HUNGRY WOLVES AND DANGEROUS PREY: A TALE OF PREY SWITCHING

by

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ABSTRACT

For 40 years wolves have subsisted on elk in Riding Mountain National Park – an intensively monitored system. During 24 continuous months of fieldwork, I uncovered a novel observation of prey switching. Wolves switched to a more dangerous alternative, moose, from the historical and vulnerable prey, elk. Generalist predators are ubiquitous but testing mechanisms of population-level prey switching in charismatic megafauna is rare. I empirically test foundational theory with long-term data on predator consumption and prey population abundance to identify processes underlying prey switching. First, the urgency of acquiring energy mediates space-use behaviour of wolves; hunger drove a fine-scale switch in prey tracking. Hunger increased the preference for moose catchability and decreased tracking of elk. Movement patterns of hungry wolves are indicative of area-restricted search behavior to promote encounter rates. Second, I tested the ideal gas law's ability to describe encounter rates between predators and prey. Wolf movement rate governed the effective speed, and consequently, encounters in the system. Winter kills increase with effective speed and total light for moose, but not for elk. There was a seasonal switch in these prey-specific relationships, where only elk kills increased with effective speed and total light in summer. Third, I express a functional response of a single predator to the abundance of two prey types, dissimilar in energy and time costs to predators when searching, attacking, and consuming prey. This model operationalizes the balance of costs and gains inherent in foragers pursuing their next meal. I simulate how optimal foraging decisions produces prey switching. Fourth, I empirically test this model with data collected on wolf diets and prey abundance in Riding Mountain National Park since 1970. Despite moose being most abundant and consumed, wolves still maintain their preference for elk over moose. The switching observations at both the population and pack level support optimal foraging predictions; wolves prefer elk but their preference for elk declined as the total prey biomass available declined. From search to consumption, my research captures echoes of broad scale population contexts resonating within the fine-scale behaviours of a predator in a multi-prey system.

CO-AUTHORSHIP STATEMENT

This thesis was completed as a PhD research project in the Department of Biology at Memorial University of Newfoundland and Labrador. I am the principal coauthor of all the chapters in this thesis. I am responsible for the ideas, project design, data analysis, writing, and manuscript preparation. My research is the result of collaborative contributions particularly my supervisor Dr. Eric Vander Wal, my colleague Sana Zabihi-Seissan, and my other coauthors on Chapter 2: Daniel Dupont, Katrien Kingdon, and Dr. Julie Turner; Chapter 3: Daniel Dupont, Katrien Kingdon; Chapter 4: Drs. Tal Avgar and Adam Ford; and Chapter 5: Drs. Paul Paquet and Adam Ford.

The data for this thesis was supported, collected, and maintained through Parks Canada and the Manitoba Government. The primary data source for this thesis is the wolf location and site investigation data collected by myself and Sana Zabihi-Seissan (Chapter 2, 3, 5). For Chapter 2, landscape layers were generated from locations of elk, moose, and white-tailed deer remotely and through aerial surveys collected by Parks Canada, Drs. Eric Vander Wal, Ryan Brook, and Erin McCance, habitat covariate layers were provided by Sean Frey and Tim Sallows at Parks Canada. Data used in Chapter 3 for wolves, elk, and white-tailed deer in Riding Mountain National Park was collected through Parks Canada and for moose in Game Hunting Area 26 was collected by Daniel Dupont and Katrien Kingdon through the Manitoba Government. Chapter 5 synthesized data collected in Riding Mountain National Park through Parks Canada and extracted wolf diet data from publications by Dr. Lu Carbyn, Dr. Paul Paquet, Dennis Meleshko, and Tim Sallows. Acknowledgements and co-authorship statements are included at the end of each chapter.

Chapter 1. I am solely responsible for this chapter, sections may be revised and included in the submission of Chapter 5 for publication.

Chapter 2. Prokopenko CM, Zabihi-Seissan S, Dupont DLJ, Kingdon KA, Turner JW, and Vander Wal E. Pangs of hunger: State drives switching and searching response of a social predator will be submitted to *Journal of Animal Ecology*.

CMP conceived the original idea for the manuscript. Data was collected and provided by CMP and SZS in RMNP. CMP conducted the analysis with assistance from JWT and KAK. CMP wrote the manuscript with input and approval from all coauthors.

Chapter 3. Prokopenko CM, Zabihi-Seissan S, Dupont DLJ, Kingdon KA, and Vander Wal E. Movement and detectability influences diel variation in kill rates in a multiprey system will be submitted to *Functional Ecology*.

CMP conceived the original idea for the manuscript. Data was collected and provided by CMP and SZS in RMNP, DLJD and KAK in GHA 26. CMP conducted the analysis and wrote the manuscript with input and approval from all coauthors.

Chapter 4. Prokopenko CM, Avgar T, Ford AT, and Vander Wal E. 2022. Optimal prey switching: Predator foraging costs provide a mechanism for functional responses in multi-prey systems. *Ecology*.

The conceptual framework was supported by discussions with all coauthors, the model was formalized by CMP and TA. CMP wrote the manuscript which was revised by all coauthors.

Chapter 5. Prokopenko CM, Zabihi-Seissan S, Paquet P, Ford A, and Vander Wal E. Empirical evidence of optimal prey switching in an apex predator will be submitted to *Ecology Letters*.

CMP conceived the original idea for the manuscript. Data was collected and provided by myself and SZS. CMP conducted the analysis and wrote the manuscript with input and approval from all coauthors.

Chapter 6. I am solely responsible for this chapter, sections may be revised and included in submission in the future.

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CHAPTER 1:PROLOGUE

Predation epitomizes the *'struggle for existence'* (Darwin 1875). Predators aim to increase their fitness through energy acquisition by consuming prey, while prey try to survive by evading predators. Predation is an interaction between species in different trophic levels, one species, the prey, is negatively affected where the predator benefits. For prey, it represents ultimate loss while for a predator it is a short-term gain and one of many repeated events. Consumer-resource interactions create competition, directly and apparently, within trophic levels and species. This thesis focuses on the response of wolves to their prey and offers a revisionist approach to foundational theory though integrating natural nuance, e.g. multiple prey, predator state, antipredator traits, spatial and temporal variation, into these models.

1.1 FOUNDATIONAL ECOLOGICAL THEORY

Early theory describing the relationship between trophic levels was developed in parallel by two ecologists (Lotka 1925, Volterra 1926). The framework described the change in prey and predator abundance due to births and deaths over time, where prey mortality is due to predation, and this consumption feeds predator growth. Lotka described predator movement using 'kinetic theory of gases', describing encounters as a product of predator movement rate, size, and densities of both predator and prey. The ideal gas law (Maxwell 1860) has provided a useful framework and null model for many biological processes including encounters between animals (Hutchinson and Waser 2007). The pattern of home range scaling with body size was supported by expectations from the ideal gas law (Jetz et al. 2004). Further, the ideal gas law provides a framework for estimating the density of animals from observations on transects or camera traps (Yapp 1956, Rowcliffe et al. 2008). Therefore, the ideal gas law is a useful formula to explain how predators encounter their prey, but to fully depict consumption rate additional details that add biological realism should be included.

The term ‘functional response’, coined by (Solomon 1949), describes the consumption rate of prey by predators as it changes with prey density and articulates the flow of energy up trophic levels. Holling (1959a, 1959b) proposed three models of functional response that comprise contemporary consumption rate descriptions (Jeschke et al. 2002). From zooplankton (Fussmann et al. 2005) to lions (Fryxell et al. 2007), a considerable effort has been directed to determining the shape of the functional response curves, and which parameters describe predator responses to prey (Jeschke et al. 2002, Uiterwaal et al. 2018), sometimes sparking longstanding debates (Abrams and Ginzburg 2000).

The simplest type of functional response, referred to as Type I, depicts a linear increase in consumption rates with increasing prey density, described by the attack rate. For example, filter feeders exhibit a constant attack rate until they reach capacity (Jeschke et al. 2004). The attack rate is the area where prey are removed over time (also more precisely termed space clearance rate; DeLong 2021). The attack rate can be further deconstructed into components such as search efficiency, encounter rate, and probability of capture success (Hebblewhite and Pletscher 2002, Fryxell et al. 2007). The Type II functional response, *i.e.* ‘Holling’s Disc Equation’, incorporates the time it takes to process prey items (*i.e.* handling time), resulting in a saturating functional response. Handling time in some cases includes digestion though it arguably may not interfere with searching for the next prey item (Jeschke et al. 2002). If a predator follows a Type III functional response it will demonstrate a sigmoid consumption response with prey density. In this case, predators will consume disproportionally less prey at low densities, then accelerate consumption rates at intermediate densities to gradually reach an asymptote due to handling time as in Type II functional response (Denny 2014). The sigmoid shape is created by the 'Hill Exponent' (Real 1977), which alters attack rate as a function of prey density but does not have a defined biological mechanism compared to attack rate or handling time parameters (DeLong 2021). Type III functional responses are thought to describe a pattern exhibited by a generalist predator that switches between prey types whereas Type II functional responses apply to specialists (Hanski et al. 1991). Yet, generalist predators are exceedingly common, while confirmation of Type III functional responses are rare in multiprey systems (Oaten and Murdoch 1975).

