



Wolf spatial behavior promotes encounters and kills of abundant prey

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Abstract

Predators use different spatial tactics to track the prey on the landscape. Three hypotheses describe spatial tactics: prey abundance for prey that are aggregated in space; prey habitat for uniformly distributed prey; and prey catchability for prey that are difficult to catch and kill. The gray wolf (*Canis lupus*) is a generalist predator that likely employs more than one spatial hunting tactic to match their diverse prey with distinct distributions and behavior that are available. We conducted a study on 17 GPS collared wolves in 6 packs in Riding Mountain National Park, Manitoba, Canada where wolves prey on moose (*Alces alces*) and elk (*Cervus canadensis*). We evaluated wolf selection for prey density, habitat selection and catchability on the landscape through within-territory habitat selection analysis. We reveal support for both the *prey habitat* and *prey catchability* hypotheses. For moose, their primary prey, wolves employed a mixed habitat and catchability tactic. Wolves used spaces described by the intersection of moose habitat and moose catchability. Wolves selected for the catchability of elk, their secondary prey, but not elk habitat. Counter to our predictions, wolves avoided areas of moose and elk density, likely highlighting the ongoing space race between predator and prey. We illustrate that of the three hypotheses the primary driver was prey catchability, where the interplay of both prey habitat with catchability culminate in predator spatial behaviour in a multiprey system.

Keywords *Canis lupus* · *Alces alces* · *Cervus canadensis* · Predator–prey game · Prey abundance · Prey habitat · Prey catchability · Hunting strategy · Spatial dynamics · Habitat selection

Introduction

Habitat structure and resource distribution shape animal space use (Johnson et al. 2002; Bjørneraas et al. 2011; Fagan et al. 2013). In the context of a mobile consumer preying on a fixed resource, the consumer selects areas associated with increased resource availability (Jung et al. 2009; Street et al.

2015). In cases where mobile consumers prey on mobile resources, both affect each other's space use. For example, predators may use space such that it maximizes their access to prey (Kittle et al. 2017), whereas prey may adjust their behavior to avoid predation (Mitchell and Lima 2002; Creel et al. 2005; Kittle et al. 2008). Various hypotheses have been proposed to explain how predators track their prey, leading to encounters, and kills. Predators can exploit the relationship between encounter rates and prey density (Holling 1959, 1966) by selecting areas of higher prey abundance where prey are more aggregated, i.e., the prey abundance hypothesis (Weckel et al. 2006). Conversely, where prey are more evenly distributed on the landscape a suitable tactic is to search prey habitat to increase the probability of encounter, i.e., the prey habitat hypothesis (Williams and Flaxman 2012; Latham et al. 2013). Predators can further increase success rates by encountering and pursuing prey in areas that facilitate kills (Hebblewhite et al. 2005; Petrunenko et al. 2016), i.e., the prey catchability hypothesis (Davidson et al. 2012). Each hypothesis may describe processes in a

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The study occurred within a novel ecological event: wolves switched from primarily feeding on elk to moose. Our results illustrate the spatial trade-offs that predators resolve in multiprey.

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multi-prey system since predators may use one or more of the resulting tactics in concert (Kittle et al. 2017).

The relationship between prey abundance and distribution with predator behavior increases in complexity in systems with multiple prey. In multi-prey systems, the abundance of individual species may fluctuate. Changes in the most abundant prey may also precipitate changes in predator diet (Sillero-Zubiri and Gottelli 1995; Weckel et al. 2006; Garrett et al. 2007). Prey abundance is an essential component of the functional response, which describes an increase in the number of available prey items leading to higher kill rates (Dale et al. 1994; Zimmermann et al. 2015), likely through encounter rates. Indeed, random encounters between predator and prey are positively related to prey abundance. However, the influence of prey abundance on predator–prey dynamics is often assessed in single prey systems despite the ubiquity of generalist predators consuming multiple prey. In multi-prey systems, predators typically have a non-linear encounter relationship with prey abundance. Predators select for areas of high prey abundance when prey abundance reaches a threshold where encounters with prey are more consistent (Kittle et al. 2017). This abundance threshold may be influenced by the degree of aggregation of the prey (Huggard 1993). Therefore, when prey are neither aggregated nor abundant, predators may use alternative space use strategies to encounter prey.

When large groups of prey are absent, predators need alternate tactics for tracking smaller prey groups with lower detectability. The prey habitat hypothesis stipulates predators select preferred prey habitat instead of selecting prey abundance. Adhering to the prey habitat hypothesis should increase the likelihood predators encounter prey when prey abundance is low. There is evidence to support the prey habitat hypothesis in large mammalian predators that select for habitat types preferred by their prey species. For example, wolves selected for forest types are considered high-quality moose habitat (Lesmerises et al. 2012). Selecting high-quality prey habitat may be an outcome of remembering where prey species were previously encountered (Janson 1998; Regular et al. 2013). Therefore, it may be advantageous for predators to track prey using the prey habitat tactic when prey are less locally abundant and aggregated in space.

In the context of a multi-prey system, tracking resources through prey abundance and prey habitat quality may be simultaneously adopted by predators in response to differences in prey populations. Species that aggregate in space (Hammond et al. 2007) may elicit the prey abundance tactic, but species that are evenly distributed in space may lead predators to adopt the prey habitat tactic to maximize encounter rates. Generalist predators that target multiple prey species could simultaneously use different tactics. To this effect, few empirical studies have tested if multiple tactics are simultaneously employed by a predator in a

multi-prey system to increase encounter rates with different prey species (but see Kittle et al. 2017).

