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Resource availability and anthropogenic disturbance alter how wolves move and feed: comparing two populations

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Abstract

Animals behave 'optimally' when they minimize their costs while maximizing their energetic gain. Optimal foraging theory predicts that with decreasing resource abundance, animals will increase 1) niche breadth, 2) territory size and movement distance, and 3) time spent at resource patches. We used optimal foraging as a guiding framework to test what drives differences in behaviour of GPS collared wolves in two predator populations. As expected, niche breadth and territory sizes were larger, movement rates were greater and cluster durations were longer in the study area with relatively lower resource abundance. Our comparative test through the lens of optimal foraging theory led to some unexpected discoveries. Specifically, differences in these responses were not explained by the density of the large primary prey (moose) but instead anthropogenic disturbance (linear feature density) was a ubiquitous influence on wolf behaviours. Wolves in higher linear feature density responded by reducing their cluster residency and increased step lengths and territory sizes with increases in linear feature density. Our work provides evidence that large carnivores can mediate changes in resources by adjusting their space use and time budgets in a way that corresponds with optimal behaviour - maximizing their energy gain and minimizing costs.

Keywords Cluster investigation, Diet composition, Optimal foraging, Wolves, Predation, Resource abundance

Introduction

Animals, whether populations, groups, or individuals, exist across a gradient of resource abundance. The spatial distribution of resources influences animal movement and space use, as animals evaluate the energetic gains from the resources against the costs to access the resources [1, 2]. Apex predators that hunt and kill large-bodied prey incur a high initial energetic cost during the hunting stage [3] and receive a high energy gain during consumption – striving to optimize the two. A useful framework to evaluate predator decisions in diverse systems is optimal foraging theory [4]. Optimal foraging theory predicts that with lower resource abundance, animals will generalize their diet and expand their territory to meet energetic needs [5]. In addition, due to the

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increased movement costs between sparse prey, predators will spend more time at a kill [1]. We applied these foundational expectations to a comparative study of behavioral observations in two predator populations that differ in their prey composition and abundance.

Variation in prey composition may lead to different dietary niches. Dietary niche classifies animals by the proportion of food items consumed and is largely constrained by the resources available to an animal. Animals are on a spectrum from generalists, which consume many resource types equally, i.e., broad niche, to specialists, which focus on resource types, i.e., narrow niche [6]. Whether a predator opts to specialize or generalize its diet depends on the availability and accessibility of the preferred prey type. Within a given population, animals have been shown to alter their dietary niche across years or seasons to reflect fluctuations in primary prey availability [7] or when environmental conditions improved the success rate in hunting an alternative prey [8]. Species with broad food preferences, or those that consume alternate food types, will have wider dietary niches when preferred resources are scarce [9]. Generalist species have also been shown to have larger range sizes and therefore should occur in more patches across a landscape than species with narrow niches, i.e., specialists [10].

Animals form their dietary niches within their home ranges, which are the spaces used to fulfill an organism's needs to survive and reproduce [11]. The size of ranges is shaped by the quantity of resources contained within, where increases in resources decreases range size [5, 12]. In western Canada, wolves (*Canis lupus*) had smaller territories in areas with more productive vegetation, assumed to have more prey [13]. Even at a fine scale, individuals adjust their home range sizes as resources change temporally. Following a wildfire and subsequent resource pulse, black bears (*Ursus americanus*) reduced their home range size [14]. In contrast to range contraction, expansion of home ranges increases the cost of moving between resource patches and defending larger territories [15]. Landscape variation in resource distribution alters the search rate to meet the same energetic threshold [16]. In response to increases in resource availability, animals decrease their home range size to increase their exploitation efficiency [17].

Within home ranges, animals should adjust their activity budgets to be more efficient, either to expend less energy or less time when moving to acquire resources. The time spent in patches is influenced by the energy spent traveling between, searching within patches, and the energy consumed within a patch [1]. For a predator, consuming a carcass (i.e., handling time) can be likened to patch residency. Accordingly, increased patch residency via handling time can offset travel costs between patches when prey are sparse. For example, wolves

exhibited longer handling times as annual prey biomass per wolf decreased [18]. Partial consumption of prey is an optimal foraging strategy when resource availability is high, the cost of searching is low, and predators are often sated; wolves consumed smaller amounts of each individual prey item when kill rates were higher [19]. At a fine scale, predators can decrease their handling of killed prey when more resources are available.

Whether it is a shorebird rejecting toxic molluscs [20] or a lion selecting for catchability over prey density [21], foraging costs shape animal behaviour. The expectation is for predators to prefer more profitable and vulnerable prey [4]. Risk of injury is a foraging cost for many predators [22]. In the case of wolves, there are significant injury risks when attacking larger and more dangerous prey. In addition, there are risks that vary across space that shape predator decisions. For example, human disturbance brings direct mortality risk to predators which generates avoidance behaviour [23]. Therefore, risks are an opposing influence to resources on predator niche breadth, space use, and time allocation.

We studied the diet and behavior of two populations of a generalist predator, the wolf, in different resource conditions. We tested how resources and risk shape niche breadth, time budgets, and range size of wolves from two populations where we completed concurrent tracking and cluster investigations. Our analysis was rooted in optimal foraging theory where we expected wolves in the study areas with less prey available would have greater 1) niche breadth, 2) home range size and movement distance, 3) time spent at patches through longer total times at kill clusters and higher revisitation to previous kills. Overall, our comparative study presents which factors drive diet and space use responses of wolves to their environment.

Study area

Riding mountain national park

Riding Mountain National Park (RMNP) is a 3,000 km² federally protected area in southwestern Manitoba. RMNP is in Treaty 2 Territory, the ancestral lands of the Anishinabe people and the homeland of the Métis Nation (Fig. 1A). Parks Canada works with First Nations from Treaties 2, 4, and 1 including Keeseekoowenin Ojibway First Nation, Ebb and Flow First Nation, Waywayseecappo First Nation, Rolling River First Nation, Tootinaowaziibeeng First Nation, Gambler First Nation, and Sandy Bay Ojibway First Nation. The border of the protected area is conspicuous against the surrounding agriculture-dominated landscape. The habitat within the park is a confluence of aspen parkland, mixed wood and boreal forest, and grassland prairie. There is a gradient in human activity decreasing generally northward, and westward. There is a network of trails, campsites, and

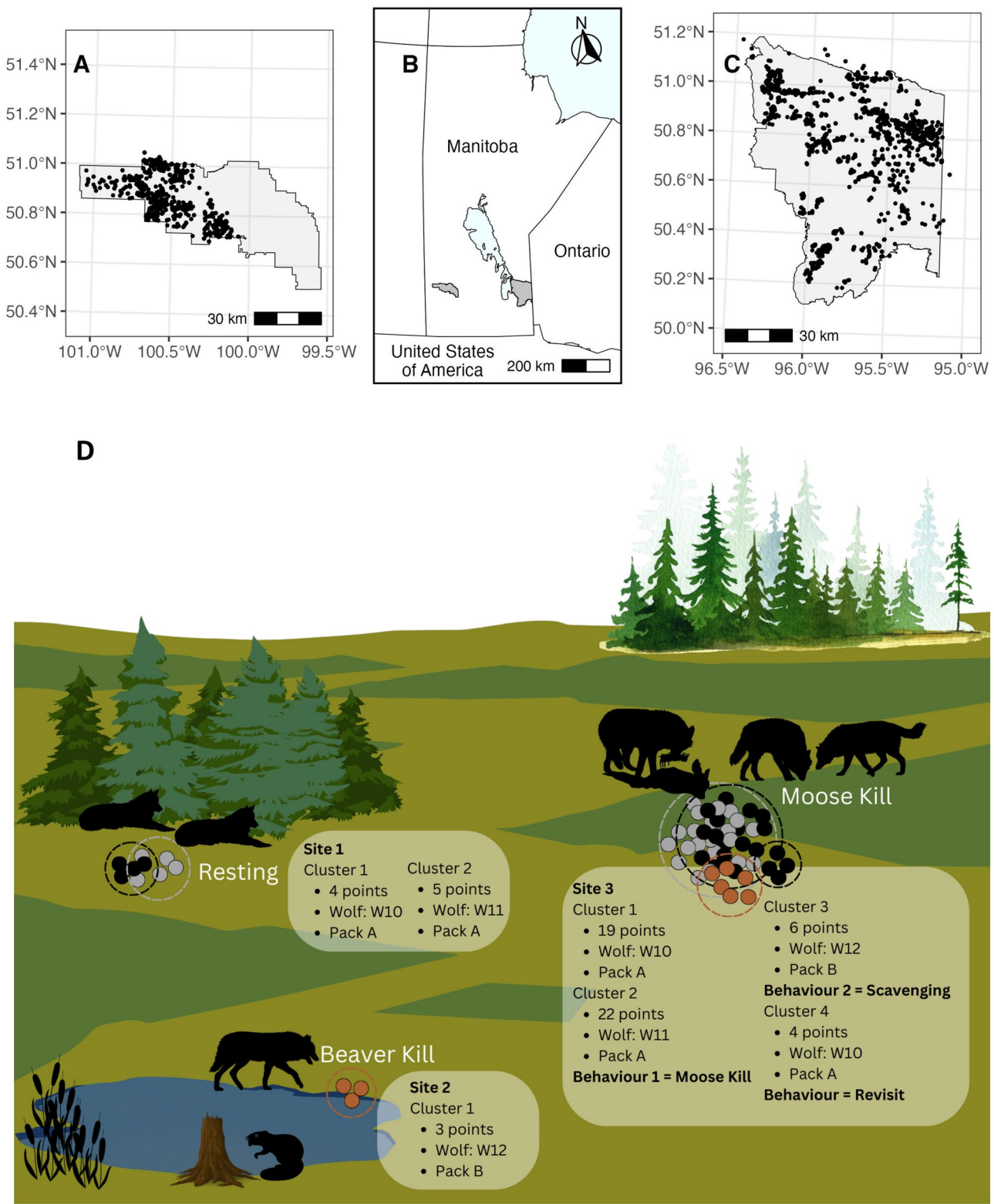


Fig. 1 (See legend on next page.)