Prey switching is the disproportionate consumption of prey that is more abundant (Murdoch 1969). Predator preference can be constant, where predators attack one type of prey more than the other regardless of their densities. The special case of switching requires a density-dependent change in preference. Here, preference is weaker when prey are rare, and stronger when the prey increase in abundance. Different mechanisms could generate this shift in preference and ultimately switching prey. We can understand diet specialization for a predator consuming different prey types through an optimization lens (MacArthur and Pianka 1966). Predators can optimize capture rates by balancing the decline of energetic gain due to resource depletion with the cost of searching (Charnov 1976b) and predator's willingness to pursue prey is mediated by its satiation (Charnov 1976a). Optimal foraging describes patterns many systems (Sih and Christensen 2001) and offers useful starting point for understanding the mechanisms of predator decisions.

Why do predators prefer one prey over another? Of course, the energy available to predators both in each individual prey item (*e.g.,* biomass) and broadly as a prey population (*e.g.,* abundance) often varies between the two prey and subsequently influences the decisions of a predator. However, additional information is needed to fully appreciate the diversity of prey and their value to a predator. Prey reduce their vulnerability to predation through antipredator traits and differ within or between species in a suite of characteristics that decrease predator success. For example, white-tailed deer (*Odocoileus virginianus*) can outrun their predators (*Canis latrans*), preventing a successful attack (Lingle and Pellis 2002). In bison (*Bison bison*), individuals who stand their ground have higher survival rates compared individuals that flee (Macnulty 2002). In many systems, there is a potential for prey to injure a predator (Mukherjee and Heithaus 2013). Foraging costs from risk of injury can shape a predators decisions (Berger-Tal et al. 2009). Thus, we can simplify the complexities of prey diversity through the prism of energetic trade-offs for the predator.

1.2 WOLVES

Wolves (*Canis lupus*) are a ubiquitous social generalist predator able to survive in variable environmental conditions by hunting diverse prey. Most populations of wolves have large ungulates as their main prey, with subsidies from small prey (Mech and Boitani 2003, Gable et al. 2018). Wolves are apex the predator for many systems with multiple prey that possess diverse antipredator traits (Mech and Boitani 2003), responding to changes in prey availability and vulnerability to maximize their success and reduce their risk (Macnulty 2002). The opportunistic, perhaps even optimal, behaviour of wolves make them a promising study species to explore predator-prey theory. Wolf-prey systems have provided empirical examples of foundational theory including trophic dynamics (Ripple and Beschta 2012), ideal gas law (Vander Vennen et al. 2016), functional response (Hebblewhite 2013), prey switching (Tallian et al. 2017), and energetics (Zimmermann et al. 2015). The current understanding of wolf ecology has been informed by observations from some cornerstone systems, one of which is Riding Mountain National Park (Mech and Boitani 2003).

The ecology of the wolves of Riding Mountain National Park has been studied since the 1970's (Carbyn 1980). During the studies that have spanned 50 years, elk have always been the main and preferred prey of wolves (Carbyn 1980, Meleshenko 1986, Paquet 1992, Sallows 2007). During my thesis research (January 2016 to January 2018), the wolf population was estimated at 70 animals and 13 packs. The fieldwork for my thesis was continuous and intensive tracking of wolves directed by GPS collars on 25 individuals in 8 packs. A notable change occurred across these studies on wolves and their prey. Certainly, there was an advancement of technology and proliferation of the data collected which supports new quantitative approaches. But there was a surprising ecological change since the previous study 16 years earlier: the main prey were not as expected, wolves had switched from elk to moose. Prey switching in a large charismatic carnivore is rare and requires long-term data to capture. The incidental observation during my work was supported by the consistent ecological monitoring in this study area.

1.3 RIDING MOUNTAIN NATIONAL PARK

Riding Mountain National Park (50°051′50″ N 100°02′10″W) is a ~3000 km^2 area in southwestern Manitoba, located on Treaty 2 territory. The establishment of the park in 1930 expelled the Anishinabe from their homelands, and until 1994, the borders of Riding Mountain wrongfully included Clear Lake IR 61A of the Keeseekoowenin Ojibway First Nation Band. Parks Canada now works with the Coalition of First Nations with Interest in Riding Mountain National Park composed of First Nations from Treaties 2, 4, and 1. In this thesis, I will discuss the history of Riding Mountain and the data that has been collected in this area for 100 years. This century of research provides us with important context to understand the ecology of present day, yet the Anishinabe have been stewards of these lands since time immemorial. Even in ‘early’ studies of Riding Mountain, western researchers benefitted from Traditional Knowledge (Banfield 1949).

Riding Mountain’s elevation of 550 to 650 m rises above the surrounding prairie which is 300 to 550 m. The geomorphology of Riding Mountain National Park is remnant of the continental glaciation of the late Pleistocene-Early Holocene, escarpments were carved by glacial rivers systems while overlying stagnation moraines were left by retreating glaciers (Clausen 2019, Teller et al 2018). Due to settler-colonial land-use practices, the borders of the park are conspicuous against the surrounding agricultural land. The habitat within the park is a confluence of aspen parkland, mixed wood and boreal forest, and grassland prairie. Dominant tree species are trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), and jack pine (*Pinus banskiana*). Grassland species include rough fescue (*Festuca scrabella*). Wildlife in Riding Mountain National Park have been monitored and studied for over a century. Here, I will present the history of the park in distinct periods 1) wolf extirpation and park establishment, 2) wolf resurgence and standardized monitoring, 3) Bovine Tubercolosis management and prey decline, and 4) the present situation.

Wolves were extirpated from Riding Mountain, and across North America, due to hunting, trapping, and poisoning by settlers (Carbyn 1980, Mech and Boitani 2003). The species was not listed in Green’s (1932) description of the park. Rare observations of wolves were recorded in the mid 1930’s and increased to a population of 20 in the late 40s (Banfield 1949). Warden surveys in the 1960’s estimated a population of around ~30 (Carbyn 1980). Predator control occurred in the park in response to public complaints throughout the 1950s and 1960s but were prohibited in the mid 1960s (Carbyn 1980). Elk (*Cervus elaphus*) in Riding Mountain are one of the last fragments of the population range across Manitoba. Elk were the most abundant and certainly the most noted ungulate in the park. In 1917, elk hunting was prohibited (Green 1933), resulting in an increase of ungulates in the area from 500 elk in 1914 to 12,000 in 1946 (Banfield 1947). From 1950 to 1974, the population fluctuated from 600 to 2000. Moose (*Alces alces*) have been present within the park since early inventories but were not estimated through surveys until 1950s, the population estimate of 1000 in 1957 tripled to 3700 over 20 years. In forested study areas like Riding Mountain, the sightability of deer biases population estimates low and they should be considered a rough relative estimate with high uncertainty (Carbyn 1983, Vander Wal et al. 2011). Mule deer (*Odocoileous hemionus*) were less abundant than white-tailed deer (*Odocoileus virginianus*) in the 1920s. In the 1940s there was a ratio of ~1:5 mule deer to white-tailed deer (Soper 1953). The beaver population was estimated at 70 individuals in 1932 (Green 1933) and declined to only rare sightings in by the 1940s. Trapping, poaching, and predation were all attributed to small and declining numbers (Green 1933) and introductions of beavers occurred in 1947 and 1958. Over the first decades following establishment of the park, wolf repopulation was supported by an abundant prey base. However, studies focused on wolf hunting of these prey were not conducted.

By 1974, the wolf population was estimated at 66 individuals from Warden surveys. Standardized annual wolf surveys began in 1983 and continue to present day. Wolves reached a peak abundance of 102 individuals in 1988. During the 1990s, wolves declined to 30 individuals but quickly recovered to 60 individuals. Parks Canada began standardized annual aerial surveys for ungulates in 1976. Since then, elk and moose fluctuated from 2000-4000 individuals each for 20 years, with elk typically more abundant than moose. Elk and moose existed at similar abundances of ~4500 individuals for a decade. During this period of high population density, a bovine tuberculosis (*Mycobacterium bovis*) outbreak occurred in cattle herds surrounding Riding Mountain, with wildlife facilitated transmission. In 1997, an *M. bovis* surveillance and eradication program began in the area which included the implementation of testing and culling elk in Riding Mountain (Shury 2015). A significant population decline began in the late 1990's for moose and elk, but was more steep for elk. Wolf predation research was completed by multiple studies that tracked wolves, investigated kill sites and collected scat samples. The findings from these studies confirmed wolves were primarily hunting and consuming elk in the park, though their diet was diverse and included moose, white-tailed deer, beaver, and other small prey (Carbyn 1983, Meleshenko 1986, Paquet 1992).

With exception of a peak population at 113 in 2011, there were ~75 wolves in the park from 2000 to 2016. The decline of the two major prey continued until 2004 where both populations were around 2300 animals, moose have fluctuated around that estimate since that time. Elk continued to decline with a population estimate in 2016-2017 around 1100 individuals. White-tailed deer have only been recorded through the standardized survey methods since 2000, observations indicated white-tailed deer have fluctuated buy increased from ~400 to 900 from 2000 to 2016. There has been an abundant population since the 1960s and 1970s with an estimated population of 3500 (Carbyn 1980). Recent beaver cache surveys conducted semianually show an increasing trend from an estimated 1700 in 2013 to 2600 in 2016 (Parks Canada Report 2016). Despite declines in prey that occurred in the 1990s, a wolf diet study confirmed elk were the primary prey in the early 2000s (Sallows 2007). As fieldwork began for this thesis research in 2016 it became apparent that moose were now being consumed more than elk.