The presence of prey on the landscape is not necessarily equivalent to prey being accessible to predators. Prey species can select habitats that reduce their predation risk (Stein and Magnuson 1976; Rachlow and Bowyer 1998; Thaker et al. 2011) creating a landscape where prey catchability depends on underlying habitat features. The prey catchability hypothesis posits that predators will select habitats where prey are easier to kill (Davidson et al. 2012). Habitat where prey are less accessible to predators may be characterized by decreased visibility of prey (Balme et al. 2007) or more opportunities for prey to evade predators (Creel et al. 2005; Hebblewhite et al. 2005; Mao et al. 2005). Hunting in such habitats is energetically more costly due to increased efforts to catch prey and subsequently fewer kills (Andruskiw et al. 2008). The importance of using the prey catchability tactic may be amplified when there is an increased risk of injury or death for the predator during a predator–prey encounter (Mukherjee and Heithaus 2013). As a result, areas that are more frequently used by prey may be less valuable to predators if the prey are risky. The prey catchability hypothesis may, therefore, also explain predator space use driven by prey catchability on the landscape (Hopcraft et al. 2005).

Gray wolves (*Canis lupus*) are a generalist apex predator that employ a range of tactics to hunt in multi-prey systems; systems that often include prey species ranging from large ungulates to small rodents (Paquet 1992; Mech and Boitani 2003). Although wolves prey on multiple species within a system, they usually have a primary prey species that can change based on different factors. Prey switching is typically thought to be driven by the number of prey (Sand et al. 2016; Tallian et al. 2017), highlighting the direct influence of prey abundance on the hunting tactics of wolves in multi-prey systems. However, the tactics adopted may rely on abundance, habitat quality, or catchability of prey at finer spatial extents. Although wolves may have primary prey species that make up the largest portion of their diet in a system, they still frequently kill alternative prey species (Huggard 1993; Metz et al. 2012). The consumption of multiple and dissimilar prey suggests predators may use simultaneous tactics, i.e., the prey abundance, prey habitat, and prey catchability hypotheses, which represents a trade-off in multi-prey systems.

We test the three predator foraging hypotheses on the two dominant prey in a multi-prey system: prey abundance, prey habitat, and prey catchability. Wolves prey on elk (*Cervus canadensis*) and moose (*Alces alces*) in Riding Mountain National Park, Manitoba. Elk are more social than moose and are found aggregated in larger groups (Altmann 1959; Vander Wal et al. 2013). Wolves should thus adjust space use to maximize encounter rates with both ungulate species based on the fine-scale abundance of both moose and

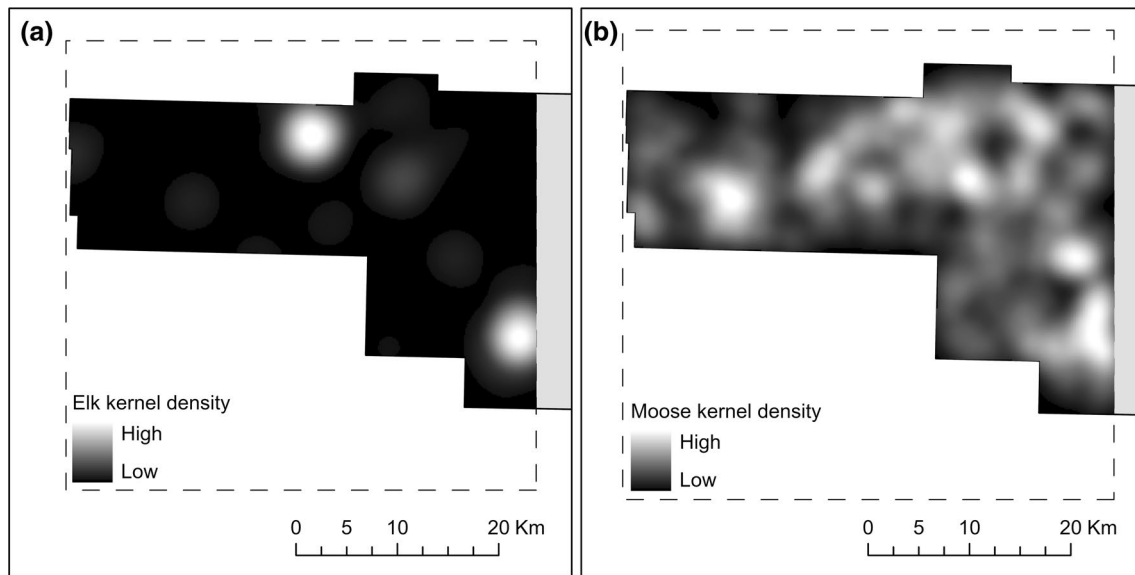


Fig. 1 Kernel density estimates for (a) elk and (b) moose abundance based on an aerial survey conducted by Parks Canada in February 2016 in Riding Mountain National Park, Manitoba. Kernel density was calculated using the Kernel Density tool in ArcGIS 10.3.1 (ESRI 2016)

elk. Encountering prey through tracking prey abundance or selecting for prey's preferred habitat is the first phase of predation, while capture success is the focus of the catchability hypothesis. Elk and moose vary in-flight responses and body size that influence ease of kill (Paquet 1992; Wikenros et al. 2009). As wolves rely on two primary prey species, and those species vary in their distribution and catchability, we predict that wolves will employ synergistic hunting tactics for the two prey:

1. Prey abundance hypothesis: we predict that wolves will select for areas of high density (animals per area) of prey species that live in more aggregated groups on the landscape, i.e., elk.
2. Prey habitat hypothesis: wolves will select for areas of high habitat quality for prey species that are relatively less dense but more evenly distributed on the landscape, i.e., moose (Fig. 1).
3. Prey catchability hypothesis: we predict that wolves select more strongly for areas where prey are easier to kill on the landscape for prey species that are more dangerous, i.e., moose.

