Evidence for optimal behavior of predators from parallel field investigations in two distinct

wolf-prey systems

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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 test these predictions by investigating clusters from GPS collared wolves

(*Canis lupus*) in two predator populations with marked differences in their prey composition and

abundance. As expected, wolves in a less abundant system increase niche breadth, territory size,

step lengths, and time spent at each kill. Our work provides evidence of optimal behavior in an

apex predator which can support population resilience across changing landscapes.

Keywords: cluster investigation, diet composition, optimal foraging, wolves, predation, resource

abundance.

Author contribution statements

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 equally by CMP and SZS in RMNP and DD and KK in GHA 26.

Data collection and processing was completed by all coauthors to various extents.

JP and CMP lead 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 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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Introduction

Animals, whether populations, groups, or individuals, exist across a gradient of resource abundance. Resource spatial distribution influences animal space use as animals evaluate the energetic gains from the resources against the costs to access the resources (Charnov 1976, Ostfeld 1990). Apex predators that hunt and kill large-bodied prey incur a high initial energetic cost during the hunting stage (Williams et al. 2014) and receive a high energy gain during consumption. A useful framework to evaluate predator decisions in diverse systems is optimal foraging theory (Prokopenko et al. 2023). Optimal foraging theory predicts that with lower resource abundance, animals will generalize their diet and expand their territory to meet energetic needs (Ford 1983). In addition, due to the increased movement costs between sparse prey, predators will spend more time at a kill (Charnov 1976). We apply these foundational expectations to behavioral observations of two predator populations with marked differences in their prey composition and abundance.

Dietary niche classifies animals by the proportion of food items consumed and is largely constrained by the resources available to an animal. Animals are either generalists, which consume many resource types equally, i.e. broad niche, or specialists, which focus on particular resource types, i.e. narrow niche (Pianka 1969). Whether a predator opts to specialize or generalize its diet can depend on the density 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 (Burstahler et al. 2016) or when environmental conditions improve the success rate in hunting an alternative prey (Mysłajek et al. 2021). Species with broad food preferences, or those that consume alternate food types, will have wider dietary niches when preferred resources are scarce (Stephens and Krebs 1986). 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 (Slatyer et al. 2013).

Animals construct their dietary niches within their home ranges, which are the space used

to fulfill an organism's needs to survive and reproduce (Burt 1943). The size of ranges is shaped

by the amount of resources contained within, where increases in resources decreases range size

(Ford 1983, Rizzuto et al. 2021). In a study across western Canada, wolves (*Canis lupus*) had

smaller territories in more productive areas assumed to have more prey (Dickie et al. 2022).

Even at a fine scale, individuals adjust their range sizes as resources change temporally.

Following a wildfire and subsequent resource pulse, black bears (*Ursus americanu*s) reduced

their home range size (Crabb et al. 2022). In contrast to range contraction, expansion of home

ranges increases costs of moving between resource patches and defending larger territories (Sells

et al. 2021). Landscape variation in research distribution alters the search rate to meet the same

energetic threshold (Mitchell and Powell 2007). In response to increases in resource availability,

animals decrease their home range size to increase their exploitation efficiency.

Within home ranges, animals will adjust their activity budgets to be more efficient. The

time spent in patches is influenced by the energy spent traveling between, searching within

patches, and the energy consumed within a patch (Charnov 1976). 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

(Gable et al. 2023). Partial consumption of prey is an optimal foraging strategy when resource

availability is high, the cost of searching is low, and predators are often satiated; wolves

consumed smaller amounts of prey when kill rates were higher (Vucetich et al. 2012). At a fine

scale, predators can decrease their handling of killed prey when more resources are available.

We studied the diet and behavior of two populations of a generalist predator, wolves, in

different resource conditions. Overall, we expect wolves in the two populations to respond

economically to their environment following optimal foraging theory resulting in predictable

variation in behavior. We determine the influence of prey biomass (energy availability) on key

population level patterns of niche breadth, time budgets, and range size of wolves via concurrent

tracking and cluster investigation. We predicted that wolves with less prey available will respond

by increasing 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.