1.4 THESIS OVERVIEW

The objective of my thesis is to study why and how predators switch prey. My research thematically spans the predation sequence from search to consumption, and the literature that formed our current paradigms from the ideal gas law to contemporary context-dependencies. I study predator searching behaviour (Chapter 2), encounters between predators and prey (Chapter 3), and the consumption rates of predators (Chapters 4 and 5) in the context of a predator at the cusp of a prey switch. In Chapter 2, I test the effect of hunger on the movement and hunting behaviour in wolves. Optimal foraging predicts that wolves will be more willing to take risks as the time-from-kill increases. Specifically, wolves will use areas of great risk due to dangerous prey, conspecifics, or humans when they are hungrier. Chapter 3 invokes the ideal gas law to test the influence of diel variation on encounters between predator and prey. I calculate the relative velocity between predators and three ungulate prey species and evaluate the influence of light on detectability. The functional response is the focus of Chapter 4, a theoretical paper that integrates optimal foraging theory directly into classic predation equations (the functional response *sensu* Holling 1959 and prey switching *sensu* Murdoch 1969). I express a functional response of a single predator to the abundance of two prey types, as it emerges from variable energy and time costs to predators when searching, attacking, or consuming prey. In Chapter 5, I test the main predictions from the theoretical model formulated and simulated in Chapter 4. Specifically (1) that predators prefer more vulnerable prey, consuming prey disproportionately more than expected by their density - wolves will prefer elk, the more vulnerable prey, over moose, the riskier prey and (2), predators exhibit a stronger preference when total prey abundance is high but are less discerning when total prey abundance is low. My work offers insight that informs future research and management, particularly as wildlife struggle to coexist in the face of rapid environmental and ecological change.

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CHAPTER 2:HUNGER DRIVES SWITCHING AND SEARCHING RESPONSE IN A SOCIAL PREDATOR

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2.1 ABSTRACT

Hunger is a frequent state for many predators and increasing hunger is likely to motivate costly behaviour to acquire necessary resources. Generalist predators must balance the costs and gains of hunting when prey differ, including increasing encounter rates and improving success rates by seeking areas with greater prey catchability. Large carnivores face threats when they interact with humans or conspecifics. We use integrated step selection analysis to describe spatiotemporal factors that influence wolf (*Canis lupus*) hunting behavior in Riding Mountain National Park, a natural area that wolves share with moose (*Alces alces*) and elk (*Cervus canadensis*). If hunger generates more risky behavior by wolves, as time-from-kill increases we expect wolves will: (1) search for and kill a prey that pose higher risk of injury, (2) use the periphery of their range, (3) use areas closer to the park boundary. Hungry wolves take more risks and hunger drives a fine scale switching in prey tracking. Movement patterns of hungry wolves are indicative of search behavior, i.e., shorter steps. Therefore, wolf space-use is directed to areas on the landscape that improve attack success of their large-bodied prey while fine-scale movement is motivated by promoting encounter rates when hungry. This work places predator behaviour at the intersection of landscape variation, movement ecology, and optimal foraging.

2.2 INTRODUCTION

Nearly half a century ago, Charnov's (1976) germinal experiment depriving mantises of food changed the way we think about foraging theory; state-dependence, such as hunger, is now foundational in movement ecology (Nathan 2008). Just as movement cannot often be disconnected from state, it also cannot be separated by the motivation to occupy a space. Habitat selection is the manifestation of evolved behaviors driven by anticipated energetic gains and cost of using a particular space. The emergent responses to the pressure to obtain resources and manage risk are offset or magnified by individual qualities, for example nutritional state (DeWitt et al. 2017). With low hunting success for large carnivores, hunger is likely a baseline state, and increasing hunger motivates risk-taking to acquire resources. For instance, hungry cougars (*Puma concolor*) were more likely to use human developed areas, which are normally avoided due to risk (Blecha et al. 2018). By incorporating state dependence into movement integrated habitat selection, we can therefore test how cooperative and cursorial hunters mediate spatial trade-offs.

As animals become hungrier foraging behaviour tips in favour of risk-taking. Hungry barn owls (*Tyto alba*) perform a risky hunting behaviour by increasing their attacks (Embar et al. 2014). Risks are posed by the resources themselves (Mukherjee and Heithaus 2013) and a more desperate predator may pursue more dangerous resources. Common starling (*Sturnus vulgaris*) consumption of toxic prey increased with decreasing energetic condition (Barnett et al. 2007). Some risky areas may become more worthwhile to hungry consumers if those areas co-occur with resources. Hungry spiders (*Pardosa milvina*) foraged when predator cues were present, while sated counterparts avoided the areas high in risk and resources (Walker and Rypstra 2003). The individual variation in risk-sensitive foraging has population implications (Sinclair and

Arcese 1995). Therefore, the ability of internal state to alter the balance between resource and risk is fundamental to descriptions of wildlife space-use.

Habitat selection and movement modelling are tools to describe how animals respond to external variation and can test expectations set by optimal foraging theory. Optimal foraging theory addresses how the energetic value of an area to an animal depends on the interplay of resource and risk (Macarthur and Pianka 1966). A fundamental assumption of both habitat selection analysis and optimal foraging theory is that animals will spend more time in areas that confer higher fitness. Mortality risk reduces the value of an area and subsequently an animal's time allocation in that area (Brown 1999). Movement enables optimal foraging by allowing animals to mediate trade-offs in space and time. For example, elk spend more time in high-risk foraging areas when wolf activity is lower (Kohl et al. 2018). Since it's conceptualization optimal foraging theory has addressed the effect of hunger on space-use behaviour (Charnov 1976, Dill and Fraser 1984). Where habitat selection analyses have been infused with optimal foraging theory in the past, there is a recent proliferation of approaches to quantify energy landscapes (Berti et al. 2022, Klappstein et al. 2022). Here we explore the internal state-dependent habitat selection and movement behaviour of an apex predator.

Hunger is an internal state that changes over fine temporal scales, which provides an opportunity to use integrated step selection analysis to test how hunger influences wolf response to spatial trade-offs in Riding Mountain National Park. If increased hunger generates more risky behaviour by wolves to expand their hunting opportunities, as time-from-kill increases we expect wolves will: (1) search for and kill prey that pose higher risk of injury, (2) use areas on the edges or outside of pack ranges where the conflict with other packs is more likely and (3) be closer to high-traffic human use areas inside the park, or venture outside the park boundary that increases the potential for human interactions.

2.3 METHODS

2.3.1 *STUDY AREA*

Riding Mountain National Park (RMNP; 50°051′50″, N 100°02′10″W) is a 3,000 km^2 conserved area in southwestern Manitoba. The conserved habitat (a confluence of prairie grassland, aspen parkland, and boreal forests) creates a distinct edge with surrounding agricultural land. During the study period (2016-2017), the wolf population was estimated from aerial and snow track surveys at ~70 individuals and 13 packs. Mortality (68% of the sample population) observed during our study were anthropogenic (trapping, poisoning, gunshot; constituting 20% of mortalities of study animals), conspecific (12%), and disease (Canine Distemper Virus; 36%) Prey defense is a source of mortality not represented in the sample population, but one unmarked individual was discovered at a kill site, succumbing to injuries due to blunt force. Aerial surveys to estimate ungulate (moose, elk, and white-tailed deer) population sizes were conducted by Parks Canada annually in the winter (Figure S1). Prey available to wolves include moose (*N* = 2,300 animals), elk (*N* = 1,100), and white-tailed deer (*Odocoileus virginianus;* N = 750*)*. There was no evidence that livestock residing outside the park were actively hunted by our collared wolves, though some wolves occasionally and opportunistically scavenged bait stations and dump sites outside the park.

2.3.2 *GPS LOCATION DATA*

We collared 35% of wolves in the RMNP population and 60% of wolf packs (at least one wolf was collared in all packs in the 'core area' on the west side of RMNP: Figure S1). Wolves in winter 2016 (*n* = 13) and 2017 (*n* = 14) were captured by Bighorn Helicopters following

Memorial University AUP 16-02-EV and fit with GPS telemetry collars (Advanced Telemetry Systems G2110E, MN USA; Followit Tellus Medium, Followit Sweden AB, Lindesberg, Sweden; Lotek Iridium TrackM 2D, Lotek Wireless Inc, Newmarket, ON, Canada; Sirtrack Pinnacle G5C, Sirtrack Limited, Hawkes Bay, New Zealand; Telonics TGW-4577-4, Telonics Inc., AZ USA). Location data was rarified to a two-hour interval to sample individuals at an equal intensity.

2.3.3 CLUSTER INVESTIGATION

Continuous and extensive fieldwork investigations determined the timing and location of wolf behaviours, including wolf killed prey. Important areas of wolf activity were indicated by an increased density of GPS locations, i.e., ‘clusters’. Clusters were identified in Python from an version of the code presented in Knopff et al. (2009) created by Warren (2008) adapted for wolves (Webb et al. 2008, DeCesare 2012, Irvine et al. 2022). In our study, the inclusion rules were set to a radius of 300m and a time of 96 hours, meaning that if a new location was within those limits from any of the locations currently in the cluster it was added.

A total of 6323 clusters were created from the locations of individuals over the study period. In the field, clusters were categorized into three classes created based on the total number of points in the clusters. Clusters were investigated by following a systematic stratified method to sample across size classes and pack territories. Clusters were most often accessed via snowmobile, quad, horseback, or on foot. Every 2-3 months a helicopter was used to visit sites not accessible from the ground. The geometric centre of the cluster (‘centroid’) and associated locations were input into a handled GPS unit to direct investigations for physical evidence. We concentrically searched an area around the centroid based on the radius of the cluster and every

GPS location of the cluster was searched within a radius of ~15m. On average, clusters were investigated within a mean of 13.8 days of occurring (median = 9 days).