(See figure on previous page.)

Fig. 1 Cluster investigations were completed in two wolf populations: **(A)** Riding Mountain National Park (RMNP) the study area with high resources and low disturbance with inset of **(B)** location of both study areas within Manitoba (gray shaded polygons) with Lake Winnipeg and Hudson Bay in blue, and **(C)** southeastern Manitoba (SEMB) the study area with low resources and high disturbance. Borders of RMNP and SEMB filled in grey with the centroid locations of all investigated clusters in black; **(D)** conceptual diagram outlining the hierarchical structure of sites, clusters and behaviors investigated and determined through field work. Sites could be composed of multiple GPS clusters from a single or multiple wolves. Clusters were generated from the GPS locations ($n > 2$) of a single wolf. Field investigations of clusters revealed primary and secondary behaviors associated with a site that could be linked to cluster characteristics

two roads in the park. Most of the human activity is concentrated at the town site along the south shore of Clear Lake, which is outside of the core study area. Hunting is permitted immediately outside of the park boundary, and agricultural land use creates an abrupt land cover change.

Wolves are the apex predators in this system and have been monitored through annual surveys, tracking, and predation studies for decades [24–26]. During the present study the wolf population was approximately 71 individuals (consistently 60–80 individuals, 23 individuals/1000 km²). Mortality in the study population was 68%, with Canine Distemper Virus being the leading cause of mortality, followed by hunting and trapping outside of the park, conspecific aggression, and injury from large prey [27]. In addition to an abundant black bear population, there are populations of coyote (*Canis latrans*), lynx (*Lynx canadensis*), and incidental sightings of cougars (*Puma concolor*) (though no confirmed breeding population). The prey base for wolves is diverse and abundant in this area including moose (*Alces alces*), elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*), beaver (*Castor canadensis*), and snowshoe hare (*Lepus americanus*). Historically, elk were more abundant than moose with populations fluctuating between 2000 and 6000 individuals (0.67 to 2 individuals/km²). A significant population decline began in the late 1990s for both species but was more substantial for elk, with moose becoming the most abundant ungulate in the park. During the study period, the populations of ungulates were estimated at around 2400 moose (0.80 moose/km²), 1200 elk (0.40 elk/km²), and 750 white-tailed deer (0.25 deer/km²). Recent beaver cache surveys conducted semi-annually show an increasing trend from an estimated 0.57 beaver caches per km² in 2013 to 0.87 caches per km² in 2016 [28].

Southeastern Manitoba

The study area in southeastern Manitoba (hereafter SEMB) is a ~7,200 km² provincial management unit (game hunting area; GHA). SEMB is bordered by Lake Winnipeg to the west, Ontario to the east, Wanipigow River to the north, and Winnipeg River to the south (Fig. 1C) and is part of the Boreal Shield Ecozone [29], which extends beyond the borders of the GHA designation and creates a continuous landscape. The landscape in SEMB is composed predominantly of coniferous and mixed

forests, interspersed with rock outcrops, rivers, lakes, and bogs.

The study area is in Treaty 1, 3 and 5 Territory, the ancestral lands of the Anishinaabe peoples and the homeland of the Métis Nation. The study area includes the traditional territories of Sagkeeng, Black River, and Holow Water First Nations, Brokenhead Ojibway Nation, and Northern Affairs communities (Bissett, Aghaming, Manigotagan, and Seymourville). The area is predominantly public land, and SEMB is used by many different user groups for both recreational purposes and resource development. There are two provincial parks in the area: Nopiming Provincial Park and Manigotagan River Provincial Park. The local economy is predominantly based on resource extraction, including past forestry activity, which has led to a network of roads including primary roads, logging roads, trails, and hydroelectric transmission line rights-of-way.

Wolves are the apex predator in this system with an average population of 128 individuals between 2012 and 2018 (range 106–141 individuals, ~17 wolves/1000 km²). Mortality in this study population was 26%, with hunting and trapping being the leading cause of mortality, followed by disease (heartworm) and drowning. The predator guild includes populations of black bears, coyotes, and lynx. The prey base for wolves in SEMB is diverse, yet spatially distinct. Moose were historically found throughout the study area, but are now found primarily in the northern half, which has led to a reduction in moose abundance and distribution in the study area. White-tailed deer densities have not been estimated in the study area. However, densities are low as SEMB lies near the northern limit of white-tailed deer distribution in eastern Manitoba (see Supplementary file S1). Secondary prey species include beavers, snowshoe hare, and woodland caribou (*Rangifer tarandus caribou*). The primary prey species for wolves in SEMB are moose, with an estimated population (unadjusted for sightability) of 1668 individuals (0.24 moose/km²) in the early 2000s. However, moose experienced a drastic decline by approximately 50% by 2010. The most recent moose survey conducted in 2020 provided a population estimate (unadjusted for sightability) of 1170 moose (0.15 moose/km²) (Supplementary file S1). The beaver cache density throughout the study area was estimated at 1.14 beaver caches per km² (Supplementary file S1).

Methods

Cluster investigations

Wolves were collared with GPS telemetry collars in RMNP (25 individuals) and SEMB (48 individuals) from 2014 to 2019 (Table S1.1). Of note, one wolf in SEMB remained collared for several months in early 2020. Wolf collars were programmed to take locations every 30 minutes, one hour, or two hours (odd and even schedules), but we rarified all locations to 2 hours for the analysis. We only used locations generated 24 hours following collaring until a mortality signal occurred (either from a dropped collar or a wolf mortality). GPS locations used were cleaned by removing round trips, unrealistically long steps, and duplicates.

Continuous and extensive fieldwork investigations determined the timing and location of wolf behaviors, including wolves killing prey, scavenging, denning, and resting (see Table 1 for full description of behaviors). Increased density of GPS locations, i.e., ‘clusters’, indicated important areas of wolf activity (Fig. 1D). To identify clusters for each individual wolf, we used an algorithm in Python, which was presented in Knopff et al. [30] created by Warren [31] and adapted for wolves [32–34]. In our study, we defined a cluster as GPS locations that occurred within a 300m radius and 96 hours of a previous location. To direct our sampling effort, we categorized clusters into three classes created based on the total number of locations in the clusters (small = 2–4 locations, medium = 5–7 locations, large = 8+ locations)

Table 1 Description of behaviors assigned to clusters during field investigations. Behaviors are presented in order of the hierarchy that was determined during the cleaning phase of our process. It is common for behaviors lower in the hierarchy to occur at sites with higher ranked behaviors. For example, most kills often include resting and scat activity. The percent of total clusters, the median and interquartile range of duration in hours and radius in meters of these clusters are presented by study area: riding Mountain National Park (RMNP, high resources and low disturbance) investigations from 2016 to 2017 and for the low resource and high disturbance area, southeastern Manitoba (SEMB, 2014–2019)

Behavior	Description	Percent	Duration (hours)	Radius (m)
Den	Dens are enclosed spaces used for birth and rearing of pups. Dens are dug into a bank/ridge/hill, under tree roots, rock cave, or abandoned beaver lodge. Sites often are on the edge of water or an open area. There are many signs of wolf activity including wolf tracks, trails, trampled vegetation, beds, prey carried from nearby kill sites.	RMNP = 3.5%, SEMB = 5.5%	RMNP = 236 [388] SEMB = 182 [386]	RMNP = 276 [208] SEMB = 241 [193]
Rendezvous	An area used for pup rearing following weaning. Similar signs of wolf activity (adults and pups) as den sites.	RMNP = 6.2% SEMB = 1.58%	RMNP = 165 [245] SEMB = 167 [342.9]	RMNP = 296.5 [143.5] SEMB = 279 [168]
Kill	A predation event from the collared wolves. Kill sites have multiple signs of wolf activity. Predominant signs are the prey remains including: a disarticulated skeleton, a gut pile, hair or hide as these are portions that are not consumed. For smaller prey evidence is scarce, sites with hair, blood, tissues, or bone fragments are assumed to be kills.	RMNP = 34.2% SEMB = 30.26%	RMNP = 56 [77] SEMB = 50 [91.5]	RMNP = 202 [145] SEMB = 196 [167]
Kill Revisit	A collared individual returning to previously identified kill site that has spatial overlap but is temporally distinct from previous cluster.	RMNP = 4.5%, SEMB = 11.18%	RMNP = 19 [43] SEMB = 16.5 [47.5]	RMNP = 188 [125] SEMB = 140 [135]
Probable Kill	Potential predation event by the collared wolves. Carcass is not observed but there is a high level of wolf and prey activity including trampled vegetation and tracks. Hair or blood may be present but does not confirm a successful kill.	RMNP = 5.0%, SEMB = 12.12%	RMNP = 36 [60] SEMB = 18 [67.5]	RMNP = 174 [157] SEMB = 146 [166]
Scavenge	Short cluster durations paired with signs of activity consistent with kill sites suggest prey was killed by another pack and scavenged by collared wolf. Carcass present without signs of kill site activity indicate prey died of other causes.	RMNP = 8.4%, SEMB = 10.33%	RMNP = 38 [94] SEMB = 45 [106]	RMNP = 184 [152] SEMB = 198 [174.8]
Resting	Sites of inactivity, lying down, or sleeping. Indicated by beds, i.e., round depressions in the vegetation or substrate. Wolf beds are confirmed by hair. Additional signs of activity are wolf tracks and scat.	RMNP = 18.9%, SEMB = 20.30%	RMNP = 14 [34] SEMB = 16 [48]	RMNP = 121 [142] SEMB = 121 [171]
Unknown/Other	Wolf activity including tracks, scat, or disturbed vegetation is observed at the site but there is no clear carcass or bed site.	RMNP = 12%, SEMB = 8.7%	RMNP = 16 [44.5] SEMB = 20 [76]	RMNP = 147 [142.5] SEMB = 126 [179]
Mortality	A wolf carcass was found at the site. A mortality location for the individual is the final behavioral site, which may also be visited by other wolves.	17 mortalities in RMNP 12 mortalities in SEMB A mortality signal was sent to researchers in the field after 12 hours of no movement recorded.		