Study Area

Riding Mountain National Park

Riding Mountain National Park (RMNP) is a 3,000 km^2 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 (Figure 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 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. During the present study the wolf

population was approximately 71 individuals (consistently 60-80 individuals, 23

individuals/1000 km^2). 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-

6000 individuals. A significant population decline began in the late 1990's 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,

1200 elk, and 750 white-tailed deer. Recent beaver cache surveys conducted semi-annually show

an increasing trend from an estimated 1700 beaver caches in 2013 to 2600 in 2016 (Parks

Canada Report 2016).

Game Hunting Area 26

Game Hunting Area 26 (hereafter GHA 26) is a ~7,200 km^2 provincial management unit,

located in southeastern Manitoba. GHA 26 is bordered by Lake Winnipeg to the west, Ontario to

the east, Wanipigow River to the north, and Winnipeg River to the south (Figure 1C) and is part

of the Boreal Shield Ecozone (Ecological Stratification Working Group 1995), which extends

beyond the borders of the GHA designation and creates a continuous landscape. The landscape

in GHA 26 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 Anishinabe

peoples and the homeland of the Métis Nation. The study area includes the traditional territories

of Sagkeeng, Black River, and Hollow Water First Nations, Brokenhead Ojibway Nation, and

Northern Affairs communities (Bissett, Aghaming, Manigotagan, and Seymourville). The area is

predominantly public land, and GHA 26 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 (ROW).

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/1000km^2). The

predator guild includes populations of black bears, coyotes, and lynx. The prey base for wolves

in GHA 26 is diverse, yet spatially distinct, with moose found primarily in the northern half of

the study area and white-tailed deer found primarily in the southern half of the study area.

Secondary prey species include beavers, snowshoe hare, and woodland caribou (*Rangifer*

tarandus caribou). 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. The primary prey species for wolves in GHA 26 are moose, with an estimated

population of 2400 individuals in the early 2000s but experienced a drastic decline by

approximately 50% in the early 2010s. The most recent moose survey conducted in 2020

provided a population estimate (unadjusted for sightability) of approximately 1200 moose. A

beaver cache survey was conducted in 2018 and the cache density throughout the study area was

estimated at 1,14 beaver caches per km2.

Methods

Detailed methods of data cleaning, niche breadth calculations, movement and home range

analysis are in section S1 of the supplemental file. Data and code (Python version 2.7.1, R

version 4.3.0) and are available on GitHub https://github.com/CMProkopenko/wolf_clusters and

will be archived on Zenodo.

Cluster Investigations

Wolves were collared with GPS telemetry collars in RMNP (25 individuals) and GHA 26 (38

individuals) between 2014-2018 following Memorial University AUP 16-02-EV (Packs collared

by year in supplemental file S2). 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 (Figure 1C). To identify clusters, we

used an algorithm in Python, which was presented in Knopff et al. (2009), created by Warren

(2008), and adapted for wolves (Webb et al. 2008, DeCesare 2012, Irvine et al. 2022). In our

study, we defined a cluster as GPS locations that occurred within a 300m radius and 96 hours of

a previous location. This cluster algorithm identified 10 628 clusters from all collared wolves in

GHA 26 between February 2014 and March 2020 and 6323 clusters in RMNP (Feb 2016 to Jan

2018).

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). Clusters were most often accessed via snowmobile, quad, or occasionally

helicopter, as well as by canoe or boat in GHA 26 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. On average, we investigated clusters within a mean of 13.8 days of the

first location occurrence (median = 9 days).

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 (Figure 1C). 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, such as lack of wolf activity, or if the collared wolf spent too short of a duration at the site

to have been responsible for the death of the animal, e.g., < 2 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 (prey hair, bone

marrow, 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. A single site could have more than one behavior, for example if we observed both kill and

resting evidence. However, we would consider "kill" to be the primary behavior and "resting" to

be the secondary. For the data cleaning protocol following fieldwork, see supplemental file S1.

Scat Dissection

We collected scat samples during cluster investigations at sites and opportunistically

when traveling to sites in the field. 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. In GHA

26, we collected 531 scat samples from February 2014 to March 2020, while in RMNP we

collected 296 scat samples from Feb 2016 – Jan 2018. Scats were stored for a minimum of 2

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 arbitrarily selected from each scat for identification. Hair color, size, and cuticular scale

pattern were used to identify prey remains(Adorjan and Kolenosky 1969, Kennedy and Carbyn

1981). This method allowed for distinctions to be made between adult and juvenile ungulate

hairs. 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.