Once clusters were investigated, unique areas were then termed ‘sites’. 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, e.g., tracks, disturbed vegetation, hair, blood. In some instances, clusters with carcasses were determined to be a scavenge based on evidence that the animal died due to another cause or if the collared wolf spent too short of a duration are the site to have been responsible for the death of the animal, e.g., 2 hours at a large ungulate kill. When possible, prey species at the site was determined and samples were collected. In the absence of a carcass other evidence from wolves or other species such as tracks, hair, beds, scat, dens were used to determine the behaviour that occurred at the site. For example, beds under a spruce tree containing wolf hair were indicative of a resting site.

A total of 1260 clusters were investigated, which translated to 598 unique sites. Often multiple clusters occurred at each unique site and multiple wolves visited the same site. Aggregate clusters of wolves were defined from spatial and temporal to determine unique kills. The primary behaviour was ‘kill’ at 181 unique sites (433 clusters designated as kills), probable kills at 24 sites, and scavenge at 46 sites. A total of 296 scat samples were collected and subsequently analyzed. Both kill site and scat data (Appendix 5) indicated moose contributed over half of the biomass in wolf diets (65% kill sites, 55% scat). Elk contributed less than half of the biomass (21% kill sites, 34% scat).

The movement and selection analysis was run for individual wolves during the winter period, January to March, resulting in an average of 190 locations per wolf-winter (Table S1). Lone wolves demonstrating extraterritorial movements outside the park or wolves without kills identified during the winter were omitted from the analysis to promote model convergence leaving 21 wolves from seven packs in this analysis.

2.3.4 INTEGRATED STEP SELECTION ANALYSIS

Integrated step selection analysis (iSSA) estimates movement and selection behaviour together to reduce bias and produce a holistic depiction of factors that motivate and modify animal space-use (Avgar et al. 2016). We used iSSA to incorporate fine-scale temporal-dependence into our models.

Used step lengths (distance between two consecutive GPS locations) were described by a gamma distribution (mean tentative shape = 0.419, scale = 218, Table S1). The directionality of steps was defined by turn angles (angular deviation from the step heading) fit with a Von Mises distribution (mean tentative kappa = 0.157, Table S1). Availability domain was informed by observed movement behaviour. We randomly sampled step lengths and turn angles from these distributions to create ten available steps for each used step. Within each strata of 11 steps, the start points are shared but the end points are distinct. Movement and selection covariates at the start point are those thought to influence the subsequent space-use decision, while those included at the end point estimate the resulting selection pattern of an animal. When step length is ln-transformed (natural log) and included in a step selection model, the resulting covariate is a modifier of the shape parameter of the original gamma distribution. The cosine of the turn angle transforms this circular measure to a linear correlation with previous step heading (-1 is backward movement, 1 is forward). In a step selection analysis, the coefficient relates to the concentration parameter of the Von Mises distribution.

We created five spatial layers of covariates to describe risk and resources experienced by RMNP wolves. We calculated the distance from the boundary of RMNP (shapefile from Parks

Canada), areas outside of the boundary were given a value of ‘0’. Only two main roads exist in the park, compared to a dense network outside. Thus, distance to road was not included in the model as it is highly correlated with the park boundary and risky areas. Risk from conspecifics was estimated continuously using distance to range centre. To estimate the centre of the wolf pack territories, we used 90% minimum convex polygons (MCPs) around all locations from individuals in each pack.

Prey catchability was calculated using a habitat selection framework where ‘used’ points were kill site locations determined from kill site investigation and available points were drawn uniformly within each pack range (Zabihi-Seissan et al. 2022). Covariates included in these models were landcover, distance to water, distance to roads, distance to maintained and unmaintained trails, distance to hard edge, and terrain ruggedness. Hard edge was calculated using the transition zone between open areas and closed canopy forest. Prey catchability layers were created for the three ungulate prey species in RMNP: elk, moose, and white-tailed deer. Models for elk and moose were conducted for years separately and matched to the wolf-year. Deer kills occurred mostly in 2017, thus, these year differences could not be accounted for. White-tailed deer kills increased in mixed wood (Table S2). Generally, moose kills increased in mixed wood and areas closer to maintained trails and elk kills increased closer to unmaintained trails and edge (Zabihi-Seissan et al. 2022).

To estimate the effect of hunger on movement and selection covariates, we calculated the time from leaving the last known kill for each location. Time from kill at the start point of the cluster was included as an interaction with the movement and selection covariates. Locations that contributed to the cluster were removed from the data used in the iSSA so that inferences reflect space-use behaviour when predators are pursuing (travelling steps) or conserving (resting sites) energy. A similar designation of hunger measured was used on cougars, specifically time since feeding activity binned into 11 intervals from 0-1 days to over 10 days (Blecha et al. 2018). In our analysis we used a continuous linear measure of hunger until 2 weeks, at which point we censored data as our confidence in no kill events occurring over these long intervals decreased (20% of the data was censored using this rule).

Step length and turn angle estimation, random step creation, and covariate extraction was completed using the *amt* package (Signer et al. 2019) in R version 4.1.0. We fit a mixed effects iSSA with individual random slopes for covariate interactions with time from kill using the *glmmTMB* package in R to fit a conditional Poisson model (Muff et al. 2020).

2.3.5 CALCULATING EFFECT SIZES

Relative selection strength (RSS, Avgar et al., 2017) provided an illustration of the effect size of selection coefficients. Specifically, we demonstrated the change in selection for prey catchability, pack range centre, and the park boundary with time from kill. We used the *predict* function to compare the selection of one location of average habitat over another location that has high values of the covariate of interest. We held the difference in the location habitat covariates constant while varying time from kill (0 to 7 days from kill). We used individual-specific random effects to present uncertainty and individual variation around population responses.

The change in speed as time from kill increases illustrates the effect of hunger on movement. We calculated speed (meters per hour) from the mean step length of the gamma distribution (meters), divided by the fix interval (2 hours). The mean step length is the shape parameter multiplied by the scale. We modified the shape parameters estimated for the random steps by the coefficients that included ln Step Length.

2.4 RESULTS

Wolf spatial behaviour changed with hunger (days from kill). Wolves selected for the catchability of their ungulate prey, but these responses were sensitive to their hunger. Wolves selected moose catchability (0.0560 [-0.474, 0.586]) and this selection increased with hunger (0.0164 [-0.0845, 0.117], Figure 1a). Wolves strongly selected elk catchability (0.0935 [-0.320, 0.507]), this response switched to avoidance as hunger increased (-0.104 [-0.215, 0.00773], Figure 1b). Similarly, deer catchability was selected (0.937 [0.511, 1.36]), until hunger increased (-0.0900 [-0.239, 0.0586], Figure 1c). The variation in these responses were greatest for moose, followed be white-tailed deer, and variation was the least for elk (Figure 1a-c). The between pack differences were greatest for moose (Figure 1a). The spatial response to areas of risk also varied with hunger. Wolves avoided areas farther from their range centre (-0.401 [-0.545, -0.256), but avoided these areas less as their hunger increased (0.00826 [-0.0214, 0.03797], Figure 1d). Wolves avoided areas farther from the park boundary (-0.157 [-0.256, -0.0572]); but selected those areas as they became hungrier (0.0261 [0.00340, 0.0488], Figure 1e). The response to pack range and park boundary had little variation within the population.

Wolf movement response was sensitive to hunger. Wolves moved slower and less directional than the estimate used to generate movement distributions for the available steps. Specifically, the coefficient for cosine of the turn angle was negative (-0.0626 [-0.118, -0.00683]) indicating wolves were less directional than the tentative kappa parameters (concentration of the Von Mises distribution of turn angle) estimated for the available steps. Further, the shape parameter of the gamma distribution of step length was lower than the available distribution as indicated by a negative ln-transformed step length coefficient (-0.0129 [-

0.0386, 0.0129]). Step lengths decreased with hunger (-0.00548 [-0.0105, -0.000426], Figure 1f). The differences in movement varied by individual with similarities between pack (Figure 1f).

2.5 DISCUSSION

Hungry wolves take risks. Foraging costs for predators can come in several forms including the risk of injury while targeting large prey, lethal encounters with conspecifics, and human conflict. As time-from-kill increases, wolves increase their selection for the most dangerous and abundant prey, moose, and decrease their selection for smaller but less abundant prey, elk, and deer. In addition to risk from prey, hungry wolves travelled farther from their range center and increased the risk from lethal competition with conspecifics. Humans may be the greatest risk to wolf survival outside the park. Wolves increase their selection for areas closer to the park boundary with increasing hunger. Therefore, hunger mediates the trade-off between energetic reward and mortality risks.

Hungry wolves demonstrated exploratory behaviour. Increased selection for areas away from pack range centre and near the park boundary is a signal that they are expanding search areas in the pursuit of resources. This exploration can come at a cost. Territory edges and human development pose mortality risk to wolves and are often avoided (Mech, 1994), but hunger reduced this spatial avoidance in our study. Cougars increase their selection for housing density when hungry, energy depletion drives them to areas of higher payoff that simultaneously pose higher risk (Blecha et al. 2018). Notably, despite moving closer to the park boundary with hunger it is extremely rare for wolves to leave the safety of the park (>75% of wolf locations are within the park, Figure S2) and when wolves are outside of the park their increased speeds are not indicative of a hunting behaviour (Figure S3). This is not surprising, as prey are more abundant within the park. Therefore, hunger can tilt the risk-reward trade-off towards more risky areas of the landscape, *if* those areas have higher energetic reward.