and randomly selected clusters from each category. We attempted to balance the investigation effort across cluster sizes by searching more small clusters to reduce bias towards large prey items in diet estimates. We mapped routes that balanced sampling different wolves, packs, areas, cluster sizes, and maximized the number of clusters visited. Clusters were most often accessed via snowmobile, quad, or occasionally helicopter, as well as by canoe or boat in SEMB and horseback in RMNP. We searched for physical evidence of wolf behavior starting at the geometric center of the cluster moving outwards from this point. We investigated a 15 m radius around each GPS fix in the cluster to account for GPS error. We spent a minimum of 15–30 minutes searching for evidence of a behaviour, dependent on cluster size and spread. On average, we investigated clusters within a mean of 13.8 days of the first location occurrence (median: 9 days, Table S2.1).

We identified unique behaviors within a single cluster corresponding to the physical evidence present at clusters (Table 1). We then termed these clusters as various 'sites' corresponding to the primary behavior identified (Fig. 1D). For example, we classified clusters as kill sites when a carcass was present coupled with a high degree of activity indicative of an interaction between predator and prey. In some instances, we determined clusters with carcasses were instead the result of scavenging based on evidence that the animal died due to another cause, including lack of wolf activity and minimal disarticulation of the carcass, often in combination with the collared wolves spending a short duration of time, e.g., less than two hours at a large ungulate kill. We determined prey species and, for ungulate prey, we determined sex and age (adult vs. calf) based on size, dentition, and hair pattern. At the site, we collected biological samples including prey hair, bone marrow, and wolf scat. In the absence of a carcass, we used other physical evidence from wolves or other species to determine the behavior that occurred at the site such as tracks, hair, beds, scat, and dens. For example, beds under a spruce tree containing wolf hair were indicative of a resting site.

Location downloads for cluster investigations occurred frequently in SEMB (every second week) and RMNP (usually twice weekly). Sequential data downloads created segments of data that broke up large clusters and thus inflated the number of smaller clusters occurring in an area. The increase in small clusters did not change the outcomes of our observations site investigation but would change the characteristics of the cluster including radius, duration, first and last point, revisits etc. Following fieldwork completion, we downloaded all location data for each wolf and reran the cluster algorithm to get a comprehensive summary of clusters. We matched the investigated site locations recorded in the field to the new

clusters with an overlap tolerance of 25 m and flagged data when investigations occurred early or late in reference to cluster formation time. A single site could have more than one behavior. We reviewed site and cluster matches to determine both the primary and secondary behavior and prey. These decisions were guided by which behavior was the primary motivation for occupying the area for a given time (Table 1). A hierarchy was outlined to prioritize behaviors occurring at sites. For example, if a beaver kill overlapped with a den or rendez-vous, the overlap clusters were assigned the primary behavior of 'den' and a secondary behavior of 'kill'. If overlapping clusters indicated a double kill (i.e., two prey individuals killed), then either the largest prey or the first location was assigned as the primary prey. The matched and joined file of all the sites was processed to identify the number of clusters and wolves at each site, first and last point of overlapping clusters, and total number of each prey species killed.

Wolves in the same pack often simultaneously visited the same site or departure/return events by a single wolf led to generating multiple clusters that overlapped in space and time. For example, a single moose kill could be associated with four individual clusters if multiple wolves visited the site or if a wolf left and returned (Fig. 1D). To further summarize wolf behavior in these two regions, we categorized unique behaviors and feeding events as sites, using the primary and secondary behaviors observed across all clusters associated with these unique events. We evaluated potential bias for large clusters by comparing the number of locations across all clusters investigated. We summarized the number of locations, duration, and radius for clusters by behavior and kill clusters by prey type in Table S2.1.

Scat dissection

We collected scat samples during cluster investigations at sites. During cluster investigations, we typically collected only the first sample we came across unless there were multiple prey found at the site or the samples were visually distinct (e.g., contained different remains, were deposited in different areas of the site). In SEMB, we collected 531 scat samples from February 2014 to March 2020, while in RMNP we collected 296 scat samples from February 2016 to January 2018. Scats were stored for a minimum of two weeks at -80°C before handling to kill any potential parasites. Scats were manually strained through a sieve to separate hair and other undigested remains from fecal matter. Twenty hairs were randomly selected from each scat sample for identification. Hair color, size, and cuticular scale pattern were used to identify prey remains [35, 36] and to distinguish between adult and juvenile ungulate hairs.

Diet analysis

We calculated the biomass composition of wolf diet as a percentage of occurrence in both scat samples and as identified at clusters. Scat composition was calculated as the percentage of scats containing a prey species relative to the total number of scats. As small prey are more likely to be overrepresented in scat data when using percentage-of-occurrence data, we adjusted biomass using the Weaver Index, $y = 0.439 + 0.008x$. Here, (y) represents the adjusted biomass value, and (x) is the live weight of the prey species identified within the scat [37]. The Weaver index transforms the frequency of occurrence of prey in scats into an estimate of the actual biomass consumed to address the bias where smaller, more numerous prey items might appear more frequently in scats. Cluster composition was calculated as the percentage of clusters where a prey species was either killed, scavenged upon, or was likely to have been consumed (i.e., probable kill, Table 1) relative to the total of these combined cluster behaviors. For clusters, we calculated biomass by multiplying the number of kills by the average weight for a given species, sex, and age (where applicable; Supplementary File Table S1.8). Of note, ungulate neonates and calves were often fully consumed, leaving little evidence for species level identification. Further, cluster investigation in RMNP encountered very few calves during the snow season. To reduce potential biases due to misclassification, and to increase sample size, all calves were combined into a general ungulate category for diet summary calculations.

We compiled all scat and cluster data to compare wolf diet composition between RMNP (2016–2017) and SEMB (2014–2020). As not all prey species are equally available across seasons, we calculated wolf niche breadth for both snow (November to April) and snow free (May to October) seasons using Levins' formula [38]: $B = 1/(\sum p_i^2)$, where p_i is the proportion of each food item that contributed to the total diet of wolves from both cluster and scat data. Prey species were classified as (1) adult ungulates; (2) neonate and calf ungulates; (3) medium-sized mammals (beavers, hares); and (4) others (bears, small rodents, plants, waste, etc.), which was composed of items that contributed less than 5% individually and 10% total to the overall wolf diet. The B index could range from 1, indicating a strong specialization to one group of prey, to four, indicating equal preying on all groups.

Space-use analysis

We quantified home ranges for each individual wolf in both snow (November to April) and snow free (May to October) seasons using 95% autocorrelated kernel density estimators (aKDEs [39, 40]); using the 'amt' [41] and 'ctmm' [42] packages in R. aKDEs account for the

temporal autocorrelation inherent in animal movement data by incorporating continuous-time movement models, which reduces bias compared to traditional KDEs that assume independence between points. While aKDEs often result in larger estimated home range areas, the increase reflects a more accurate utilization distribution by correcting for oversampling in dense, autocorrelated clusters [39, 42]. Thus, aKDEs provide more realistic and less biased estimates of space use in high-resolution tracking data.

We fit a continuous time movement model for each individual and season using an Ornstein-Uhlenbeck process to account for the autocorrelation in the tracking data [43, 44]. The estimates of the wolf home ranges were then conditioned on the same movement models, ensuring each home range was tailored to the animal's movement behavior [39, 42]. To account for multiple collared individuals in the same pack, we generated density-weighted pack level home ranges for each season and year. We calculated pack-level home ranges by first rescaling individual seasonal home ranges to values between 0 and 1, then taking the average of all individuals within a given pack and year. These pack-level aKDEs were rescaled by taking each raster cell value and dividing by the sum of all raster cells to create a density-weighted estimate.

Prior to calculating aKDEs, GPS locations used were cleaned by removing duplicate fixes, and unrealistically long steps. While uncommon, any step length greater than 15km within a 2hr period was flagged and visually assessed using 'leaflet' [45] to determine if the step was part of the individual's true trajectory or if it was the result of an erroneous location. A flagged step was removed if the GPS location at either the start or end point was deemed an outlier. For all remaining steps, we calculated the average step length for individual wolves across both snow and snow free seasons. We included steps associated with all behaviours and movement states to test for differences in general movement requirements of wolves across packs and populations.

When calculating aKDEs, we additionally visually assessed and removed any extra-territorial forays that deviated outside the general pattern of territorial space use. Extra-territorial forays were identified by long step lengths, locations outside of a reasonable range size, and with no recursive movements. As well, we ensured that individual seasons had greater than 50 GPS locations [13]; locations in RMNP ranged from 104 to 2336 (median 1086) and in SEMB locations ranged from 54 to 3253 (median 915). Wolves in RMNP experienced high mortality from canine distemper during the course of the study which reduces step length and increases tortuosity [27]. Given this disease often impacted the space use and movement of the entire pack, all data up to the day

of a confirmed mortality was included in home range estimates. There was a trade-off between reducing the data informing snow-free space use estimates and biasing the estimates because of wolf condition. We included all data up to the day of a confirmed mortality in our movement and territory measures, noting this may be a factor that reduces home range size and step length in the snow-free season. Two wolves in SEMB were identified as lone wolves during the study and travelled extensively throughout the study area during the year. Home ranges were reported for these two individuals (Supplementary file S2) but were not included in further analyses or summary statistics for the region.

