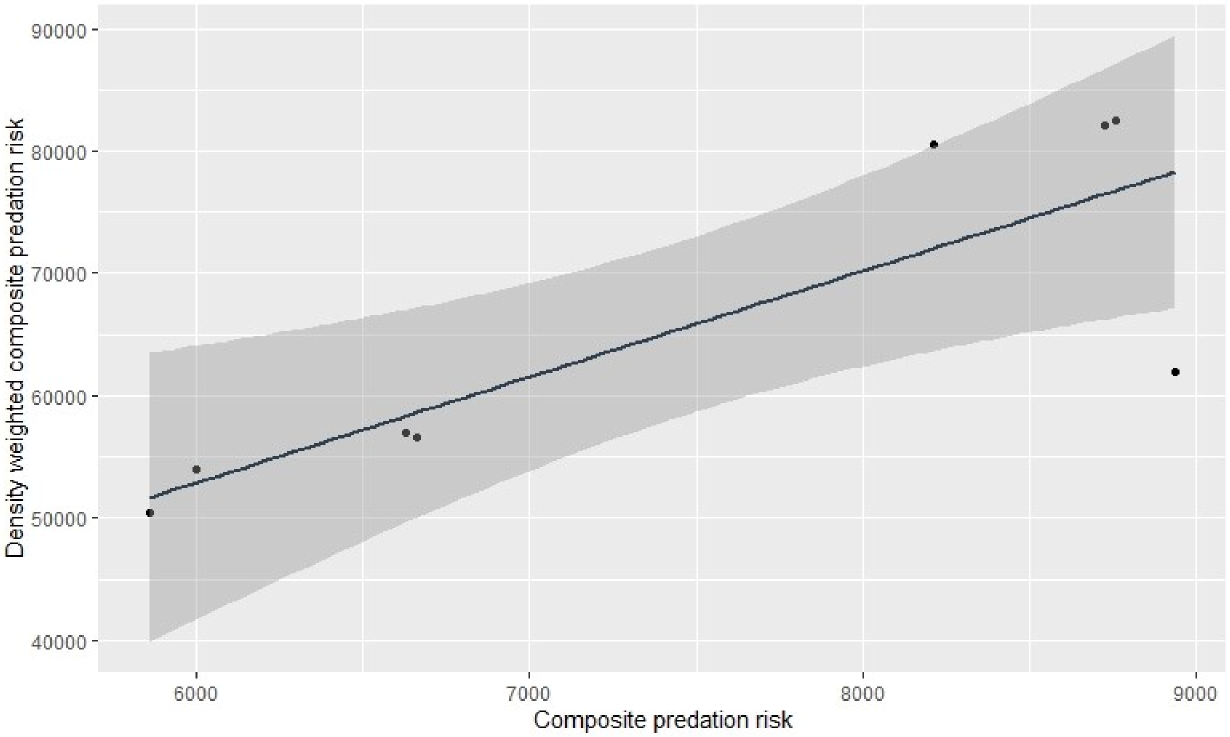

Figure 3.4 Regression to describe the relationship between composite predation risk and density-weighted composite predation risk

Relative contribution of composite predation risk to explain spatial variation of density weighted composite predation risk for describing non-ideal resource use for fawn white-tailed deer. The regression is across summed probabilities of paired raster observations within equally sized bins (*n* = 8). Upper Peninsula of Michigan, USA, 2013–2015

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APPENDIX A

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The work in Chapter I "Interference competition between wolves and coyotes during variable prey abundance" is attributed to Tyler R. Petroelje, Todd M. Kautz, Dean E. Beyer, Jr., and Jerrold L. Belant and is reprinted and modified from its original form first published in Ecology and Evolution, https://doi.org/10.1002/ece3.7153.