Early movement pattern studies offer guidance to understand a predator's response to heterogeneous resource distribution (Turchin 1966). Specifically, predators are expected to spend more time in areas of high resource density (Fauchald and Tveraa 2006). Area-restricted search behaviour corresponds with decreased movement rates when foraging (Kareiva and Odell 1987). Therefore, our results indicate wolves are increasing their search effort when hungry by slowing their movement. Foundational prey theory (*i.e.* law of mass action and functional response) and empirical evidence supports the expectation that increased speed increases encounter and kill rates (Vander Vennen et al. 2016). Both these patterns can be true, as the assumptions of iSSA and the law of mass action operate under different simplifying assumptions. We model spatially biased movement behaviour at a 2-hour time scale, which violates the assumptions of instantaneous measures in a homogenous system from the law of mass action. Both approaches are valid and can be synthesized to understand the spatial and temporal mechanisms of foraging responses.

Hungry wolves responded to a trade-off between ease of capture with probability of encounter. Predators exhibit varied strategies to improve hunting success including: tracking areas of abundance or habitat to encounter prey; selecting for areas that facilitate movement; and focusing efforts on prey that are more vulnerable or areas that increase prey capture (Balme et al. 2007, Kittle et al. 2017). This population of wolves select for prey spatial catchability at the within-territory scale (Zabihi-Seissan et al. 2022). At the step-level, satiated wolves strongly selected for deer and elk catchability and have a variable selection for moose catchability. Hungry wolves demonstrated a switch in their spatial prey tracking; selection for moose increases while the selection for elk decreased. The response to deer was variable between individuals and packs. Interestingly, the spatial behaviour of wolves parallels the change in kill rates and diet composition in this population.

The variation in fine-scale spatial behaviour corresponds to the environmental pressures acting on the wolf population in RMNP. This study period was the first to observe a population-level switch from elk to moose. Wolves in RMNP have demonstrated a historical preference for elk that have only recently switched due to a resurgence in moose abundance that surpassed elk. Further, deer abundance is increasing but distribution is concentrated to southern edges and closer to human disturbance (Zabihi-Seissan 2019). The most conserved selection response in our study to prey was to elk, followed by moose, and then deer. This pattern could be indicative of behaviour adaptation to new environmental conditions, specifically prey abundance and distribution. In support of this, the responses to established risks of conspecifics and human disturbance had low variation. If foraging behaviour is a labile trait, it is under the hungry condition that there is more variance, which generates opportunity for selection.

Cohesion of social groups emerges from a balance of risks and rewards (Krause et al. 2002, Silk 2007). In our results, pack similarities emerge from individual wolf responses to the environment. Social carnivores are more cohesive when hunting larger and more dangerous prey (Smith et al. 2008, MacNulty et al. 2014). This study population of wolves in RMNP are more cohesive in areas used be larger prey and at kill sites of large prey (Zabihi-Seissan et al. 2022). These social constraints are likely contributing to the notable variation in patterns by pack for risky selection for moose catchability, the more abundant and risky prey, but not elk. Further, groupmates aid in defense of resource loss from scavengers or mortality risk from other large predators (Caraco and Wolf 1975, Vucetich et al. 2004). Packs share similar genetics and environmental conditions, which both influence space-use. Owls in the same nest, regardless of genetic relatedness were more similar (Bombieri et al. 2018). The processes generating the phenotypic patterns in selection and movement within and between wolf packs should be investigated further.

Habitat selection is the manifestation of evolved behaviors driven by anticipated rewards and risks of using a particular location in space. By incorporating state-dependence into movement integrated habitat selection we illustrate how individual cooperative hunters have evolved to acclimate to increased risk as they become hungrier. This work adds to the building evidence that energetic trade-offs shape spatial responses (Berti et al. 2022, Klappstein et al. 2022) with added detail that hunger mediates those choices (Berger-Tal et al. 2009, Embar et al. 2014, Blecha et al. 2018). Overall energy depletion can influence population distributions and survival as desperation makes risks more appealing.

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2.7 AUTHOR'S CONTRIBUTIONS

CMP conceived the original idea for the manuscript. Data was collected and provided by CMP and SZS in RMNP. CMP conducted the analysis with assistance from JWT and KK. CMP wrote the manuscript with input and approval from all coauthors.

Table 2.1. Population-level coefficients from the integrative step selection model fit with individual-specific differences (Muff et al., 2020) testing the change in wolf selection of resource or risk and movement behaviour with increasing hunger (days from kill). Bold coefficients indicate confidence intervals that do not overlap zero.

	Covariate	Coefficient [CI]
Selection		
Prey	Moose catchability	0.0560 [-0.474, 0.586]
	Moose catchability : Days from kill	0.0164 [-0.0845, 0.117]
	Elk catchability	0.0935 [-.320, 0.507]
	Elk catchability : Days from kill	-0.103 [-0.215, 0.00773]
	Deer catchability	**0.937 [0.511, 1.36]**
	Deer catchability : Days from kill	-0.0900 [-0.239, 0.0586]
Conspecific	ln Distance from range centre	**-0.401 [-0.545, -0.256]**
	ln Distance from range centre: Days from kill	0.00826 [-0.0214, 0.0380]
Human	ln Distance to park boundary	**-0.157 [-0.256, -0.0573]**
	ln Distance to park boundary : Days from kill	**0.0261 [0.00340, 0.0488]**
Movement		
	cos Turn Angle	**-0.0626 [-0.118, -0.00683]**
	ln Step Length	-0.0129 [-0.0386, 0.0129]
	ln Step Length: Days from kill	**-0.00548 [-0.0105, -0.000426]**

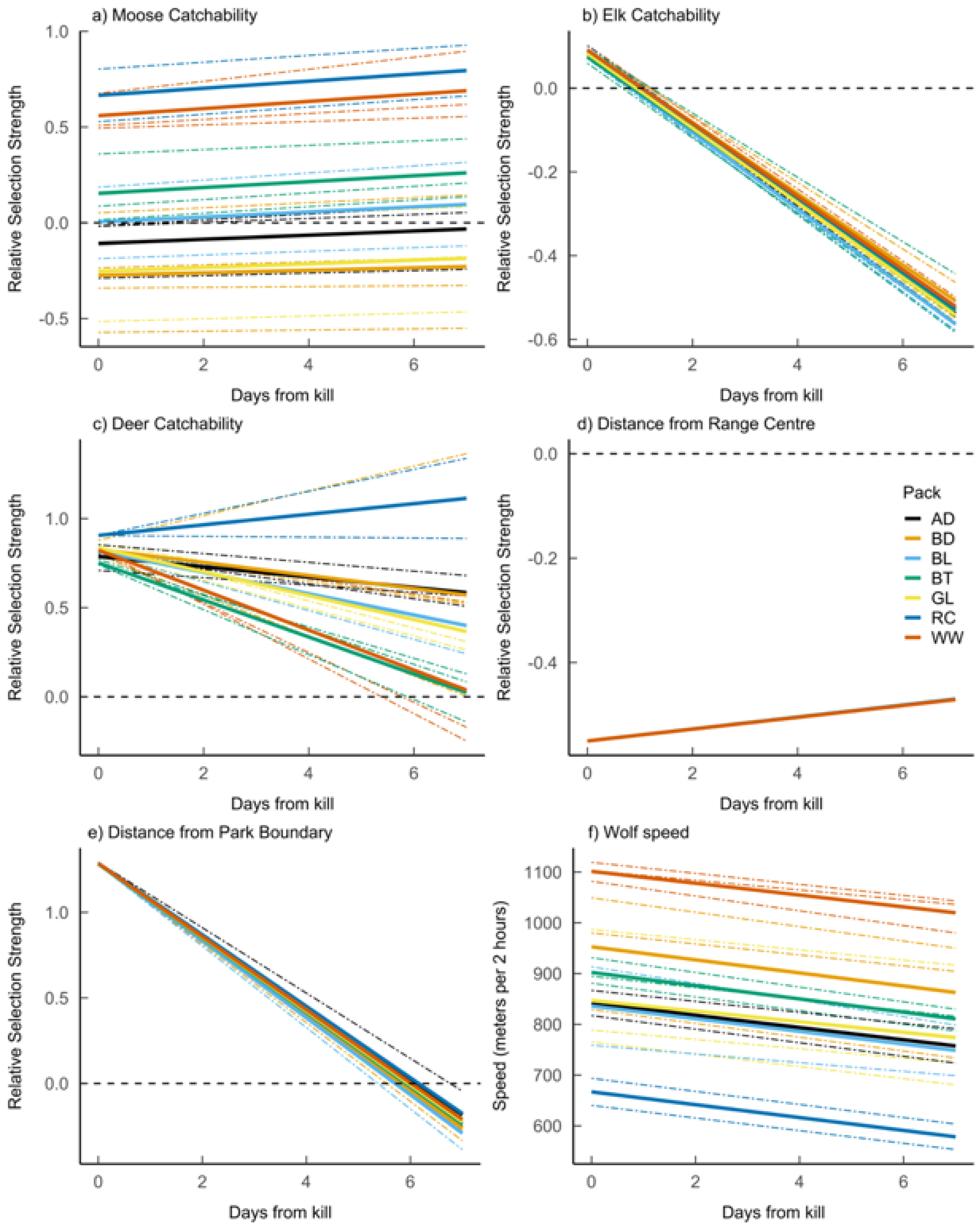

Figure 2.1. Natural log-transformed Relative Selection Strength (ln-RSS) for location x_1 over another location x_2 as time from kill increases (0 to 7 days). The ln-RSS for individual wolves is

displayed as dashed lines coloured by pack. The dashed line at zero indicates no difference in selection between the two locations. The two locations are identical (including time from kill) except for differences in the value of a single habitat variable a) max (x_1=1) versus mean estimate (x_2=0.253) in moose catchability, b) max (x_1=1) versus mean estimate (x_2=0.137) in elk catchability, c) max (x_1=1) versus mean estimate (x_2=0.142) in deer catchability, d) max (x_1= 10 km) versus mean estimate (x_2=8.61 km) from the edge of the individual's pack range, e) min (x_1 = 0 km) versus mean estimate (x_2=8.42 km) from the boundary of Riding Mountain National Park. f) Movement response (speed, meters per 2 hours) of wolves as a function of time from the final point in the previous kill cluster (0 to 7 days). Speed is calculated from the tentative shape and scale parameters of the gamma distribution of step length and modified by ln-transformed step length coefficients from the model output.