Model covariates

To account for factors that can impact wolf home range size, diet, cluster behaviour, and movement, we extracted model covariates from within the seasonal aKDE boundaries of individual wolves. For both snow and snow free seasons, we first calculated the area of individual aKDEs, niche breadth indices from investigated clusters, and average step length. We calculated the 3-year average moose density (moose/km²) within each aKDE using the results of aerial ungulate surveys in each region, averaged across three years of data (supplementary file S1). We also calculated average linear feature density (km/km²) and the average proportion of moose-preferred habitat (i.e., deciduous and mixed forest). Finally, we summarized yearly pack and population sizes, also calculating population density (wolves/1000 km²).

Mixed effects models

Using mixed effects models, we modelled the patch residency time (natural log Cluster Duration of kills in hours) and the patch returns (count of returns to kills during cluster period) by the average weight (kg) of prey found at the kill site, moose density in each home range corresponding to the wolf at the cluster, linear feature density in each wolf range, pack size, wolf population density in the study area for that year, season, and study site with a nested random effect for wolf and pack.

We modelled niche breadth, the natural log of step length (m) and the natural log of home range size (km²) by season (snow or snow free), pack size, population density, linear feature density, proportion of combined deciduous and mixed forest, moose density, and study area. For each model, we included a random effect for pack affiliation.

These general linear mixed effects models were completed using `lmer()` from *lme4* [46] and results were plotted using the *effects* package [47, 48] and *ggplot* [49] in R [50].

Results

Cluster investigations

The cluster algorithm identified 11,804 clusters from all collared wolves in SEMB between February 2014 and March 2020 and 6,458 clusters in RMNP (February 2016 to January 2018). In both RMNP and SEMB, we investigated 16% of the total GPS clusters (RMNP: 1061/6458 clusters; SEMB: 1897/11804) generated during the study periods. Wolf GPS clusters ranged in size from 2 to 275 locations (RMNP 17 ± 28 , SEMB 15 ± 23). Small clusters (2–4 locations) occurred more frequently, and we visited a higher total number but smaller proportion of small clusters (Fig. 2A, B, and C). Investigation rates increased with the number of locations and peaked around a proportion of 0.7 for clusters that had 20–60 locations, then declined as cluster size continued to increase (Fig. 2C). We identified 549 unique sites from the 1061 clusters we investigated in RMNP and 1091 sites from the 1897 investigated clusters in SEMB. Reproductive behaviors, den and rendezvous were associated with the largest clusters (Table 1, Fig. 2D and E). In comparison, resting clusters had some of the fewest locations and duration (Table 1, Fig. 2D and E).

The dominant primary behavior identified at clusters during investigations was kill (34% of investigated clusters in RMNP, 30% in SEMB), followed by resting (19% of investigated clusters in RMNP, 20% in SEMB) for both study areas (Table 1).

Diet composition and niche breadth

We summarized wolf feeding behaviors at GPS clusters into kill, probable kill, and scavenge sites. Wolves in both RMNP and SEMB fed on a wide variety of species (Table 2). Both scat analysis and site investigation revealed over 90% of wolf diet consisted of adult ungulates (RMNP: elk, moose, white-tailed deer; SEMB: moose, white-tailed deer), ungulate calves, and beavers, as well as snowshoe hares in SEMB. Niche breadth calculations at the population level indicated that wolves from RMNP had a more specialized diet compared to wolves in SEMB (Table 2). Similarly, at the individual level, niche breadth was higher in SEMB (3.03 [0.58, 5.49]) but increased in RMNP during snow free periods (0.81 [0.41, 1.21]; Supplementary S3, Table S3.3). Overall, in SEMB, wolves consumed fewer adult ungulates, but more beavers, hares, and ungulate calves (Table 2). However, niche breadth did not significantly differ with average moose density, pack size, or population density.

Comparing the biomass for the top five prey species in each study area shows moose constituted the highest proportion of wolf diet in both study areas, across sample types and seasons (Fig. 3). In RMNP, we observed similar diet proportions in scat samples for moose and elk in snow free seasons, with increased disparity during snow

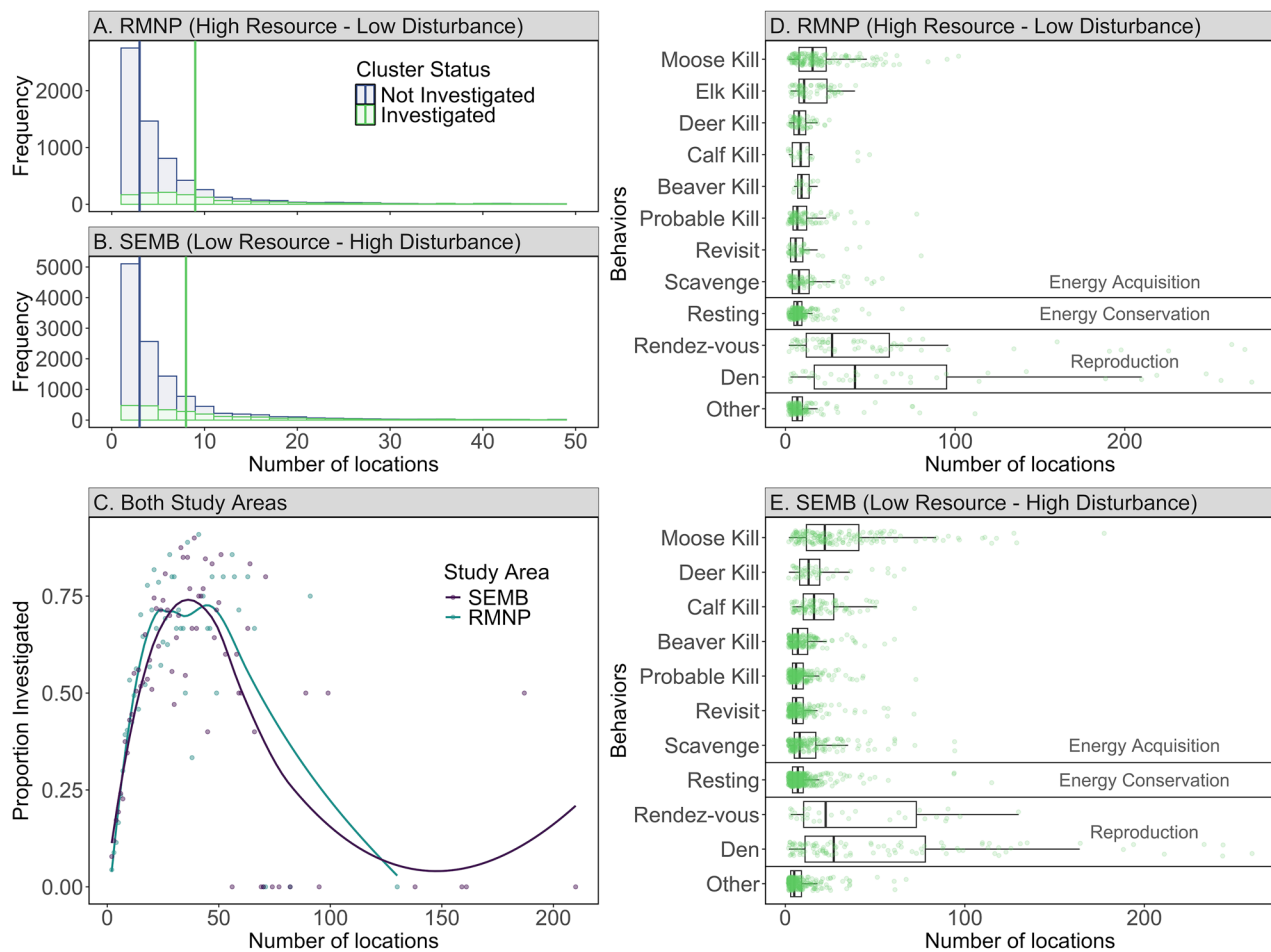


Fig. 2 Cluster size, defined by the number of GPS locations (2-hour schedule) included in the clusters investigated and not, proportion investigated, and behaviors at the clusters for the high resource and low disturbance area: riding Mountain National Park (RMNP) investigations from 2016 to 2017 and for the low resource and high disturbance area: southeastern Manitoba (SEMB) from 2014 to 2019. Histograms depicting the count of clusters that were investigated and not investigated by the number of locations for **(A)** RMNP (high resource – low disturbance) and **(B)** SEMB (low resource – high disturbance). Vertical lines indicate median number of locations for all clusters investigated (9 locations for RMNP, 8 locations for SEMB) and not investigated (3 locations for both study areas) note: x-axis was limited to 50 locations to remove long tail of 0 or 1 occurrence extending to 200 locations. **(C)** Scatterplot and line (loess smoothing method in ggplot2) showing the relationships between proportion of clusters investigated and the number of locations in clusters for both study areas. Boxplots and points of behavior categories at clusters of different sizes for **(D)** RMNP (high resource – low disturbance) and **(E)** SEMB (low resource – high disturbance). Primary behaviors and prey were used to define the categories on the y axes. Horizontal lines divide behaviors further from top to bottom into energy acquisition, energy conservation, reproduction, or other. Definitions of behaviors with key signs observed at clusters during investigations are in Table 1

seasons (Fig. 3). There were smaller seasonal shifts in wolf diet in RMNP at the population level and the overall beaver diet percentage was much lower in RMNP compared to SEMB, but we observed an increase in calf percentage in snow free seasons. In SEMB, scat biomass data indicated a seasonal shift in percentage of moose in wolf diet that was not as strongly indicated by kill site data (Supplementary S2, Figure S2.2). Specifically, the percentage of beaver biomass increased in snow free months, particularly in scat samples. We observed a seasonal shift in diet across almost all packs in SEMB (Fig. 4) where beaver and ungulate calves comprised a much higher percentage of wolf diet in snow free months.