Methods

Study site and species

Riding Mountain National Park is an insular protected area surrounded by agriculture (3000 km²; 50°51'50"N 100°02'10"W). Riding Mountain is primarily composed of

aspen parkland and boreal forests, dominated by tree species such as trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), and jack pine (*Pinus banksiana*). Wolves are the apex predator in this system followed by black bears (*Ursus americanus*). The wolf population was estimated at 72 individuals in 2016 and 70 in 2017 (0.024 wolves per km²; Sallows 2016). The wolf population has a high turnover and is geographically isolated because of human disturbance (Stronen et al. 2012). Prey species of wolves have been historically abundant in Riding Mountain (Carbyn 1980); these species include elk, moose, white-tailed deer (*Odocoileus virginianus*) and beavers (*Castor canadensis*). Elk and moose have historically been, and still are, the two main prey species for wolves in the park (Sallows 2007). Elk and moose populations sizes are estimated at an average of 1200 and 2300 individuals, respectively (0.4 elk per km² and 0.77 moose per km²; 2016 and 2017) through annual winter surveys (Vander Wal et al. 2013; van Beest et al. 2014). For this population-level analysis, we omitted white-tailed deer as they are less abundant in the park and in our kill site observations. White-tailed deer abundance is lower than the other two ungulate species within the park, their population is estimated at around 750 individuals (0.25 deer per km²; and their distribution is concentrated near human development within the park, by campgrounds, townsites, and the park boundary (Sallows 2016; Sallows et al. 2017). White-tailed deer were primarily consumed by a single pack in 2017 (Supplementary File 1, Table S1 and Figure S6) which was found outside of the main ungulate survey area (100% coverage). Thus, we

focused on the two main ungulate prey during the winter for this analysis.

Data

Wolf data

Wolves were captured using net guns from a helicopter (Memorial University AUP 16-02-EV). Wolves in the western portion of Riding Mountain were fitted with GPS collars in three packs and one lone wolf in Jan-Feb 2016 ($n=13$), and in six-packs Jan-Feb 2017 ($n=14$) representing 60% of packs in the park and 100% coverage of packs in the western 'core' area. Stable wolf territories in Riding Mountain range from 51.1 km² to 266.4 km² (Table 1). Packs with extraterritorial forays have territories an order of magnitude larger 2179.2 km² and 3377.2 km² and were omitted from habitat selection analysis. Analysis was conducted on a total of $n=9$ wolves from three packs in 2016 and $n=8$ wolves from three packs in 2017. In a population of 70 with high turnover, this represents 11% of the population included in our analysis. A map of the pack territories can be found in (Supplementary File 1 Figure S1). All GPS locations were rarified to a 2 h fix rate to sample all wolves equally (Fieberg et al. 2021; Northrup et al. 2021).

Ungulate aerial survey data

Prey abundance and habitat were assessed using visual observations recorded during annual ungulate survey conducted by Parks Canada over a two- or three-day period in the winter (January or February) when animal sightability is greatest (Vander Wal et al. 2011), Parks Canada conducts an annual ungulate survey using a helicopter (Sallows 2016)

where observers on either side of the aircraft counted moose and elk within 200 m of the aircraft and recorded the spatial location of observed individuals and group size. The survey transects are flown north–south at intervals of approximately 400 m resolution and the extent spans the territories of collared wolves (western Riding Mountain, Supplementary File 1 Figure S2).

Analysis

We tested the influence of three different prey metrics: density, habitat selection, and kill sites on wolf habitat selection using a within-territory (third order; Johnson 1980)) habitat selection analysis (see Fig. 2 for an overview). Habitat selection analysis determines the intensity of space use measured at the level of individuals, populations, or species by comparing used vs. available habitat units as they vary across geographical space (Manly et al. 2007; Northrup et al. 2021).

Prey abundance hypothesis

To test the Prey Abundance Hypothesis, we used density by calculating the local count of animals over the area sampled. We converted visual observations from the 100% coverage ungulate survey into quantifiable density by partitioning the area covered by the survey into a 400 m × 400 m grid using the Create Fishnet tool from ArcGIS 10.3.1, ESRI 2016. The mean density for each cell was calculated averaging values from 2015 to 2017 as the input for 2016 wolf models and from 2016 to 2018 for 2017 wolf models. Although this data is a snapshot in time of the distribution of moose and elk

Table 1 Summaries of pack territory size and of prey density found associated with three (2016) and five (2017) collared packs in Riding Mountain National Park, Manitoba from January–February 2016 and 2017. Mean, range and standard deviation of densities shown

Pack	Year	Pack territory size (km ²)	Moose density (individuals/km ²)			Elk density (individuals/km ²)		
			Mean	Range	Std. dev	Mean	Range	Std. dev
Baldy	2016	128.4	3.9	2.1–25	2.6	4.1	2.1–16.7	3.4
Baldy	2017	2179.2	4.2	2.1–27.1	2.6	7.3	2.1–66.7	9.3
Gunn Lake	2016	253.5	4.2	2.1–14.6	2.5	3.8	2.1–10.4	2.6
Whitewater	2016	194.6	4.8	2.1–18.8	3.4	8.6	2.1–56.3	8.7
Birdtail	2017	255.4	4.1	2.1–27.1	2.6	6.6	2.1–66.7	10.2
Block	2017	94.0	4.4	2.1–18.8	3.1	8.9	2.1–14.6	4.5
Lake Audy	2017	51.1	–	–	–	–	–	–
Ranch Creek	2017	266.4	4.2	2.1–18.8	2.7	3.4	2.1–8.3	1.9
Spruce Lake	2017	3377.2	4.3	2.1–12.5	2.4	13.3	2.1–47.9	12.5

correspond to survey cells (400 m × 400 m) that had at least one observed moose or elk, respectively, during the aerial surveys from 2015 to 2017 for 2016 and from 2016 to 2018 for 2017