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CHAPTER 3:MOVEMENT AND DETECTABILITY INFLUENCES DIEL VARIATION IN KILL RATES IN A MULTIPREY SYSTEM

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3.1 ABSTRACT

Encounter rates are a hinge on which population trajectories of predators and prey pivot. We accept the simplifying assumptions of the ideal gas law to empirically test multiprey predation dynamics. We examine diel variation in kills of moose (*Alces alces*), elk (*Cervus canadensis*), and white-tailed deer (*Odocoileus virginianus*) by wolves (*Canis lupus*) in Riding Mountain National Park, Manitoba. Wolf movement rate governed the effective speed of predators and prey. During the snow season, kills increase with effective speed and sunlight for moose and white-tailed deer, the current and emergent primary prey species in this system. Effective speed did not affect kills for elk, the historic prey species in the snow season. A switch occurred in response during the snow-free season, elk kills increased with effective speed and sunlight, and moose kills decreased with sunlight. Our fine scale diel patterns of kill rates indicate population level patterns of predation in this system.

3.2 INTRODUCTION

Encounter rates are a hinge on which population trajectories of predators and prey pivot. Predator behaviour promotes hunting success, whereas prey seek to avoid this risk by responding to where and *when* they might be captured. For example, the 'landscape of fear' is not static as elk adjust their behaviour through space and time (Kohl et al. 2017, Palmer et al. 2017) in response to wolf activity periods. Increased predator activity therefore begets an increase in kill rate; in fact movement rate is found to overwhelm the effects of prey density, prey movement, and detectability when describing kill rates (McPhee et al. 2012, Vander Vennen et al. 2016a). Here we study multiprey predation dynamics by accepting the assumptions of the ideal gas law to model the relationship between the diel variation in encounter rates with movement and detectability.

Despite the complexities of kill rates in natural systems, the ideal gas law has been useful for understanding many ecological processes (Hutchinson and Waser 2007). The description of collision rates between two moving particles, here animals, has been used to characterize predator-prey encounter rates as

$$\varphi = DvN \qquad \text{eqn 1}$$

where encounter rates (φ) are linearly related to the distance at which a predator can detect a prey (D), and the effective speed of the system (v) which is calculated from the speeds of both predator and prey, and their density (N). Using this linear relationship, Vander Vennen et al. (2016) found that diel variation in kill rates of prey were strongly predicted by predator speed. However, the application of the ideal gas law applied to a single prey system, such as the one studied by Vander Vennen et al. (2016), provides opportunities to build in more biological complexity.

Animal movement varies across diel and seasonal cycles. Predators exhibit peaks of increased activity, often defined by movement rates, during twilight (dawn and dusk) periods (Theuerkauf et al. 2003a, Eggermann et al. 2009b, Eriksen et al. 2011). Twilight activity of wolves has been linked to increased prey capture success and injury avoidance through improved visual acuity of wolves and detectability of prey in crepuscular light (Asa and Mech 1995). Prey species such as ungulates exhibit a similar diel activity rhythm due to foraging and ruminating cycles (Reisenhoover 1986). Kill rate varies across hourly diel periods that reflect activity, while monthly or seasonal variation in kill rate may be due to resource availability, prey vulnerability, and/or life history (Prugh et al. 2019). Indeed, important differences between seasons mediate killing times in wolf-ungulate systems. For example, movement behaviour is altered in ungulates and wolves during periods of offspring rearing (Merrill and David Mech 2003, Tsunoda et al. 2009, Eriksen et al. 2011). Thus, we evaluated predator-prey dynamics across temporal scales.

Wolves (*Canis lupus*) are generalist predators that live in multi-prey systems and have been a model species to test core elements of predator-prey theory for decades, which offers a valuable foundation to expand the depictions of these processes. Wolves in Riding Mountain National Park (RMNP) in Manitoba, Canada, are supported by a diverse and abundant ungulate prey base, predominantly moose (*Alces alces*), elk (*Cervus canadensis*), and white-tailed deer (*Odocoileus virginianus*). Differences in prey morphological and behavioural traits may influence their catchability during the search and attack phases, which in turn could disrupt the predictions generated by the ideal gas law and thereby, classical functional response models. Using wolves and their prey in RMNP, we integrate the ideal gas law with biologically relevant details about wolves and their prey to establish the mechanisms driving temporal variation in kill rates of predators in complex systems. We test the response of kill rates in a multiprey system to fine scale temporal variation in detectability and speed between seasons. We empirically tested the ideal gas law: (1) Are kill rates a product of predator and prey movement rates?; (2) Does visual acuity play a role in predation success?; (3) Are these relationships context-dependent either due to prey species or season specific differences? Determining the mechanisms driving temporal variation in this system can help us identify core components of kill rates that are broadly applicable.

3.3 METHODS

The GPS data were collected in Manitoba, Canada (Memorial University AUP 16-02-EV). Riding Mountain National Park is a protected area in southwestern Manitoba (3,000 km^2; 50°51′50″N 100°02′10″W). Elevation in the study area is around ~600 m, the habitat is a composition of aspen parkland and boreal forests, with trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), and jack pine (*Pinus banskiana*). There is an abundant population of black bears (*Ursus americanus*) and sightings of cougars (*Puma concolor*) are incidental with no breeding population. During the study period (2016-2017), population sizes of elk and moose were estimated at an average of 1,100 and 2,300 individuals respectively (0.4 elk per km^2 and 0.77 moose per km^2) through annual winter surveys (Vander Wal et al. 2013, van Beest et al. 2014). White-tailed deer abundance was lower than the other two ungulate species within the park, their population is estimated at around 750 individuals (0.25 deer per km^2). A network of trails, campsites, and two roads occur throughout the park. Most of the human activity is concentrated at the town site, outside of the core study area.

Game Hunting Area (GHA) 26 is located in eastern Manitoba and provides a comparable wolf-multiprey system. Here the primary prey are moose, which provides movement estimates of moose in RMNP. GHA 26 is located in the Boreal Shield Ecozone (Ecological Stratification Working Group 1995), most of which is crown (public) land (7,200 km^2; 50°40′59″N 95°42′05″W). This part of eastern Manitoba is characterized by an interspersion of rock outcrops, bogs, lakes and rivers, with an average elevation of 260 m. Habitat include black spruce, white spruce, tamarack larch (*Larix laricina*), balsam fir (*Abies balsamea*), jack pine, trembling aspen, paper birch (*Betula papyrifera*), black ash (*Fraxinus nigra*), and balsam poplar (*Populus balsamifera*) (Palidwor and Schindler 1995). Large mammals in GHA 26 include moose, white-tailed deer and boreal woodland caribou (*Rangifer tarandus caribou*) and a large predator guild of wolves, black bears, and coyotes (*Canis latrans*). Two provincial parks are in the area, Nopiming Provincial Park and Manigotagan River Provincial Park. GHA 26 is used by many different groups for recreational purposes and resource development. The local economy is predominantly based on resource development.

GPS location data

Wolves were collared in RMNP in 2016 (13 individuals in 4 packs) and 2017 (14 individuals in 5 packs). Animals were captured by Bighorn Inc., contracted through Parks Canada, using net gun immobilization via helicopter (Memorial University AUP 16-02-EV). All collars were Iridium based from the following companies: ATS (1), Lotek (4), Televilt (14), Telonics (6), Sirtrack (2). In 2016, collars took relocations every 2 hours, 8 collars sampled locations on odd hours while 5 collars sampled locations on even hours. The odd and even schedules were distributed between packs with at least one collar following each schedule in a pack. In 2017, collars were programmed with an hourly fix rate, which were then rarified to 2 hours matching the arrangement of the other collars, schedules were randomly assigned to an individual wolf and distributed within pack. From 2003-2016, 50 elk were equipped with GPS collars with 2-hour fix rates. In 2013, 16 collars with 2-hour fix rates were deployed on white-tailed deer, for a total of 72 elk-years and 16 deer-years. We used 15 moose-years of data from GHA 26 at a 2-hour fix rates (2012-2018, n = 15) to estimate the movement patterns of moose in RMNP. We partitioned dependent and independent variables for four prey species (moose, elk, white-tailed deer, and beaver) into one-hour time bins for two seasons (summer and winter). Thus, for each season and prey type there were 24 bins to which we assigned the following variables: total number of kills, detectability (*D*), and effective speed (*v*).

Cluster creation and site investigation

Continuous and extensive fieldwork investigations determined the timing and location of wolf behaviours, including wolf killed prey. Important areas of wolf activity were indicated by an increased density of GPS locations, i.e., 'clusters'. Clusters were identified in Python from an version of the code presented in Knopff et al. (2009) created by Warren (2008) adapted for wolves (Webb et al. 2008, DeCesare 2012, Irvine et al. 2022). In our study, the inclusion rules were set to a radius of 300m and a time of 96 hours, meaning that if a new location was within those limits from any of the locations currently in the cluster it was added.