Diet Analysis

We calculated the composition of wolf diet as both percentage of occurrence in scat and

at clusters. This was calculated as either the percentage of scats containing a prey species relative

to the total number of scats or 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 cluster behaviors.

We compiled all scat and cluster data to compare wolf diet composition between RMNP

(2016-2017) and GHA 26 (2014–2019). As not all prey species are equally available across

seasons, we calculated niche breadth (*B,* Levins 1968) for both snow (November to April) and

snow free (May to October) seasons. We classified wolf prey into the 4 general groups. The B

index, therefore, 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 and snow free seasons

using 95% autocorrelated kernel density estimators (aKDEs; Fleming et al. 2015, Noonan et al.

2019) using the amt (Signer et al. 2019) and ctmm (Calabrese et al. 2016) packages in R.

Results

Cluster Investigations

In both RMNP and GHA 26, we investigated 16% of the total GPS clusters (RMNP: 1061/6433

clusters; GHA 26: 1897/11804) generated during the study periods. We identified both the

primary and secondary behaviors at each cluster and calculated various spatial and temporal

metrics that could provide a link between behavior and remotely sensed data.

Wolf GPS clusters ranged in size from 2 to 275 locations. Small clusters (2-4 locations)

occurred more frequently, and we visited a higher total number but smaller proportion of small

clusters (Figure 2A, 2B, and 2C). 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 (Figure 2C). Reproductive behaviors, den and rendezvous were

associated with the largest clusters (Table 1, Figure 2D and 2E). In comparison, resting clusters

had some of the fewest locations and duration (Table 1, Figure 2D and 2E).

The dominant primary behavior identified at clusters during investigations was kill (363

clusters in RMNP, 674 in GHA 26), followed by resting (201 clusters in RMNP, 385 in GHA 26)

for both study areas (Table 1). Time spent at kill clusters varied between prey species and study

areas (Figure 2, Table S2.1). In RMNP, wolves spent the most time on average at large ungulate

kills including moose (68 hours) and elk (60 hours) but less time at small ungulate kills such as

white-tailed deer (22 hours) and calves (26 hours). In contrast, wolves in GHA 26 spent longer at

kills of most ungulate prey including moose (92 hours), calves (63 hours), and white-tailed deer

(22 hours). However, wolves spent less time at beaver kills in GHA 26 with clusters lasting a

median of 22 hours compared to 46 hours in RMNP. GHA 26 wolves had more kill revisits than

RMNP (Table S2.1).

Wolves in the same pack often simultaneously visit the same site or departure/return

events by a single wolf can lead to generating multiple clusters that overlap in space and time.

For example, a single moose kill can be associated with 4 individual clusters if multiple wolves

visit the site or if a wolf leaves and returns (Figure 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 identified 549 unique sites from the 1061 clusters we investigated in RMNP and

1091 sites from the 1897 investigated clusters in GHA 26.

Diet composition and niche breadth

We summarized wolf feeding behaviors at GPS clusters into unique kill, probable kill, and

scavenge sites. Wolves in both RMNP and GHA 26 fed on a wide variety of species (Table 3).

Both scat analysis and site investigation revealed over 90% of wolf diet consisted of adult

ungulates (RMNP: elk, moose, white-tailed deer; GHA 26: moose, white-tailed deer), ungulate

calves, and beavers, as well as snowshoe hares in GHA 26. Niche breadth calculations indicated

that wolves from RMNP had a more specialized diet compared to wolves in GHA 26 (Table 2).

Overall, in GHA 26, wolves consumed fewer adult ungulates, but more beavers, hares, and

ungulate calves to increase the dietary niche breadth.