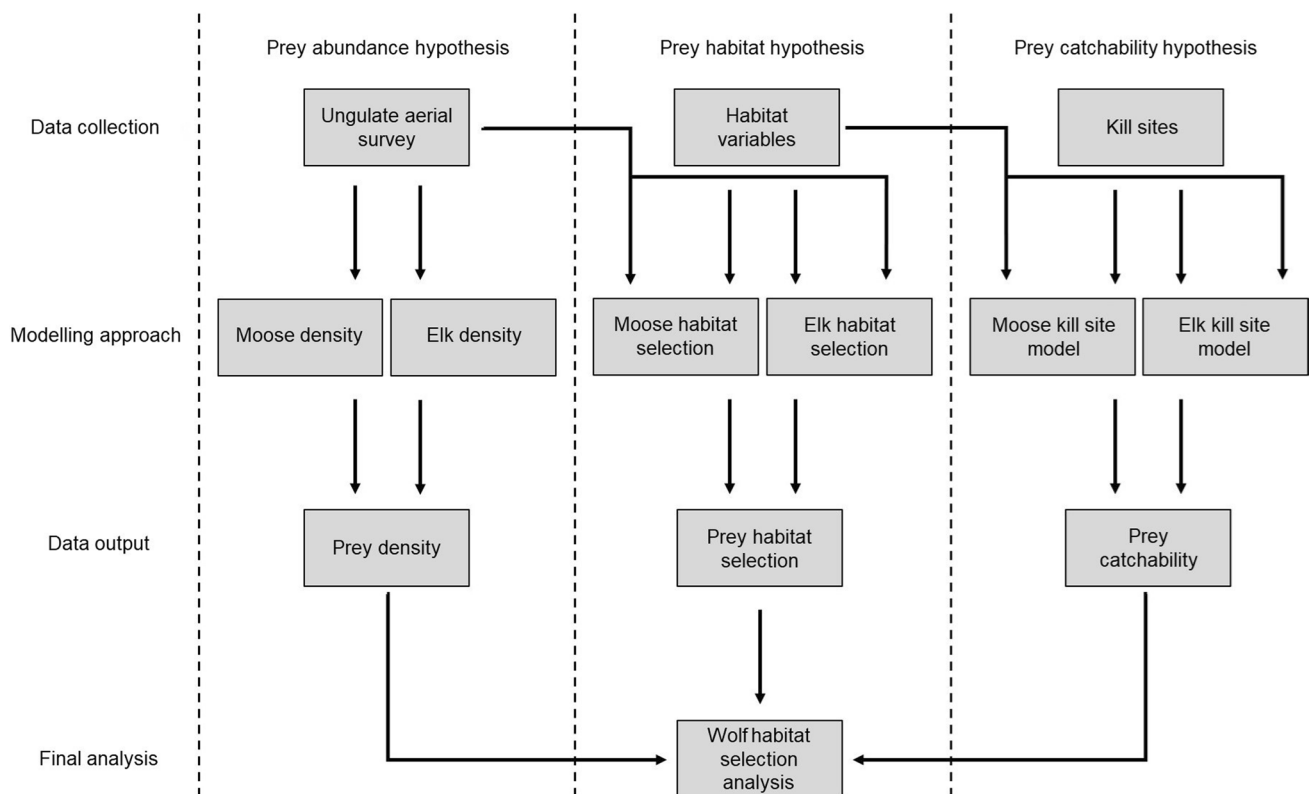


Fig. 2 Flow chart of methods used to generate the three different prey distribution metrics to test the use of the prey abundance, prey habitat and prey catchability tactics by wolves ($n = 17$) in six wolf packs in Riding Mountain National Park, Manitoba, from January–February

2016 and 2017. Columns within dotted lines represent steps to generate the prey distribution metrics for each of the three hypotheses governing the tactics (i.e., prey abundance hypothesis, prey habitat hypothesis and prey catchability hypothesis)

densities, the values are representative of the general distribution of moose and elk winter densities in Riding Mountain (Vander Wal et al. 2011; van Beest et al. 2014).

Prey habitat hypothesis

We used the winter survey data to construct models of moose and elk habitat selection on the landscape using land cover classes and distances to features as explanatory variables in the models (Supplementary File 1 Table S4).

We used georeferenced visual observations from the 100% coverage ungulate survey (Supplementary File 1 Figure S2) conducted by Parks Canada from 2016 and 2017 to gather locations for the moose and elk habitat selection analyses. Validation of aerial survey data with GPS data was completed for elk in Riding Mountain previously where coefficient estimates are similar in direction and magnitude of effect (seven out of 10 confidence intervals overlap: Supplementary File 1 Figure S8). A similar exercise was done in a previous study for elk in Riding Mountain (Fig. 2 in van Beest et al. 2014). We classified each moose or elk observation as a used point in the habitat selection models (van Beest et al. 2014; Street

et al. 2015). A uniform distribution of points was generated every 600 m for each species and each year along the transect lines to model available points for the habitat selection models (Street et al. 2015).

We built one a priori habitat selection model for moose and elk, respectively. Covariates included in the model for both prey species were: proportion of land cover type (Manitoba Remote Sensing Centre 2004) within 200 m (i.e., coniferous forest/bog, marsh/grassland, mixed wood forest and open deciduous forest), distance to water, distance to roads, distance to maintained and unmaintained trails, and terrain ruggedness. Distances were included in the model as natural logarithm transformed distance + 1 to account for the decay in animal response to proximity to features (Prokopenko et al. 2017). Terrain ruggedness was calculated using the Terrain function found in the R package “raster” (Hijmans et al. 2017). Year was included in the models as an interacting covariate with all other covariates to allow for variation in the effect of habitat features on species distribution between years. We checked for potential correlation between covariates in the models (Supplementary File 1 Figure S7).