A total of 6323 clusters were created from the locations of individuals over the study period. In the field, clusters were categorized into three classes created based on the total number of points in the clusters. Clusters were investigated by following a systematic stratified method to sample across size classes and pack territories. Clusters were most often accessed via snowmobile, quad, horseback, or on foot. Every 2-3 months a helicopter was used to visit sites not accessible from the ground. The geometric centre of the cluster ('centroid') and associated locations were input into a handled GPS unit to direct investigations for physical evidence. We concentrically searched an area around the centroid based on the radius of the cluster and every

GPS location of the cluster was searched within a radius of ~15m. On average, clusters were investigated within a mean of 13.8 days of occurring (median = 9 days).

Once clusters were investigated, unique areas were then termed 'sites'. 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, e.g., tracks, disturbed vegetation, hair, blood. In some instances, clusters with carcasses were determined to be a scavenge based on evidence that the animal died due to another cause or if the collared wolf spent too short of a duration are the site to have been responsible for the death of the animal, e.g., 2 hours at a large ungulate kill. When possible, prey species at the site was determined and samples were collected. In the absence of a carcass other evidence from wolves or other species such as tracks, hair, beds, scat, dens were used to determine the behaviour that occurred at the site. For example, beds under a spruce tree containing wolf hair were indicative of a resting site.

A total of 1260 clusters were investigated, which translated to 598 unique sites. Often multiple clusters occurred at each unique site and multiple wolves visited the same site. Aggregate clusters of wolves were defined from spatial and temporal to determine unique kills. The primary behaviour was 'kill' at 181 unique sites (433 clusters designated as kills), probable kills at 24 sites, and scavenge at 46 sites. The time bin for individual kills was determined from the time of first fix in each cluster, assuming this represents the time of encounter (corresponding with Tallian et al., 2017; Vander Vennen et al., 2016a). We tallied kills per hour for each prey type (white-tailed deer, elk, and moose separately).

We found 42 white-tailed deer, 33 elk, and 89 moose kills. To study the effect of seasonality on these dynamics, year-round kills were split into two periods, snow and snow-free. The snow season was from November to April, which included 34 white-tailed deer, 22 elk kills, and 63 moose kills. Less kills were identified during the snow-free season (May to October) due to a decline in active collars and an increase in prey diversity. Eight white-tailed deer, 11 elk, and 26 moose kills were found during the snow-free season.

Movement rates and detectability varied with kill rates over time. Hourly movement rate was calculated for both wolves and their prey by dividing step length (distance between two consecutive locations) by time between locations. Speed was assigned to the time bin containing the start point. If the GPS collar fix schedule interval was longer than an hour, we rounded up by assigning the same average to all bins until the next step. GPS collar fix schedule variation (e.g. odd vs. even hours) created hourly variation over the diel cycle to provide continuous sampling over our time bins even for coarser fix rates. The effective speed of each prey type, *v*, was calculated following:

$$v = \sqrt{v^2{}_{predator} + v^2{}_{prey}} \qquad \text{eqn 2}$$

Finally, detectability, D, was estimated as the average proportion of sunlight (L) or crepuscular light (c) in each time bin. We modeled eqn 1 using *glm* in program R, first performing a log linear transformation that turns the multiplicative relationship between kill rates and the variables influencing kill rates into a cumulative one (Vander Vennen et al. 2016a):

$$\ln(kills) = \ln(v) + \ln(L) + \ln(c) \qquad \text{eqn 3}$$

To determine prey specific effects of species, a three-level categorical variable was included as a fixed-effect and interacted with the natural log of effective speed, *ln(v)*, sunlight, *ln(L)*, and crepuscular light, *ln(c)*.

There was a high correlation between effective speed and crepuscular light (r =0.6 in snow season, r = 0.65 snow-free season see Appendix 1 Figure S3 and S4). Due to this we ran a full model with effective speed and 1) both light levels, 2) sunlight, or 3) crepuscular light.

3.4 RESULTS

The diel cycle of wolf speeds was shorter (Figure 1, panel b) and had a narrower range in the snow season (0.26-0.58, mean = 0.44, median = 0.45 km/hr) compared to the snow-free season (0.13-0.64, mean = 0.40, median = 0.46 km/hr). Moose had the slowest average speeds (snow mean = 0.032 km/h, snow-free mean = 0.064 km/hr) followed by white-tailed deer (snow mean = 0.078 km/h, snow-free mean = 0.11 km/hr), and elk (snow mean = 0.11 km/hr, snow-free mean = 0.12 km/hr). White-tailed deer had the strongest cyclic pattern of their daily speeds, with a peak occurring at dusk (Figure 2).

The model with effective speed and daylight performed best (as evaluated from AIC in Appendix 1 Table S1; output of the full model in Table S2 and S3).

Snow Season - White tailed deer kill rates increased with effective speed (4.24, 95% CI [1.24, 7.25]) and sunlight (0.7, 95% CI [0.05, 1.34]). Elk kill rates were not influenced by effective speed (-0.922, 95% CI [-4.09, 2.24]), sunlight (0.03, 95% CI [-0.62, 0.68]). Moose kill rates increased with effective speed (3.99, 95% CI [1.00, 6.98]), and sunlight (1.02, 95% CI [0.37, 1.66]).

Snow-free Season - Elk kill rates increased with effective speed (1.90, 95% CI [0.27, 3.52]) and sunlight (0.83, 95% CI [0.10, 1.56]). Moose kill rates decreased with sunlight (-0.96, 95% CI [-1.70, -0.23]) and white-tailed deer kill rates were not related to sunlight (0.39, 95% CI [-0.34, 1.12]). Effective speed did not affect kill rates for moose (-0.57, 95% CI [-2.14, 1.01]) and white-tailed deer (1.35, 95% CI, [-0.21, 2.90]).

3.5 DISCUSSION

Here we empirically test the ideal gas law by modelling the influence of effective speed and detectability on the diel variation of kill rates of predators and prey. We assume kill rate frequency approximates encounter rate frequency over the diel period. During the snow season, kill rates increase with effective speed and sunlight for moose and white-tailed deer, the current and emergent primary prey species in this system. In contrast, effective speed did not affect kill rates for elk, the historic prey species. However, there was a switch in response during the snow-free season, where elk kill rates increased with effective speed and sunlight, but moose and white-tailed deer did not. The population context of this system resonates within the fine scale diel patterns of predation captured in this study.

Predation begins with a searching predator seeking to encounter prey. For many species, movement is a fundamental component of the search for resources. Kill rates, which we assume were proportional to encounter rates, increased with effective speed. Our findings agree with other systems; kill rates increase with wolf movement and activity periods and where predator movement rates were much greater than their prey (Theuerkauf et al. 2003b, Eggermann et al. 2009c, Vander Vennen et al. 2016a). Though prey movement rates varied across the 24-hour period and between prey species, these relative differences did little to alter effective speeds (Figure 2). Predators 'outrun' prey to govern effective speed, yet prey movement is an effective evasion strategy by being less predictable to a predator and thereby reducing encounters (Mitchell and Lima 2002). Accordingly, predation risk increases movement rates in prey (Pusenius et al. 2020). The assumption of ideal gas law, and our analysis, is that movement is random. A realistic depiction of movement would be non-random and biased. For example, habitat use of predators is more intense in areas that promote encounter and capture of prey (Zabihi-Seissan in review, Balme et al., 2007; Hopcraft et al., 2005). In response to predators, prey change their habitat selection to prioritize safety (Latombe et al. 2014). Movement rate precipitates encounter rates and subsequently kill rates, but there are additional factors that mediate predator and prey actions and reactions.

A common antipredator strategy is to avoid detection, *i.e.* crypsis and camouflage (Stevens and Merilaita 2009). We assumed light levels affects a predator's ability to visually perceive prey and found detectability had a positive relationship with kill rates. There is evidence that visual cues alone can prompt a predator attack; a white-tailed deer visual decoy was attacked by wolves (Gable and Gable 2019). In addition, moonlight was associated with wolf kills (Theuerkauf et al. 2003b). However, sunlight is correlated with other factors such as temperature, which influences the habitat selection and movement of predators and prey (Theuerkauf et al. 2003b, Street et al. 2015). Prey use many non-visual forms of crypsis as well, including sound and smell (Ruxton 2009), and wolves primarily detect prey through olfaction (Mech and Boitani 2003). An oft cited trade-off of group formation in response to predation risk is 'detection-dilution'(Hebblewhite and Pletscher 2002), as it is thought that large groups are more conspicuous in scent. A comprehensive evaluation of how detectability influences encounters would require an appraisal of other sensory modalities and how the relative importance of these modalities changes with proximity to prey. Predators likely use a mix of memory and perception when hunting for prey, directing their search to areas of past encounters then using proximate perception to identify which areas and prey to target. These nested complex processes summarize and simplify to encounter rates.