Comparing the biomass for the top five prey species in each study area shows moose

constituted the highest proportion of wolf diet across study area, sample type and season (Figure

3). In RMNP, we observed similar diet proportions in scat samples for moose and elk in snow

free seasons, with increased disparity during snow seasons (Figure 3). Cluster data revealed

beaver and calves made up a higher percentage of the diet in snow free seasons. In GHA 26, scat

biomass data indicated a seasonal shift in percentage of moose in wolf diet that was not as

strongly observed in the cluster data. 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 GHA 26 (Figure 4) where beaver and calves comprised a much higher percentage of wolf diet

in snow free months. There were fewer observable seasonal shifts in wolf diet in RMNP. Beaver

diet percentage was much lower compared to GHA 26 overall, but we observed an increase in

calf percentage in snow free seasons.

Home range and step length

Across both study sites, wolf packs typically had smaller home range sizes during snow

free seasons and wolves in RMNP had smaller home ranges than wolves in GHA 26 (Figure 4).

In RMNP home ranges had a median area of 202.9 km^2 (range: 67.4 to 1736 km^2) in snow free

seasons compared to 294.8 km^2 (range: 159.1 to 4116.7 km^2) in the snow seasons. Wolves in

GHA 26 had median home range sizes of 552.0 km^2 (range: 88.6 to 4445.9 km^2) and 934.4 km^2

(range: 233.0 to 4076 km^2) in snow free and snow seasons respectively. RMNP wolves moved

less over the 2-hour time periods (median = 125 m, mean = 793 m) than GHA 26 wolves

(median = 154 m, mean = 1077 m), see supplementary file Figure S2.5. RMNP did not adjust

their movement seasonally, compared to GHA 26 (Figure S2.6)

DISCUSSION

In our comparative study of two populations, wolves increased their diet breadth, home

range size and movement distances, and patch residency time in areas with less prey. Wolves in

areas with lower resource availability were more generalized than wolves in the research rich

areas. The shift to pulses in smaller bodied prey was greater in the low resource population

compared to the high resource population. Time budgets between the two populations differed:

wolves spent more time at kills in low resource areas. Wolves spatially responded by increasing

movement rates and territory sizes with decreasing resource availability. We find responses at

the population and pack level follow the fundamental expectations of animals attempting to

maximize energy acquisition and minimize time expenditure supporting our predictions from

optimal foraging theory.

Wolf niche breadth increased with decreasing prey abundance, as expected from optimal

foraging theory. At a population-level, wolves in RMNP overlap with a higher density of

ungulate prey populations than GHA 26. Wolves in RMNP consumed primarily large ungulate

prey. In comparison, wolves in GHA 26 had a broader niche breadth and more generalized diet,

consuming more calves and small mammals. Wolves have the potential to expand their diet

when ungulate prey are not available to include diverse alternative prey, such as fish (Darimont

et al. 2003) or marine prey (Roffler et al. 2021). In GHA 26, beavers were the most frequently

consumed prey item, contributing 25% of consumed biomass in the snow free period, in contrast

to RMNP that focused on large ungulates throughout the year. In many wolf systems, beavers are

an important subsidy for wolves and can increase recruitment (Gable et al. 2018). Here, wolves

adjusted their diet to smaller prey in the area with lower resources more than those in the high

resource area, as expected from optimal foraging theory.

Optimal foraging predicts increased competition in areas of low resource abundance will

drive individuals to add new items to their diet, widening their trophic niche, and forming a

population of generalist foragers (Stephens and Krebs 1986). Alternatively, we could view this

through competition theory, where increased competition leads to stable coexistence through

niche differentiation, reducing dietary overlap between competitors (Schoener 1974, Pianka

1981). Both RMNP and GHA 26 both have black bear populations that are a potential competitor

for wolves though in some instances were a prey item (Table 2). Competition and resource

availability are not mutually exclusive but are inherently linked as a consumer selects resources.

For example, caribou consume vascular plants when available but predation or competition push

caribou towards consuming lichen (Webber et al. 2022). Assessing the various factors that

contribute to the niche breadth within a species will strengthen our descriptions of critical habitat

and help to predict distributions of animals.