Prey catchability hypothesis

To model Prey Catchability on the landscape, we completed habitat selection analysis with kill site investigations conducted in GPS collared packs during the winters of 2016 and 2017 (January–April). Clustered GPS locations were visited on the ground to confirm the presence of a kill site (Webb et al. 2008). Parameters used to determine a cluster consisted of a maximum of 300 m between two locations within 96 h producing (the algorithm can be provided upon request; Warren 2008). Clusters were visited along a random stratified sampling procedure where we attempted to visit the same amount of large and small clusters. Most clusters were accessible via snowmobile, but a helicopter was used on multiple occasions for sites that were not accessible on foot or by snowmobile. When clusters were visited, observations were recorded, and samples were collected, we referred to the areas as an investigated ‘site’ (Supplementary File 1 Figure S4) with assigned behavioural categories (*e.g.*, resting, kill). Of the 104 kill sites investigated in January–April 2016 and 2017, 57% were moose and 21% were elk, the remaining prey items during this period were white-tailed deer, and a single beaver kill (Supplementary File 1 Table S1, Figure S5 and Figure S6).

Kill sites were ‘used’ locations on the landscape and determined territories for corresponding wolf packs by generating 100% minimum convex polygons using Home Range Tools for ArcGIS (Rodgers and Carr 2015) to create kill site habitat selection models. Three packs were removed from the elk and moose kill site analyses due to not having enough kills to inform the models or extraterritorial forays of collared individuals (Table 1, Supplementary File 1 Table S1). We chose a spatial grain to match our scale of inference with the scale of the predation process. Wolf pursuit distance is 70 to 160 m on average (Paquet 1992; Wikenros et al. 2009) and the average radius of clusters at kill sites is 206 m. The buffer for the habitat included in the layer was a 200 m radius, rasterized to 30 m pixels. We used 100% MCPs to determine the extent of available habitat on the landscape by generating uniform grids of locations (600 m × 600 m) to simulate available locations within each pack’s territory. This uniform sampling method is an alternative to random sampling and has been found to reduce bias (Warton and Shepherd 2010; Aarts et al. 2012; Renner et al. 2015; Proko-penko et al. 2017).

Covariates in the models describing moose and elk catchability were the proportion of land cover type (Manitoba Remote Sensing Centre 2004) within 200 m: coniferous forest/bog, marsh/grassland, mixed wood forest and open deciduous forest. We used distance to water, distance to roads, distance to maintained and unmaintained trails, distance to hard edge and terrain ruggedness. Hard edge consisted of transition zones between open cover and closed

cover habitats and has been documented to influence prey catchability on the landscape (Bergman et al. 2006). Year was included in the models as an interacting covariate with all other covariates to allow for variation in the effect of habitat features on species catchability between years (see Supplementary File 1 Figure S9 for yearly fluctuation in snow depth).

Wolf habitat selection analysis

The used locations for the models were from 17 collared wolves in January and February giving a total of $n=4157$ after removing locations outside of the park and outside of the area covered by the 100% coverage ungulate survey (Supplementary File 1 Figure S1) were excluded from the analysis. The corresponding packs for these collared wolves were the Gunn Lake, Baldy and Whitewater packs in 2016, and the Birdtail Valley, Block and Ranch Creek packs in 2017. We narrowed the temporal extent of this analysis to increase our confidence in the prey covariates calculated from the aerial survey, which were conducted during this period. Territories for individual wolves were identified by generating 100% minimum convex polygons using Home Range Tools for ArcGIS (Rodgers and Carr 2015) and portions outside of the park and the area covered by the 100% coverage ungulate survey were removed due to the stark change in a habitat outside of the park and the lack of prey observations outside of the 100% coverage ungulate survey area. We generated uniform grids of locations (150 m × 150 m) to define available habitat and prey distribution within individual territories.

We tested the effect of prey density, prey habitat selection and prey catchability on wolf resource selection using six a priori generalized linear mixed models with a binomial distribution using the R package lme4, including models with interactions (Bates et al. 2015). All six models included individual ID nested within pack ID as a random effect. The predicted values of elk catchability resulted in some extreme values in areas where there is a combination of low marsh/grassland near hard edges. Thus, we reduced these predictions to the 99.9th percentile (affecting 80 predicted values out of a total of 130,127 locations). The six models were selected to determine which combinations of prey density, prey habitat selection and prey catchability best explained wolf resource selection (Table 2). We ensured that there was no correlation between model covariates (Supplementary File 1 Figure S7). Confidence intervals were calculated via bootstrap ($n=200$) method in R using the lme4 package. This method approximates the confidence intervals of the fixed effects based on the estimated curvature of the likelihood surface (Bates et al. 2015). The final model was cross validated using a k-fold cross-validation test (Roberts et al. 2017) where each pack was treated as spatially independent

since their territories did not overlap in 2016 and overlapped minimally on two occasions in 2017. (Supplementary File 1 Figure S1 and Table S3).

Results

Prey spatial covariates

Prey density

Mean elk density values within the 400 m × 400 m cells were more aggregated compared to the mean moose density values (Fig. 1, Table 1). These results highlight that elk are more aggregated and found in larger groups relative to moose (Fig. 1, Table 1). Moose were consistently found in smaller groups illustrated by the small variance and lower average density in the cells.

Prey habitat selection

Moose avoided combined coniferous forests and bogs, open deciduous forests, and roads in both 2016 and 2017. In 2016, moose also avoided open water and maintained trails, while in 2017 moose also avoided mixed wood forests (Supplementary File 1 Table S4). Elk avoided mixed wood forests in both 2016 and 2017. Elk avoided maintained trails and streams in 2016 but was selected for in 2017. The opposite was true for combined marsh and grasslands, combined coniferous forests and bogs, and roads, where elk avoided them in 2016 but selected for them in 2017. In 2016 alone elk selected for unmaintained trails while avoiding open deciduous forests and terrain ruggedness. In 2017, elk was selected for combined marsh and grasslands, combined coniferous forests and bogs, and roads, while avoiding mixed-wood forests, maintained trails, and streams (Supplementary File 1 Table S4).