Home range and step length

Individual aKDE home ranges were larger in SEMB (8.61 [5.07, 12.16]; Supplementary S3, Table S3.3). In RMNP, home ranges decreased in the snow free season (−5.05 [−1.02, −0.08]) and increased with linear feature density (8.19 [4.82, 11.56]; Fig. 5). We did not find evidence that wolf home range size changed with prey nor conspecific density in either population. In RMNP individual home ranges had a mean area of 236.4 km² (median: 125.0 km², SD: 387.8 km²; range: 1.17 to 1742.5 km²) in snow free seasons compared to 556.5 km² (median: 210.0 km², SD: 1119.0 km²; range: 100.5 to 4398.7 km²) in the snow seasons (Fig. 6). Excluding lone wolves, wolves in SEMB

Table 2 Diet composition and niche breadth calculations of wolves in Riding Mountain National Park (RMNP; 2016–2017) and southeastern Manitoba (SEMB; 2014–2019) from scat samples and at investigated sites identified as kill, probable kill or scavenge sites. Composition is reported as the percent occurrence, as well as total samples in brackets, calculated for each data source and study site. Dashed lines (-) indicates the species is not found in that region. We analyzed dietary niche breadth calculations year-round and separately for snow (November–April) and snow-free (May–October) seasons. Niche breadth values could range from one, indicating a strong specialization to one group of prey, to four, indicating equal preying on all groups

	RMNP (High Resources – Low Disturbance)		SEMB (Low Resources – High Disturbance)	
	Site	Scat	Site	Scat
Season	Dietary Niche Breadth			
Snow	1.18	1.43	2.95	2.14
Snow-Free	2.54	2.52	2.20	3.28
Year-Round	1.54	1.80	2.66	2.82
Species	Diet Composition			
Moose Adult	44.91% (119)	34.39% (54)	21.27% (151)	33.39% (185)
Deer Adult	16.98% (45)	10.19% (16)	9.58% (68)	11.91% (66)
Elk Adult	15.47% (41)	27.39% (43)	-	-
Unknown Ungulate Adult	2.26% (6)	0	0	0
Adult Ungulate Total	79.6% (211)	71.97% (113)	30.8% (219)	45.3% (251)
Moose Calf	2.64% (7)	1.91% (3)	10.28% (73)	7.4% (41)
Deer Calf	0.75% (2)	0	0.42% (3)	0.54% (3)
Elk Calf	0	0.64% (1)	-	-
Unknown Ungulate Calf	2.26% (6)	0	0	0
Calf Ungulate Total	5.66% (15)	2.55% (4)	10.7% (76)	7.94% (44)
Beaver	10.19% (27)	17.83% (28)	42.11% (299)	32.67% (181)
Snowshoe Hare	0	0	9.3% (66)	3.61% (20)
Medium Mammals Total	10.19% (27)	17.83% (28)	50.6% (381)	37.48% (187)
Grouse	0.75% (2)	0	1.55% (11)	0
Goose	0.38% (1)	0	0.28% (2)	0
Duck	0	0	0.14% (1)	0
Raven	0	0	0.14% (1)	0
Bird Total	1.43% (4)	0% (0)	2.12% (16)	1.62% (9)
Marten	0	0	0.14% (1)	0
Mink	0.38% (1)	0	0	0
Muskrat	0	0	0.28% (2)	0
Unknown Rodent	0	3.18% (5)	0	2.17% (12)
Small Mammal Total	0.38% (1)	3.18% (5)	0.40% (3)	2.17% (12)
Bear	0.75% (2)	1.27% (2)	1.97% (14)	1.62% (9)
Fish	0	0	1.69% (12)	3.43% (19)
Vegetation	0	3.18% (5)	0	0
Human Disposal	1.14% (3)	0	0.53% (4)	0
Unknown	1.13% (3)	0	0.28% (2)	1.62% (9)

had mean home range sizes of 849.7 km² (median: 529.4 km², SD: 1039.2 km²; range: 88.97 to 4463.3 km²) and 961.4 km² (median: 698.7 km², SD: 865.54 km²; range: 111.3 to 4397.0 km²) in snow free and snow seasons respectively (Fig. 6).

We found evidence of longer step lengths in SEMB (5.59 [4.52, 6.67]), particularly during snow free periods (0.18 [0.08, 0.29]; Supplementary S3, Table S3.3). Our results indicate step lengths increased as linear feature (0.29 [0.01, 0.57]) and wolf density increased (0.68 [0.14, 1.21]; Fig. 5) in SEMB. In RMNP, wolves increased step lengths with increased linear feature density (1.69 [0.66,

2.71]), moose density (0.4 [0.03, 0.78]), and proportions of deciduous-mixed forest (2.11 [0.69, 3.54]; Fig. 5). RMNP wolves moved less over the 2-hour time periods (median: 124.9 m, mean: 779.8 m, SD: 1238.6 m) than SEMB wolves (median: 141.3 m, mean: 1111.4 m, SD: 1810.6 m; Supplementary S2, Figure S2.5). We did not find evidence that RMNP movement changed seasonally, unlike the changes observed in SEMB (Figure S2.6).

Cluster duration analysis

Cluster duration increased with increasing weight of prey killed for both study areas (RMNP: 0.402 [0.271,

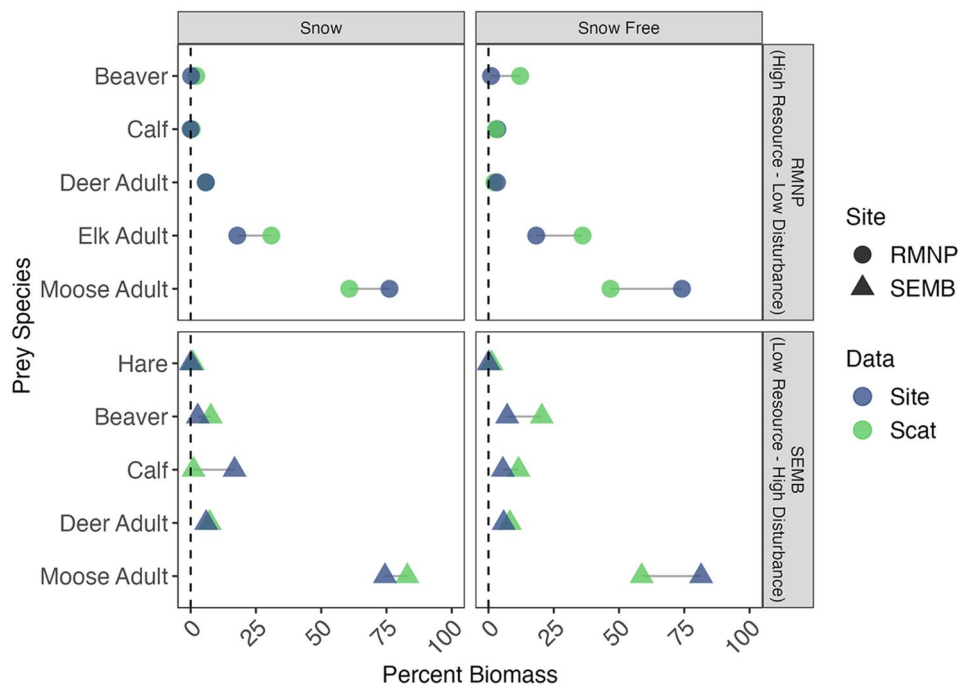


Fig. 3 Seasonal percent biomass contribution of prey type to gray wolf diet in Riding Mountain National Park (RMNP, high resources and low disturbance) (2016–2017) and southeastern Manitoba (SEMB, low resources and high disturbance) (2014–2019) determined through two data sources; kill site investigations of clusters from collared wolves (i.e., site) or found in wolf scat samples collected at all site types (i.e., scat)

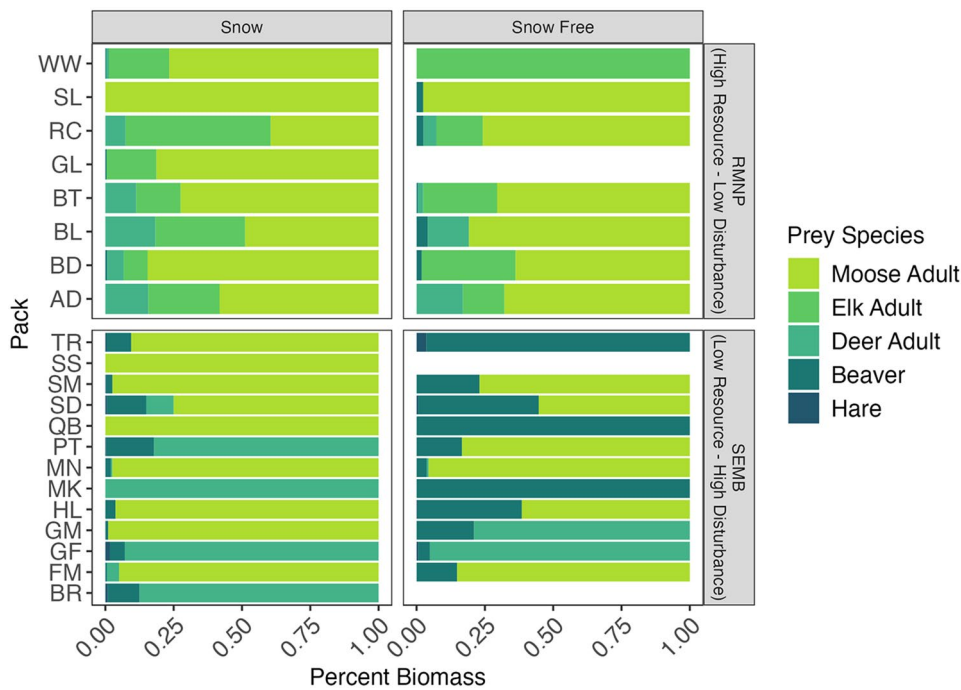


Fig. 4 Seasonal percent biomass contribution of prey type to gray wolf diet across packs in Riding Mountain National Park (RMNP; 2016 – 2017; $n=8$) the study area with high resources and low disturbance and southeastern Manitoba (SEMB; 2014–2019; $n=13$) the area with low resources and high disturbance determined through kill site investigations of clusters from collared wolves