Territories were larger in the study area with less abundant prey, supporting the idea that

wolves expand their distribution to meet energetic needs. Similarly, territories of wolves across

the boreal forest decreased with increasing resource density (Dickie et al. 2022); wolves in low

resource conditions had territory sizes of less than half that of wolf territories in high resource

conditions. In our study, year-round territory sizes of resident wolf packs spanned from 137.9 to

2621.7 km^2 in RMNP. The territory sizes in RMNP fall below or at the low end territory size of

precious estimates from wolves across the boreal (Dickie et al. 2022) indicating the resources in

RMNP are higher. In GHA 26, territories were 213.9 to 12901.3 km^2 indicating lower resource

conditions than RMNP. In addition, step lengths (2hr scale) were shorter for RMNP than for

GHA 26. Smaller territories come with reduced defense and movement costs (Sells et al. 2021),

which we find with reduced movement distances in RMNP. Thus, the wolves in RMNP

experience multiple energetic benefits compared to wolves in GHA 26.

In addition to resource availability, anthropogenic disturbance can alter space use

behavior, but high resource density and low disturbance were co-occurring factors in our study;

RMNP was an area with reduced disturbance and smaller territories compared to GHA 26.

Increasing linear features on the landscape decreased wolf territories almost twice as much as

increasing resources due to improved resource exploitation via movement efficiency (Dickie et

al. 2022). Alternatively, linear features can fragment habitats and be perceived as a risk, which

would in turn erode habitat quality. In support of this, wolves in Italy increased their territory

sizes with road density (Mancinelli et al. 2018). Wolf space use behavior, specifically their

territory size, was characteristic of differences resulting from resource abundance, but the high

resource area coincided with being a protected area with a distinct border.

The time budgets of wolves differed between the two populations. Overall, RMNP

wolves spent less time at large kills and scavenging than GHA 26 wolves. In addition, there were

limited revisits of kills in RMNP, which we interpret as wolves opting for new kills instead of

spending time at previous kills. This behavior aligns with the expectation from Marginal Value

Theorem that consumers reduce their time within resource patches as resource abundance

increases (Charnov 1976). A prey item could be compared to a 'patch' for carnivores. For

example, wolves meeting their energetic needs reduced the amount of each prey item consumed

and not the number of prey killed (Zimmermann et al. 2015). Indeed, partial prey consumption is

an optimal foraging strategy that could be generating shorter times at kills in RMNP.

Handling times generally increase with the size of prey, yet there were important

exceptions between species and study areas that do not follow this pattern. For example, RMNP

tended to spend longer at beaver kills than white-tailed deer. The time at a kill includes both the

time it takes to chase and subdue prey with consumption and digesting time. Wolves have been

found to use alternative techniques when hunting beavers including sit and wait tactics

associated with ambush hunting (Gable et al. 2021) However, given that some attempts lasted up

to 30h (mean 4h; Gable et al. 2021), this is a costly tactic in a temporal budget. In support of this,

RMNP wolves spent twice as long at beaver kills than GHA 26 wolves, a prey GHA 26 wolves

consumed over twice as much as RMNP wolves. Beaver kills were the only incidence where

RMNP wolves had a longer average time at kill sites. Future work in our system will focus on

decomposing the predation sequence and calculating population metrics such as kill rates and

predation rates.

We found evidence for all predictions at different scales of behavior, but there is likely a

hierarchical organization to how animals respond to resource limitation which we did not test.

For example, the behavioral response to low resources could begin with adjustments to

movement rate and activity which propagates to changes in territory size. Future work could

describe the sequence of animals adjusting their behavior as resources change. Further, we

identified that the low resource population used the full suite of predicted responses, indicating

that these animals may be approaching a threshold where no further behavioral adjustment is

possible. Identifying the threshold of animal behavioral limitation brings these responses to their

population-level consequences. Consumers can mediate changes in resources by adjusting their

space use and time budgets to behave optimally by maximizing their energy gain and minimizing

costs. However, wildlife are restricted by human disturbance (Tucker et al. 2018) and conflict

increases when humans and wildlife overlap spatially (Teichman et al. 2013). Determining where

and how consumers, specifically large carnivores, will survive with future changes can inform

the management of these populations.

 TABLES

404   **Table 1.** Description of behaviors assigned to clusters during field investigations. Behaviors are presented in order of the hierarchy

405   that was determined during the cleaning phase of our process. It is common for behaviors lower in the hierarchy to occur at sites with

406   higher ranked behaviors. For example, most kills often include resting and scat activity. The total count of clusters, the median

407   duration in hours, and median radius in meters of these clusters are presented by study area.