Prey catchability

There was a higher propensity for wolves to kill moose in mixed wood forests and elk closer to unmaintained trails and hard habitat edges (Supplementary File 1 Table S4).

Wolf habitat selection

The best-supported model describing space use by wolves included prey habitat selection, prey density and prey catchability of both moose and elk, and an interaction between moose catchability and moose habitat selection (mean k-fold = 0.93; Fig. 3, Table 2, Table 3). Wolves showed a neutral response to moose density ($\beta = 0.06$; 95% CI [- 0.34;

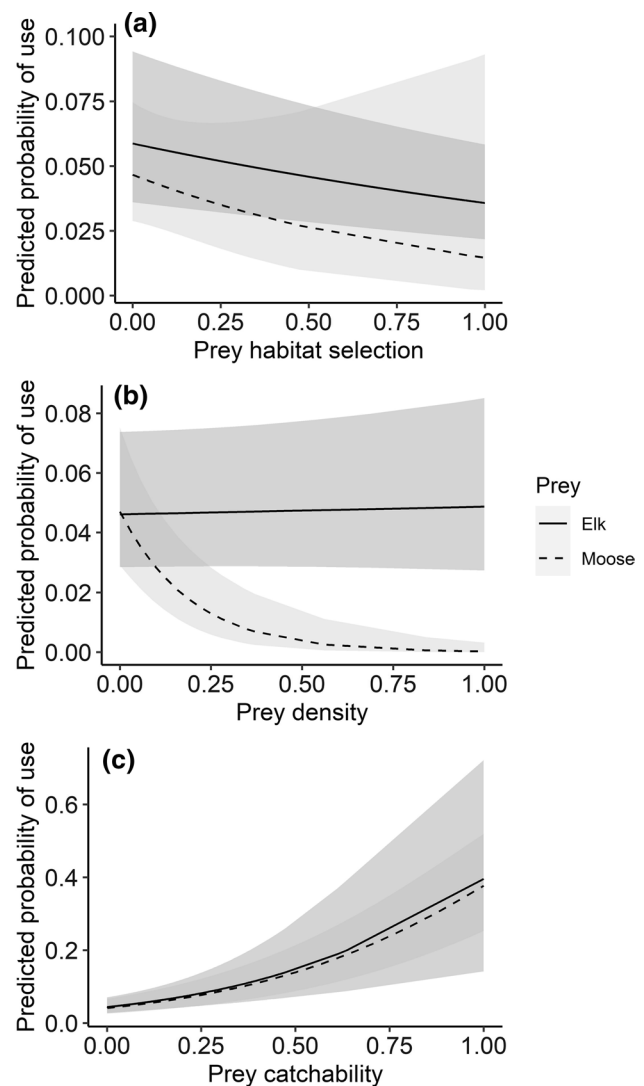


Fig. 3 Predicted probability of wolf ($n=17$) space use in six wolf packs in Riding Mountain National Park, Manitoba, Canada from January to February 2016 and 2017, in relation to moose and elk (a) habitat selection and (b) density, and (c) catchability on the landscape. Gray bands correspond to 95% confidence intervals. All three prey distribution metrics were standardized between 0 and 1 for comparison. Original units for prey density were individuals/km² while prey habitat and prey catchability did not have units due to being unitless selection values. The y-axes are at different scales to allow for a better comparison between the effects of moose and elk distribution. Predicted values and 95% confidence intervals were generated using the ggeffects package in R (Lüdtke 2018)

0.36]), elk habitat ($\beta = -0.90$; 95% CI [- 3.88; 1.12]), and the interaction between elk habitat selection and elk catchability ($\beta = -6.93\%$; CI [- 23.04; 9.19]). A neutral response indicates there was neither selection nor avoidance. Wolves significantly selected for areas where elk catchability was high ($\beta = 2.69$; 95% CI [2.29; 3.05]; Fig. 3c). However, wolves significantly avoided areas where moose catchability was high ($\beta = -5.18$; 95% CI [- 8.58; - 1.89];