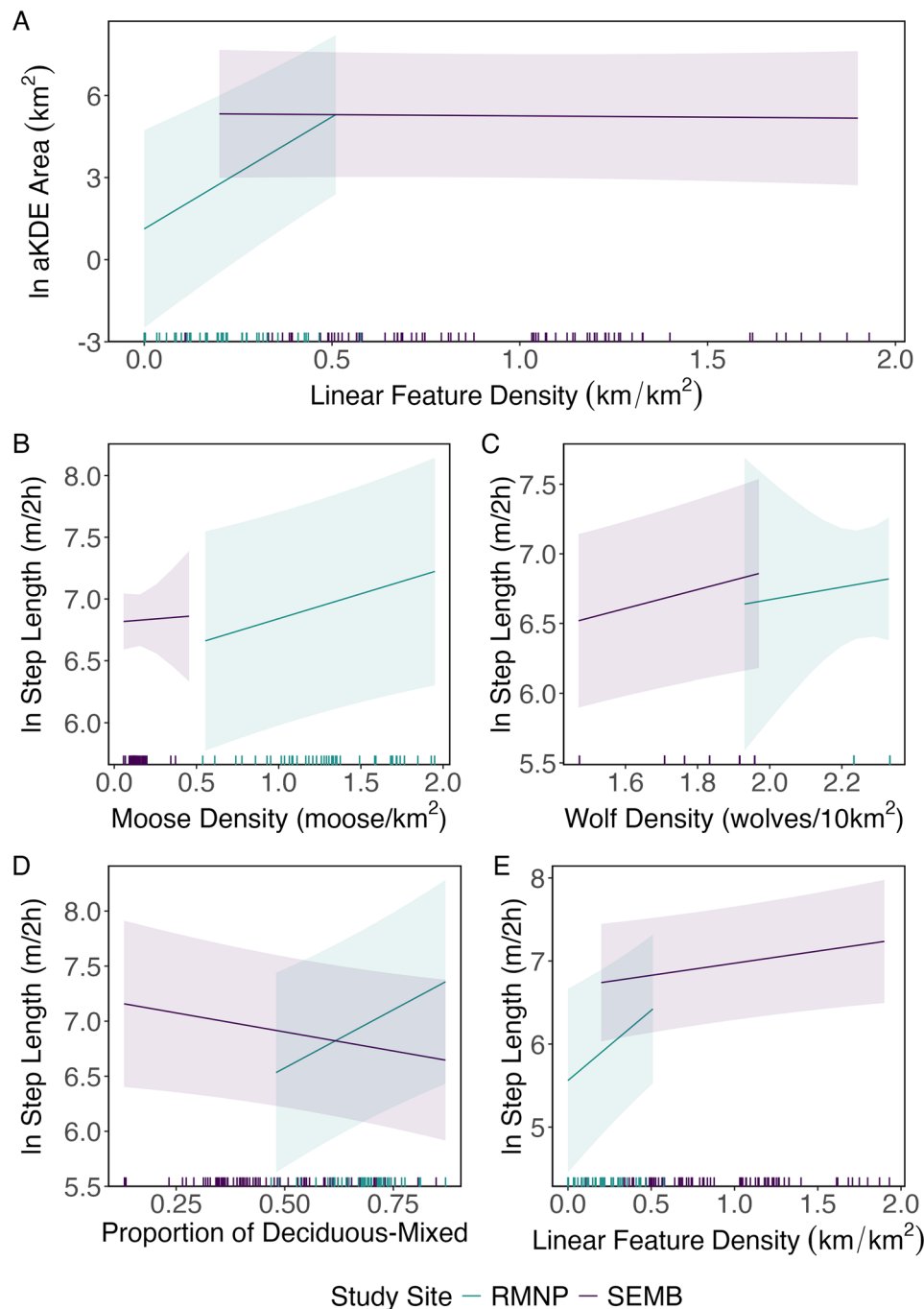


Fig. 5 (A) Natural log of individual aKDE home range size in response to linear feature density in both study areas, as well as the natural log of individual wolf step length (m/2 h) in response to (B) moose density, (C) wolf density, (D) proportion of deciduous-mixed forest and (E) linear feature density. Predicted responses have been fit to the data range for to reflect our range of inference and input data points for each study area Riding Mountain National Park (RMNP, high resources and low disturbance) and southeastern Manitoba (SEMB, low resources and high disturbance) are indicated as a rug on the x-axis

0.534]; SEMB: 0.31 [0.247, 0.373]; Fig. 7). Pack size (-0.058 [-0.17 , 0.055]) and linear feature density (-0.836 [-3.736 , 2.065]) did not influence cluster duration in RMNP (Supplementary S3, Table S3.1). In SEMB, cluster duration decreased with larger pack size (-0.068 [-0.118 , -0.018]) and when home ranges overlapped with

higher linear feature density (-0.81 [-1.296 , -0.323]). There was no evidence that moose density (RMNP: -0.147 [-0.833 , 0.539]; SEMB: -1.627 [-4.519 , 1.266]), wolf density (RMNP: 1.846 [-3.765 , 7.457]; SEMB: 0.224 [-1.16 , 0.711]) and proportion of deciduous mixed forest (RMNP: 0.485 [-3.144 , 4.114]; SEMB: -0.397 [-1.771 ,

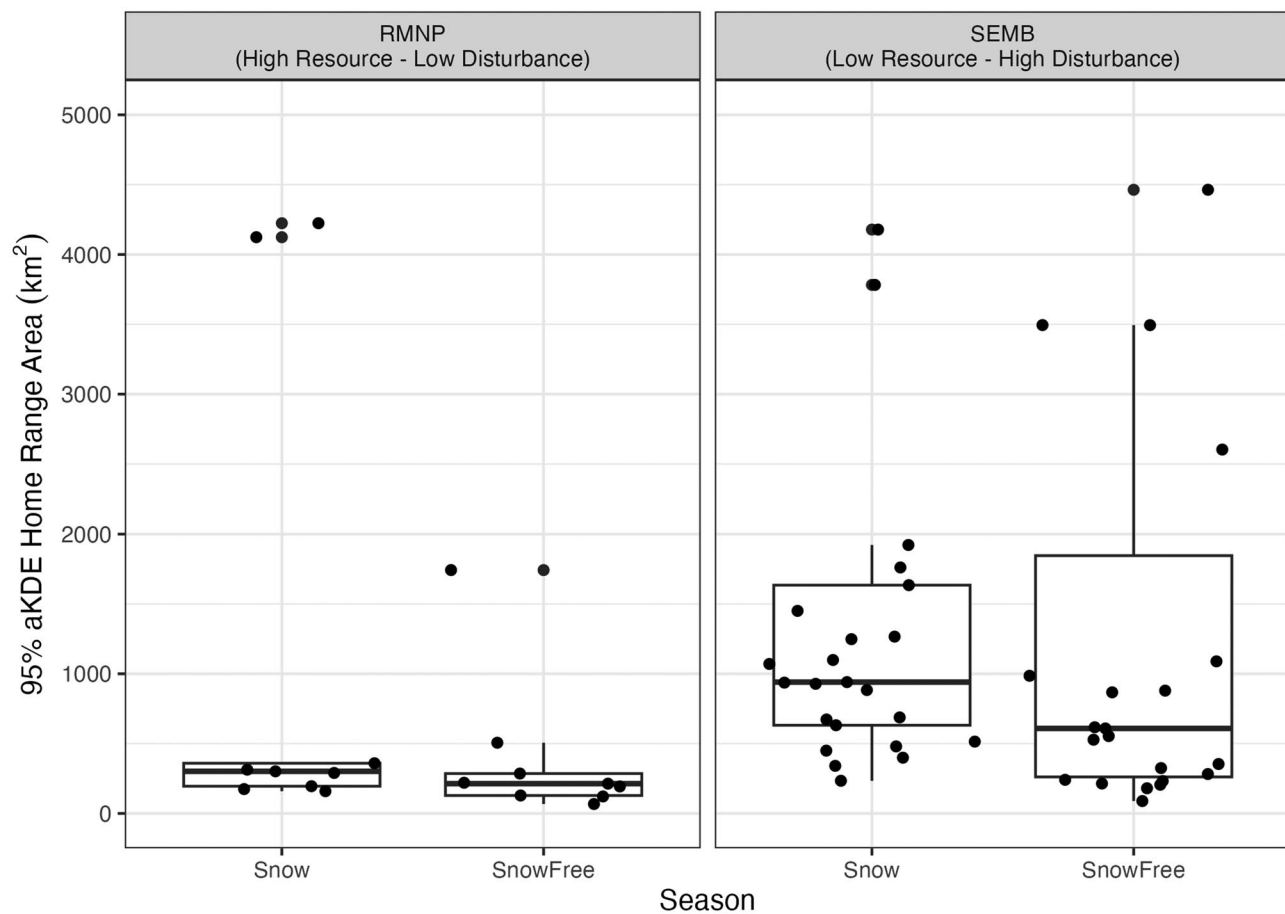


Fig. 6 Home range areas (km²) of gray wolf packs in the study area Riding Mountain National Park (RMNP; 2016–2017; $n=8$) and southeastern Manitoba (SEMB) (2014–2019; $n=13$) calculated from 95% aKDE isopleths. Home range sizes greater than 5000 km² were included in the boxplot calculations but not included in the figure for visualization purposes. See supplementary file table S2.2 for all values

0.977]) within home ranges influenced cluster duration for either study area (Table S3.1). Cluster duration was longer in the Snow Free season for RMNP (0.551 [0.264, 0.837]) but not in SEMB (0.075 [−0.133, 0.283]). We did not find evidence of a difference between the two study areas, SEMB was significantly positive (4.488 [2.595, 6.381]) and was greater but the estimates overlapped with RMNP which had wide confidence intervals that included zero (−2.221 [−17.573, 13.13]). The same model covariates but with cluster returns as the response yielded similar results (see Table S3.1 for the outputs of both models). The two response variables are correlated where longer cluster durations allow for more returns or departures and returns generate a longer cluster duration (See Fig. 8).