Behavior	Description	Count	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 = 31, GHA 26 = 105	RMNP = 166, GHA 26 = 182	RMNP = 224, GHA 26 = 241

Rendezvous	An area used for pup rearing following weaning. Similar signs of wolf activity (adults and pups) as den sites.	RMNP = 60, GHA 26 = 30	RMNP = 151, GHA 26 = 267	RMNP = 279, GHA 26 = 241
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 = 363, GHA 26 = 674	RMNP = 56, GHA 26 = 50	RMNP = 202, GHA 26 = 196
Kill Revisit	A collared individual returning to previously identified kill site that has spatial overlap but is temporally distinct from previous cluster.	RMNP = 48, GHA 26 = 212	RMNP = 19, GHA 26 = 16	RMNP = 188, GHA 26 = 140
Probable Kill	Potential predation event by the collared wolves. Carcass is not observed but there is a high level of	RMNP = 95, GHA 26 = 230	RMNP = 20, GHA 26 = 18	RMNP = 151, GHA 26 = 146

wolf and prey activity including trampled vegetation and tracks. Hair or blood may be present but does not confirm a successful kill.

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 = 89, GHA 26 = 184	RMNP = 38, GHA 26 = 45	RMNP = 184, GHA 26 = 198
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 = 201, GHA 26 = 385	RMNP = 14, GHA 26 = 16	RMNP = 121, GHA 26 = 121
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 = 161, GHA 26 = 260	RMNP = 18 , GHA 26 = 32	RMNP = 155, GHA 26 = 146

| 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 GHA 26
A mortality signal was sent to researchers in the field after 12 hours of no movement recorded. |

410 **Table 2.** Diet composition and niche breadth calculations of wolves in Riding Mountain National Park (2016-2017) and Game

411 Hunting Area 26 (2014-2019) from scat samples and at investigated sites identified as kill, probable kill or scavenge sites.

412 Composition is reported as the percent occurrence, as well as total samples in brackets, calculated for each data source and study site.

413 Dashed lines (-) indicates the species is not found in that region. We analyzed dietary niche breadth calculations year-round and

414 separately for snow (November-April) and snow-free (May-October) seasons.

	RMNP		GHA 26	
	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)

FIGURES

Figure 1. Cluster investigations were completed in two wolf populations A) RMNP with inset of

B) location of both study areas within Manitoba and C) GHA 26. Borders of RMNP and GHA 26

 filled in grey with the centroid locations of all investigated clusters in black; D) Conceptual

423 diagram outlining the hierarchical structure of sites, clusters and behaviors investigated and

424 determined through field work. Sites could be composed of multiple GPS clusters from a single

425 or multiple wolves. Clusters were generated from the GPS locations (n>2) of a single wolf. Field

426 investigations of clusters revealed primary and secondary behaviors associated with a site that

427 could be linked to cluster characteristics.

Figure 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 Riding

Mountain National Park investigations from 2016 to 2017 and for Game Hunting Area 26 from

2014 to 2019. Histograms depicting the count of clusters that were investigated and not

investigated by the number of locations for A. RMNP and B. GHA 26. Vertical lines indicate

median number of locations for all clusters investigated (9 locations for RMNP, 8 locations for

GHA 26) 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 and E. GHA 26. 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.

Figure 3. Seasonal percent biomass contribution of prey type to gray wolf diet in RMNP (2016 -

2017) and GHA 26 (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).

Figure 4. Seasonal percent biomass contribution of prey type to gray wolf diet across packs in

RMNP (2016 - 2017; n = 8) and GHA 26 (2014-2019; n = 13) determined through kill site

investigations of clusters from collared wolves.

458   **Figure 5.** Home range areas (km2) of gray wolves in RMNP (2016 - 2017; n = 8) and GHA 26

459   (2014-2019; n = 13) calculated from 95% aKDE isopleths. Home range sizes greater than 5000

460   km2 were included in the boxplot calculations but not included in the figure for visualization

461   purposes. See supplemental file Table S2.2. for all values.

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A wolf (*Canis lupus*) at a scavenging site of a hunter killed moose (*Alces alces*) visited by

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cluster investigation in October and picture captured in April 2015 when the wolves returned to

the site again.