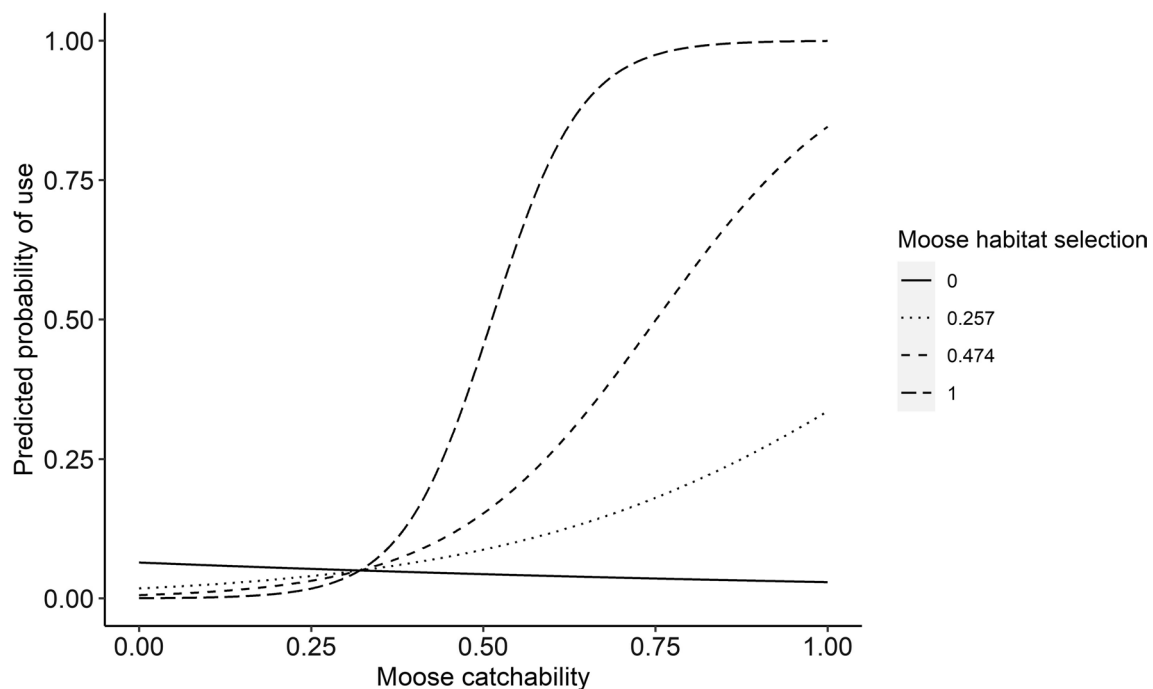


Fig. 4 Predicted probability of wolf ($n=17$) space use in six wolf packs in Riding Mountain National Park, Manitoba, Canada from January to February 2016 and 2017, in relation to the interaction between moose habitat selection and catchability on the landscape.

Prey habitat and prey catchability did not have units due to being unitless selection values and were standardized from 0 to 1. Predicted values were generated using the `ggeffects` package in R (Lüdtke 2018)

Fig. 3c), moose habitat selection was high ($\beta = -0.83$; 95% CI $[-1.08; -0.57]$; Fig. 3b), or where elk density was high ($\beta = -5.29$; 95% CI $[-8.35; -2.93]$; Fig. 3a). Wolves strongly selected areas that were simultaneously habitat moose selected and high moose catchability ($\beta = 16.16$; 95% CI $[8.98; 21.78]$; Fig. 4, Table 3). Indeed, the selection coefficient for the interaction between moose habitat and moose catchability was 8 times greater in magnitude than elk catchability.

Discussion

We tested three hypotheses describing predator space use for two dominant prey in a multiprey system: prey abundance, prey habitat, and prey catchability. The prey abundance hypothesis predicted that wolves would select for elk density because the elk were more aggregated on the landscape. However, wolves avoided elk density. Avoidance of elk density becomes more intuitive when considering the predator–prey space race at the resolution of the analysis. The prey habitat hypothesis predicted wolves would select for

Table 2 Models considering effects of prey habitat selection, density and catchability on wolf space use with their respective K, Δ AIC, Δ AIC weight, log likelihood, Marginal R², conditional R² and mean k-fold. Data used in the models were from collared wolves ($n=17$)

Model	Variables	K	Δ AIC	weight	logLik	K-fold
Model 6	$M_D + E_D + M_H \times M_C + E_H \times E_C$	11	0.00	0.96	−15,400.13	0.93
Model 4	$M_D + E_D + M_H + E_H + M_C \times E_C$	10	6.33	0.04	−15,404.29	0.92
Model 1	$M_D + E_D + M_H + E_H + M_C + E_C$	9	18.50	0.00	−15,411.38	0.93
Model 3	$M_D + E_D + M_H \times E_H + M_C + E_C$	10	19.91	0.00	−15,411.09	0.91
Model 5	$M_D \times M_V + E_D \times E_C + M_H + E_H$	11	20.13	0.00	−15,410.20	0.93
Model 2	$M_D \times E_D + M_H + E_H + M_C + E_C$	10	20.16	0.00	−15,411.21	0.93

M_H moose habitat selection, E_H elk habitat selection, M_D moose density, E_D elk density, M_C moose catchability, E_C elk catchability

Table 3 Coefficients, standard errors, 95% confidence intervals (generated using bootstrap with 200 iterations) and *p*-values of variables of the top model considering effects of prey distribution on collared wolf (*n* = 17) space use in six wolf packs from January to February 2016–2017 in Riding Mountain National Park, Manitoba. Coefficients with significant *p*-values (*p* < 0.05) and confidence intervals that do not overlap zero are bolded

Variable	Coefficient	St. Error	95% CI	<i>P</i> -value
Intercept	– 2.77	0.26	– 3.29; – 2.36	< 0.001
Moose density	0.06	0.18	– 0.34; 0.36	0.74
Elk density	– 5.29	1.28	– 8.35 ; – 2.93	< 0.001
Moose habitat	– 0.83	0.15	– 1.08 ; – 0.57	< 0.001
Elk habitat	– 0.90	1.13	– 3.88 ; 1.12	0.43
Moose catchability	– 5.18	2.06	– 8.58 ; – 1.89	0.01
Elk catchability	2.69	0.17	2.29 ; 3.05	< 0.001
Moose habitat × catchability	16.16	3.90	8.98 ; 21.78	< 0.001
Elk habitat × catchability	– 6.92	8.22	– 14.39; 4.82	0.40

moose habitat because abundance would not be a dependable cue for an evenly distributed prey. Wolf response was neutral for elk and weak for moose habitat alone. We found support for the prey catchability hypothesis; wolves selected areas of high elk catchability and had the strongest selection for areas of high moose catchability in moose habitat. The interactive effect between moose catchability and moose habitat selection demonstrates that our hypotheses were not mutually exclusive. Rather, as wolves increased their chances of encountering and killing prey by using areas where their primary prey moose are simultaneously predictable within their selected habitat and catchable. For example, wolves can select to hunt in areas where moose select to be that are also areas where moose are easier for wolves to catch.