Discussion

Optimal foraging theory guided our comparative test of two wolf-prey systems with parallel field investigations. We tested if differences in responses between the two populations were driven by trade-offs in energy

acquisition and expenditure in distinct environments. We predicted with decreasing prey there would be increases in 1) niche breadth, 2) home range size and movement distance, 3) time spent at patches through longer total times at kill clusters and higher revisitation to previous kills. There were general trends that followed our expectations for study area differences. The niche breadth and territory sizes were larger, movement rates were greater and cluster durations were longer in the study area with lower resource abundance (southeastern Manitoba; SEMB) relative to the region with higher resource abundance (Riding Mountain National Park; RMNP). However, the differences in these responses were not explained by the density of the large primary prey (moose). We considered a prey item to be a resource 'patch' for wolves. Thus, cluster duration at a kill site is considered analogous to time in patch. Instead, we found wolves respond to the local resource availability at a patch (prey size), the depletion rates (pack size), and disturbance (linear feature density) when allocating time in a patch. Wolves also adjusted their course scale space use

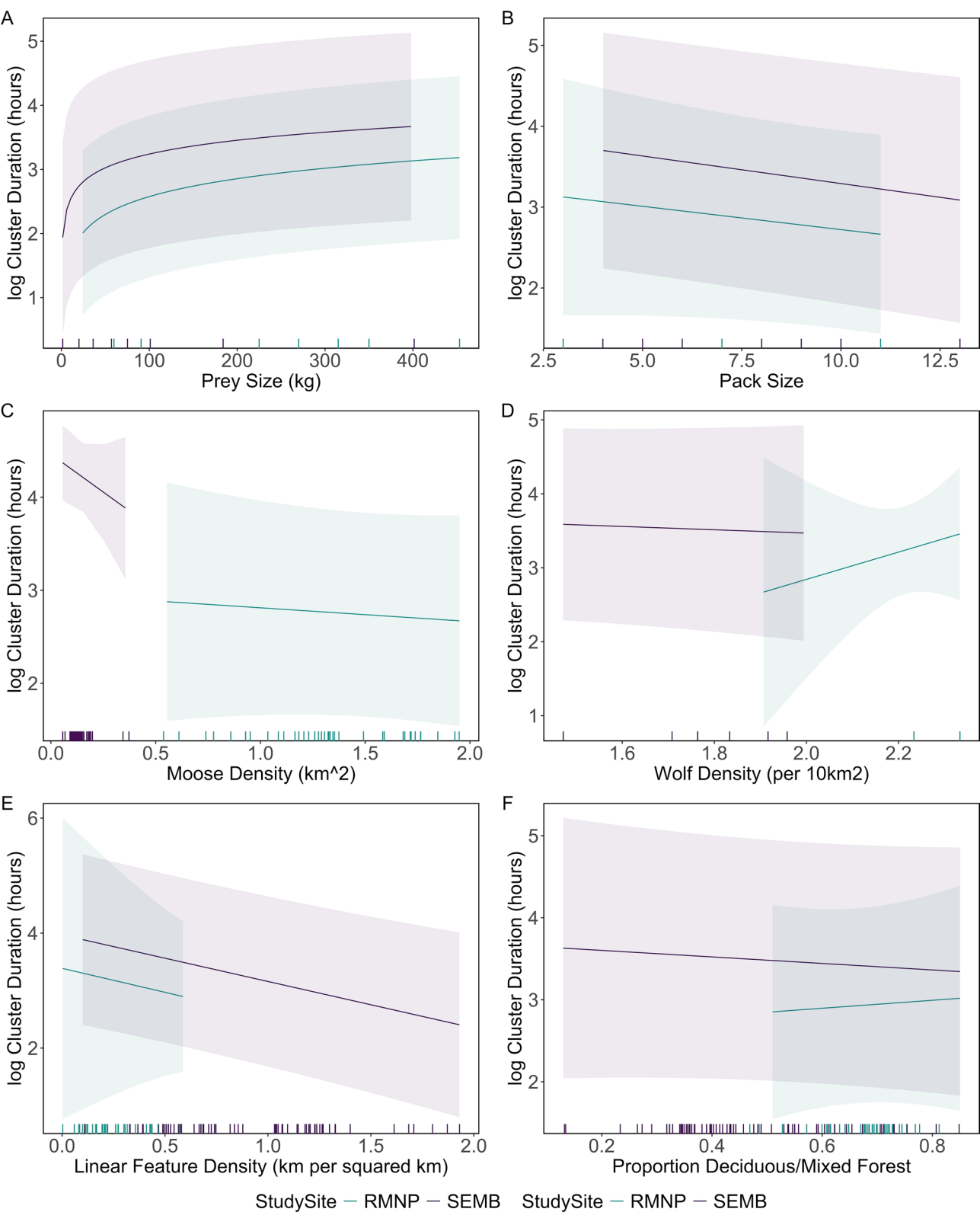


Fig. 7 Time spent in a patch (cluster duration in hours) response to (A) resources within the patch estimated as prey size, (B) patch depletion through pack size, (C) resource availability estimated as moose density, (D) resource competition through wolf density, (E) anthropogenic risk in the form of linear feature density, and (F) landcover composition, specifically the proportion deciduous and mixed forest. Predicted responses have been fit to the data range for to reflect our range of inference and input data points for each study area Riding Mountain National Park (RMNP, high resources and low disturbance) and southeastern Manitoba (SEMB, low resources and high disturbance) are indicated as a rug on the x-axis



Fig. 8 A wolf (*Canis lupus*) at a scavenging site of a hunter killed moose (*Alces alces*) visited by collared wolves. Reconyx camera deployed by Daniel Dupont north of Bissett (SEMB) during the first cluster investigation in October and picture captured in April 2015 when the wolves returned to the site again

and movement rates in response to season and linear feature density. While wolves did not adjust their space use to conspecifics at the pack-level, there was some impact of population size on movement rates. Thus, our comparative test through the lens of optimal foraging theory led to some unexpected discoveries and insights.

Optimal foraging theory predicts that predators will broaden their dietary niche as preferred prey become scarce. Wolf territories in RMNP overlapped with higher densities of ungulate prey compared to those in SEMB and primarily consumed large ungulates. In comparison, wolves in SEMB exhibited a broader niche breadth and more generalized diet, including a higher proportion of calves and small mammals. However, our results indicate that prey availability and composition may influence wolf diet more strongly than prey density alone. Notably, niche breadth did not correlate with moose density, suggesting other factors may be more influential. Wolves are known to diversify their diet when ungulate prey are scarce, incorporating alternative food sources such as fish [51] or marine prey [52]. Prey composition varied substantially between regions and among individual packs within each region. In SEMB, beavers were the most frequently consumed prey item during the snow-free period, contributing 25% of the biomass consumed, whereas RMNP wolves relied more consistently on large ungulates throughout the year. SEMB had fewer unique ungulate populations and individual packs within SEMB

showed more variation in diet than those in RMNP, likely reflecting localized differences in prey availability and habitat. Similarly, in urban systems, the diet of individual coyotes reflected their local territories, which generated variation in the population's dietary niche [53]. Some SEMB packs consumed high proportions of beaver and small mammals, while others incorporated more ungulates, indicating flexible foraging strategies at the pack level in response to limited or patchy resources. However, the density of these secondary prey populations were not incorporated into the models of the present study and should be tested more explicitly in the future.

Encounter rates between predators and prey species can be shaped both by large-scale space use decisions and by fine-scale movement behaviour. However, contrary to our prediction, we found a limited response of home range size and step length to either moose density or prey habitat. As an exception, RMNP wolves increased their step lengths with increasing moose density and prey-preferred habitat. Encounters between predators and prey often increase with increased predator movement rates and increased prey density [54]. Wolves may therefore increase their movement rates in areas with more prey to further promote encounters. In a wolf-moose system in northern Ontario, encounter rates were predominantly influenced by wolf movement, where kill rates increased with movement rates [55]. In an area of high prey density, we expected wolves would have to move

less overall to encounter prey. The qualitative differences between step lengths of wolves supported this expectation, where wolves in RMNP moved shorter distances on average than SEMB. These results suggest two movement responses to prey density: a fine scale adjustment of step length to increase encounter rates in RMNP and a coarse scale increase in overall movement rates in the low prey density context of SEMB.