Encounter and kill are the two critical components of hunting success. Accordingly, the interaction of moose habitat and moose catchability had the strongest effect on wolf space use. Prey catchability has been shown to be an important predictor of space use for a variety of predators across systems (Messier and Barrette 1985; Patterson and Messier 2001; Hopcraft et al. 2005; Balme et al. 2007; Petrunenko et al. 2016). When prey are larger than their predators they pose a greater foraging risk (Mukherjee and Heithaus 2013). Ungulates injure or kill wolves in confrontations, and wolves alter space use to increase the catchability of both of their large prey, moose and elk (Mech and Boitani 2003; Mukherjee and Heithaus 2013). While catchability was important for predators when hunting both prey species, we expected species-specific responses to the encounter-centric mechanisms of the prey abundance hypothesis and the prey habitat hypothesis given the relative differences in prey abundance and distribution in Riding Mountain.

We predicted predator spatial tactics would differ between prey due to differences in distribution and social behavior of prey influencing encounter rates. However, we based our prediction on prey spatial distribution without considering the total prey abundance within the region and the relative differences between prey abundance. In a multi-prey system in Ontario, wolves selected for moose locations when local

moose density was high and avoided areas where their secondary prey, caribou (*Rangifer tarandus*), occur and forage (Kittle et al. 2017). Historically in our study system, elk surpassed moose in abundance in Riding Mountain and were the primary prey species for wolves (Carbyn 1983). During this study, moose were more abundant relative to elk and kill sites demonstrated that moose were the primary prey species for wolves during this time (Supplementary File 1 Figure S6). The pattern in abundance and kill rates was reflected in the spatial tactics that focused on moose. Predators will not always shift hunting behavior to the most abundant prey. Instead, their primary or preferred prey is determined by both its abundance and catchability. Wolves relied on elk as their primary prey in Yellowstone National Park, USA, and maintained their preference for elk even with an increase in abundance of a more dangerous prey, bison (*Bison bison*; Tallian et al. 2017). In Riding Mountain, wolves followed the catchability hypothesis by using the landscape to facilitate capturing moose, which ultimately facilitated a switch in prey. Thus, these spatial behaviors are sensitive to both the availability (*i.e.*, abundance and habitat) and accessibility (*i.e.*, catchability) of prey to predators.

Prey density and prey habitat can be simultaneously exploited by predators (Castillo et al. 2012). However, wolves must prioritize which areas to frequent with multiple prey on the landscape. Wolves in a moose and caribou system avoided caribou (Kittle et al. 2017). Notably, the spatial antipredator behavior of these two prey differ. Though caribou were secondary prey to moose and existed at a low density, as were elk in our study, caribou space out and away from predators as opposed to elk which aggregate. In addition, there can also be a disconnect between prey density and prey habitat selection that may be explained by the “leap-frogging” hypothesis (Sih 2005). Here, prey select lower-quality resources to avoid predation and therefore trade-off the benefits of high-quality resources to reduce predation risks (Mitchell and Lima 2002; R. Heithaus and M. Dill 2006). Further, prey mediate their individual risk of predation through conspecific density by trading off detection with

dilution (Hebblewhite and Pletscher 2002). Thus, the highest densities of prey might not be the most selected habitat of either predators or prey.

The counter-intuitive result of wolves strongly avoiding elk density in this study could be driven by the avoidance behaviour of the prey occurring at a finer resolution than our analysis. A key difference between our density measures and other studies testing similar hypotheses is the scale at which they were estimated. When wolves selected for moose density in Northern Ontario, the resolution at which density was estimated was much coarser at 5 km apart (Kittle et al. 2017) compared to 400 m in our study. Predators respond to prey density by adjusting territory size according to how many prey are available (Valeix et al. 2012). Consistently, predators reduce territory size in areas with high prey availability and increased prey access (Dickie et al. 2022). In comparison, Riding Mountain territories are strikingly smaller (51 km² to 266 km²) than other high-productivity wolf systems (3186 km² to 4878 km² during the winter; Dickie et al. 2022). This indicates wolves in Riding Mountain have adjusted their space use to resource abundance at a coarse-scale when forming territories. Within territories, predators and prey mutually influence each other's space use (Schneider and Piatt 1986; Rose and Leggett 1990; Mitchell and Lima 2002), while predators try to increase the chances of encounter and the prey attempt to reduce these chances a spatial game emerges. Our finding of prey density avoidance by wolves highlights the importance of considering scale when studying spatial predator–prey relationships.

The prey catchability hypothesis was supported by wolf space use behaviour observed in Riding Mountain, similar to other systems involving large mammalian carnivores (Hopcraft et al. 2005; Balme et al. 2007; Davidson et al. 2012). When tracking their primary prey, wolves appear to trade-off between encountering and capturing prey by using space that is both predictable moose habitat but also habitat where moose are vulnerable. Focusing on the intersection of space where moose are likely to be and be catchable increases the probability of encountering, and subsequently capturing prey. Adopting the tactic best suited for their primary prey, wolves in this system also rely on the catchability tactic to track a secondary prey due to the lack of large elk herds. We attribute the counterintuitive avoidance of elk density by wolves to a prey response to avoid predators instead of indicating a viable predator hunting tactic. Therefore, wolf behavior is motivated by prey habitat and catchability which represent spatial trade-offs between encounter versus kill, and availability versus accessibility when hunting multiple responsive prey.

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Author contribution statement SZS and CMP formulated the idea, conducted fieldwork, and designed the analysis. SZS conducted the analysis. SZS and CMP wrote the manuscript. EVW provided conceptual and editorial advice.

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Availability of data Input data for the wolf habitat selection analysis and metadata of raw locations is available online at <https://github.com/CMPProkopenko/wolfspace>

Code availability Code will be available at <https://github.com/CMPProkopenko/wolfspace>.

Declarations

Conflict of interest Not applicable.

Ethics approval All applicable institutional and national guidelines for the care and use of animals were followed (Memorial University AUP 16-02-EV).

Consent to participate Not applicable.

Consent for publication Not applicable.

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