Changes in movement rates can emerge from at least two non-exclusive mechanisms. First, animals may spend more time within resource patches, in which case reduced step lengths reflect increased residency time in high-value areas [56], which when applied to predators, could indicate longer handling times. Alternatively, movement rates may vary as a function of landscape structure, where increased patch density reduces the distance traveled between patches [57] even if encounter rates remain constant. Therefore, shorter step lengths do not necessarily imply lower prey encounter rates but may instead reflect differences in patch use or handling time. Future work that incorporates fine-scale behavioural state classification or cluster-based analyses would help disentangle whether observed differences in movement primarily reflect time spent within patches versus movement between them. Notably, the fine-scale differences in movement rates we observed did not scale up to detectable differences at the home range level, suggesting that population-level space use may be buffered against these behavioural mechanisms.

Animals are typically acquiring resources in the presence of risk, and they respond to both considerations when adjusting the time they spend at a location [58]. We applied this idea to a large carnivore where prey items were 'patches'. We found evidence that wolves adjust their time budgets in response to patch-level resource availability (prey size) and landscape-level risk (linear feature density). There are challenges that include increased chase distances and risk of injury when a predator is consuming larger prey which could increase cluster duration [4, 22, 59]. In addition, large kills provide more resources to wolves and following Marginal Value Theorem, higher resources in a patch leads to a longer time in a patch [1]. Wolves use alternative techniques when hunting beavers including sit and wait tactics associated with ambush hunting [60]. However, given that some beaver kills lasted up to 30 h (mean 4 h [60]), this may be a costly tactic when balancing time spent and resources gained.

The duration of time a predator spends at a cluster can be interpreted through the lens of Marginal Value Theorem, which we did here by estimating patch residency time using cluster duration. In addition, cluster duration could be considered as an estimate of prey handling time, which is an important parameter dictating satiation of kill rates and predation rates [61]. Handling is the time

it takes to actively chase, subdue, and consume the prey [61–63]. Digestion of prey is a passive process distinct from the active prey handling [61]. All of these behaviours, in addition to others, might be included within the time wolves spend at a kill cluster and thus might not fit more strict definitions of handling time. However, there is valuable insight to be gained through estimates of predator functional responses and prey predation rates by informing parameters using these empirical data.

The tension between cost and gain shapes foraging strategies in social consumers. Wolf packs cooperate to capture prey, but more individuals will deplete the resources more quickly, setting up a tension between cooperation and competition. Wolves are more cooperative with larger prey [64], sharing both the risks of hunting dangerous prey and the greater energetic reward. In southeastern Manitoba, wolves decreased time in patches with increasing pack size, likely due to accelerated resource depletion with more individuals at the same patch. We did not find evidence that wolves in either study area responded to a landscape-level measure of competition, i.e., wolf density. Except wolves moved more as wolf density increased in SEMB (Fig. 5). Indeed, there may be a population-level response in wolf population size to resource availability (numerical response [65]), that we did not test for.

Anthropogenic linear features, such as roads and seismic lines, can elevate perceived risk for large carnivores, in turn influencing space use and movement [66, 67]. Between our two study regions, linear feature density differs drastically. RMNP has fewer and more spatially confined linear features, largely outside the park boundary, which may influence wolves to expand their home ranges with linear feature density, thus shifting their core space use to avoid disturbance. This risk-avoidance strategy has also been found in other populations where wolves expanded their territories in response to high road density [68]. In contrast, SEMB has a pervasive network of linear features across the entire landscape, limiting wolves' ability to spatially avoid risky zones.

Linear features can instead increase foraging efficiency, especially in low-resource environments, thereby reducing home range size [13]. Further, smaller territories come with reduced defense and movement costs [15]. In RMNP, wolves benefit from higher resource availability and less pervasive disturbance, supporting overall smaller home ranges and reduced movement distances, consistent with predictions from optimal foraging theory [69]. Wolves in SEMB had overall larger home ranges and moved more compared to those in RMNP, particularly as wolf population density increased. Low prey density in SEMB may cause wolves to cover larger areas to access resources, therefore moving more to meet their energetic demands. For this wolf population, the prevalent network

of linear features provides movement corridors, possibly to increase prey encounters, or the ability to defend territories with fewer energetic costs. This dynamic generates an interactive effect where linear feature-induced risk and resource scarcity jointly shape wolf movement and space-use while wolves balance travel costs, risk exposure, and prey encounter rates.

Importantly, not all linear features exert the same ecological effects. Wolves often avoid high-risk linear features, such as paved roads, but may actively select low-risk features that offer movement advantages, including trails [70, 71]. In this context, behavioral responses to linear features reflect a nuanced risk-reward trade-off. In home ranges with high densities of linear features, reduced time spent at wolf clusters may indicate either increased perceived risk or efficient travel corridors enabling more rapid prey access. Under optimal foraging theory, risky patches diminish net energetic returns, lowering their value and leading wolves to reduce the time spent in such areas [72]. However, where linear features reduce travel cost between distant resource patches, they may also increase landscape-level foraging efficiency. Our results likely reflect both mechanisms where wolves across both populations increased their movement as linear feature density increased. Wolves in RMNP could use spatial avoidance strategies including increasing home range size and movement when in the presence of largely high-risk linear features. In contrast, wolves in SEMB experienced a wide range of high and low-risk linear features, moving more in high densities and reducing time spent at clusters. In this study, these patterns demonstrate how wolf responses are influenced by both landscape features and energetic trade-offs when making space-use decisions in complex, human-modified environments.

The effect of several covariates may have been difficult to detect because wolves in the two systems experienced completely distinct environmental conditions. Future work should include more populations that vary in resource abundance and disturbance to further disentangle the drivers of these foraging behaviours. Further, we compared these two areas spatially during a single period of time, but the context within each study area is not static. Specifically, RMNP was experiencing high mortality rates due to Canine Distemper Virus, which is known to cycle through populations. A disease outbreak can be a pervasive top-down influence on systems [73] and within RMNP during this study period, animals altered space use behaviour and decreased movement rates [27]. Therefore, follow up studies in both areas would clarify whether our findings are consistent within and between study populations.

We provide a quantitative analysis of foraging and space use behavior in two wolf populations that exist on

opposite ends of the resource abundance and anthropogenic disturbance spectrums. Our comparative study of two areas with parallel field investigations provided insight into the ubiquitous influence of anthropogenic disturbance. Our results suggest that wolves respond more to anthropogenic disturbance than resource abundance in two very distinct contexts. Wildlife movement is restricted by human disturbance [74] and the spatial overlap between humans and wildlife provides potential for conflict [75]. However, in landscapes with low human disturbance, such as RMNP, wolves appear capable of adjusting their movement in response to both prey density and preferred habitat. These conflating results indicate that in relatively intact landscapes with high prey densities, wolves retain the ability to exhibit adaptive spatial responses, potentially optimizing foraging efficiency and maintaining their ecological role. Determining where and how consumers, specifically large carnivores, will survive with future changes can inform the management of these populations.

Abbreviations

aKDE	Autocorrelated Kernel Density Estimator
RMNP	Riding Mountain National Park
SEMB	Southeastern Manitoba

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40462-026-00650-0>.

Supplementary Material 1

Acknowledgements

We respectfully acknowledge that RMNP is in the ancestral lands of the Anishinabe people and the Homeland of the Métis Nation, within Treaty 2 territory and Parks Canada works with First Nations from Treaties 2, 4, and 1. We would like to acknowledge that our research in Eastern Manitoba occurs within Treaty 3 and 5 Territory and within the Homeland of the Métis Nation. Funding and logistic support for this project was provided primarily by Parks Canada Agency (Riding Mountain National Park of Canada), with additional support from the Fish and Wildlife Enhancement Fund, and the Nature Conservancy of Canada. We thank T Sallows, KJ Kingdon, D Bergeson, R Robinson, R Baird, and R Grzela from Parks Canada and A Critchley and R Sandstrom from Shoal Lake Aviation for their contributions during data collection in RMNP. We are grateful for all the field technicians who assisted with data collection including S Graham and S Walmsley. The work in southeastern Manitoba would not be possible without the support of Manitoba Wildlife and Fisheries Branch, Manitoba Hydro, the Fish and Wildlife Enhancement Fund, Lac du Bonnet Wildlife Association and local communities. In particular, we thank K Leavesley, V Harriman, K Rebizant, D Brannen, D Bulloch, and J Matthewson for their continued support. Thank you to I Lavoie, A Scott, S Graham, J Budzinski, S Böttcher, M Erich, C Clayton, M Ewacha, N Kaminski, R Bartel, and J Dupont for field support and many others. Members of the Wildlife Evolutionary Ecology Lab at Memorial University of Newfoundland and Labrador and the Wildlife Restoration Lab at University of British Columbia Okanagan graciously provided comments on earlier versions of this manuscript.

Author contributions

Conceptualization for the paper was led by KK and CMP with support from DD and EVW. Field methods development was led by DD supported by SZS CMP and KK. Cluster investigations were led by CMP and SZS, supported by BC, in Riding Mountain and DD and KK in eastern Manitoba. Data collection

and processing was completed by all coauthors to various extents. TMN developed scat identification protocols and analyzed prey composition. JP and CMP led the development of code to clean collar locations and clusters and modified the cluster algorithm. Analysis and visualization was led by CMP and KK supported by BC, JWT and DD. EVW supported coauthors through supervision and lead funding acquisition. CMP and KK lead the writing of the original draft and received comments from all coauthors.

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Data availability

Data and code (Python version 2.7.1, R version 4.3.0) are available on GitHub https://github.com/CMPProkopenko/wolf_clusters and will be archived on Zenodo.

Declarations

Ethics approval

All field methodology was approved by Memorial University Animal Care Committee and conducted under AUP 16–02-EV issues in February 2016 and renewed every 3 years. We ensured the collaring followed established guidelines including collar weights being well under the suggested limit of 5% [76].

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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