Kill rates are temporally variable; between hours throughout the day, and between seasons throughout the year. We found that the relationships between encounters with movement rate and detectability switched from being positive for white-tailed deer and moose, but not elk, in the snow season to being positive for only elk in the snow-free season. Further, kill rates of moose decreased with sunlight in the snow-free season. The magnitude of effects was much stronger during the snow season than the snow-free season. We acknowledge seasonal differences in results could be due to sample sizes being reduced in snow-free months due to a decline in our sample population. However, many other ecological mechanisms account for seasonal differences in predation. The factors influencing encounters, speed, and detectability change due to environmental and biological cycles across seasons. For example, snowfall decreases wolf activity and speed (Droghini and Boutin 2018). Antipredator movement response decreases with body condition over the winter, moose in late winter had a weaker movement response compared with early winter (Oates et al. 2019). Further, kill rates from one season do not predict kill rates in another (Metz et al. 2012), indicating the importance of including multiple seasons in predation studies when possible. During denning periods, wolves demonstrate central place foraging movements (Ylitalo et al. 2021). Breeding females moved more during activity periods, though hunting and not reproduction was the main driver of movement (Theuerkauf et al. 2003b). Movement was supressed at high temperatures (>20°C) in the summer (Theuerkauf et al. 2003b). Perhaps some decoupling of moose with wolf activity periods was due to temperature driven behaviour, as most moose were killed at night during the snow-free season. From spring to fall, wolves have a more diverse diet comprising adult ungulates, calves, beavers (*Castor canadensis*) , and other small prey. In our study, beaver kills often co-occurred with wolf den sites, wolf rendezvous sites, or large ungulate kills sites, confounding our ability to estimate the time of kill as we did for ungulate prey. Further, we did not have movement rates or activity data for beaver. Though wolf speeds will still be much greater than beavers, beaver activity periods are very indicative of risky times as they have areas of spatial refuge (McClintic et al. 2014, Bartra Cabré et al. 2020). We recommend that future work increase sampling and attempt to survey prey availability and accessibility during the snow-free months to provide a more robust test of seasonal differences.

Kill rates increase with density until a saturation point due to handling time (Holling 1959). For a discussion of how to incorporate density and handling time into this analysis framework see Appendix 2. Similarly, encounter rates nonlinearly increase with density; in another wolf elk system this threshold was 3.27 elk/km^2 (Martin et al. 2018). Prey density in RMNP around this threshold: average moose density in the studied packs territories is 1.5 moose/ km^2 ranging from .04 to 3.4 moose/km^2, and average elk density is 0.39 elk/km^2, ranging from 0.02 to 1.2 elk/km^2 (Zabihi-Seissan et al. *in review*). In addition, wolf territories in this system are small (median area of the 95% MCP of stable territories from November to April location 230 km^2, ranging from 130 to 500 km^2) compared with other wolf populations considered to be in highly productive systems (3,186 km^2 to 4,878 km^2 during the winter; Dickie et al. 2022). Thus, encounter rates likely play an even more significant role in wolf behaviour in other systems compared with RMNP. In RMNP, catchability may have a greater influence on which prey are ultimately killed in this system. The three prey in this analysis vary in their body size, energetic payoff, flight responses, and danger to wolves. Underlying prey switching is the trade-off between energetic gains and costs presented by diverse prey (Prokopenko et al. *in review*). In RMNP, white-tailed deer, elk, and moose have been prey for wolves for decades. However, a shift occurred in population trends and subsequent kill rates over time. Elk were the most abundant and the primary prey for wolves when wolf research began in the area (Carbyn 1983, Paquet 1992). During the winter kill rates of wolves on elk are potentially incidental and opportunistic, as they are not related to wolf activity periods. This result is paralleled in wolf selection behaviour (Zabihi-Seissan et al. Accepted), where wolves select for moose habitat and catchability (encounter and attack), but only elk catchability (attack). There was a switch in the snow-free season where kill rates of elk were the only prey described by effective speed and sunlight. In multiprey systems, the predator encounter and kill rates contain multitude mechanisms including availability and accessibility.

Our study was conducted in a protected area. In areas with increased anthropogenic pressures, the relationship between movement and predation can be disrupted. For example, when human harvest was the main mortality cause for moose, moose did not respond to predation by changing movement rates (Wikenros et al. 2016). This is in contrast to other systems where predation is a larger mortality factor and prey do respond by increasing movement rates (Gude et al. 2006, Pusenius et al. 2020). If predation is a dominant factor, then anthropogenic disturbance in the form of linear features can increase predator movement and potentially intensify predation (McKenzie et al. 2012, Dickie et al. 2017). In addition, disturbances can displace prey species, which will alter local densities and subsequently encounter rates (Holling 1959, Avgar et al. 2011). Habitat modification creates open areas and edges which promote kills (Bergman et al. 2006). Further, anthropogenic disturbance creates light, sound, and scent pollution which could interrupt multiple modalities relied upon by predators and prey (Polo-Cavia et al. 2016, Kern and Radford 2016, Fleming and Bateman 2018). Finally, human activity can alter diel activity patterns in wildlife (Patten et al. 2019); thus, further tests of these relationships should be done in disturbed landscapes.

We present a multiprey test of the ideal gas law through a temporal prism, where we find speed and detectability increase diel kill rates. Movement rates are maximized at times when sunlight is declining; the positive relationship with both factors may represent behaviours occurring at this confluence of both detectability and effective speed. There is a dynamic interplay between risking times and risky places (Smith et al. 2020). Simultaneous collaring of predators and prey examining precise conditions affecting encounters and kills will further disentangle these relationships.

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3.7 Author's Contributions

CMP conceived the original idea for the manuscript. Data was collected and provided by CMP and SZS in RMNP, DD and KK in GHA 26. CMP conducted the analysis and wrote the manuscript with input and approval from all coauthors.

Table 3.1. Model coefficients for the relationship between wolf kills with movement rate and light conditions for the three ungulate prey (white-tailed deer - WTD, elk, and moose) in Riding Mountain National Park. Bold values indicate where 95% Confidence Intervals do not overlap zero.

	Snow			*Snow-free*		
	Estimate	95% CI		Estimate	95% CI	
Intercept (WTD)	-1.07	-2.27	0.13	-0.44	-1.22	0.35
Elk	1.94	0.19	3.70	-0.32	-1.46	0.82
Moose	0.45	-1.24	2.14	1.69	0.57	2.81
Effective Speed:WTD	**4.24**	**1.24**	**7.25**	1.35	-0.21	2.90
Effective Speed:Elk	-0.92	-4.09	2.24	**1.90**	**0.27**	**3.52**
Effective Speed:Moose	**3.99**	**1.00**	**6.98**	-0.57	-2.14	1.01
Sunlight:WTD	**0.70**	**0.05**	**1.34**	0.39	-0.34	1.12
Sunlight:Elk	0.03	-0.62	0.68	**0.83**	**0.10**	**1.56**
Sunlightt:Moose	**1.02**	**0.37**	**1.66**	**-0.96**	**-1.70**	**-0.23**

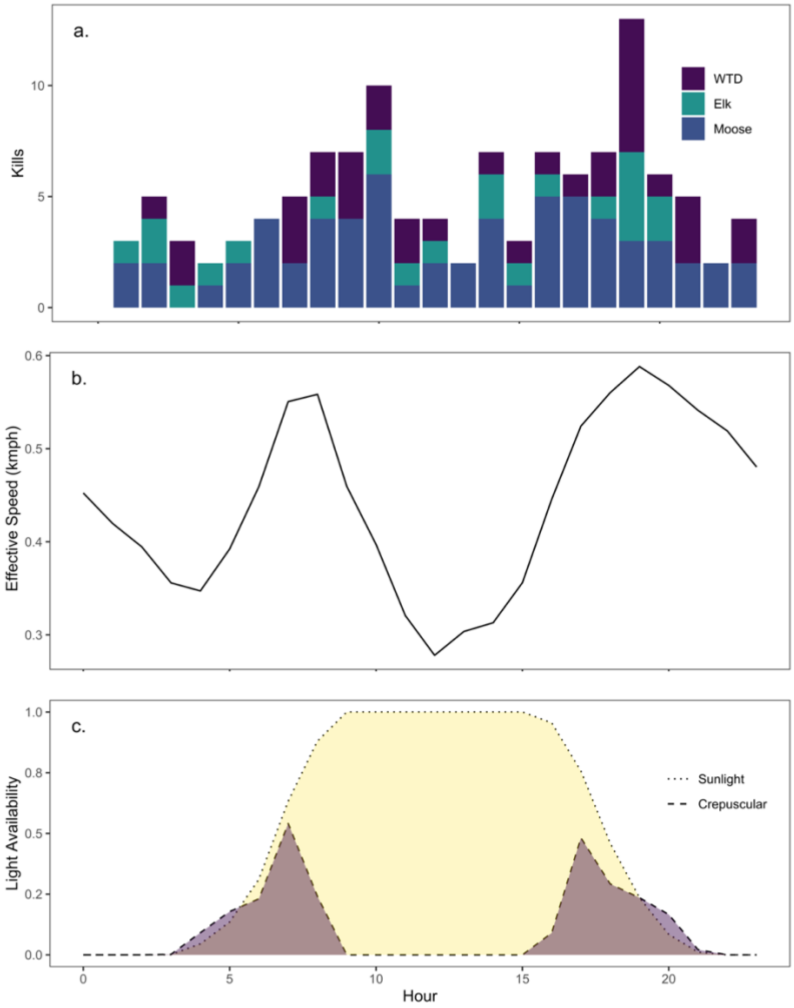

Figure 3.1. Temporally dynamic covariates used to explain diel variation in a) kill rates are b) effective speed (*v*, calculated from wolves, elk, white tailed deer, and moose) and c) detectability (*D,* which was measured as proportion sunlight availability (L, and crepuscular light (c, purple). Total number of kills per hour are the dependent variable explained by factors interacting with prey species that vary between hours. We identified kill clusters and animal speed from GPS locations, detectability was determined from the proportion of sunlight and crepuscular light occurring each day and averaged across the year. Data in figure is from snow season, snow-free season is presented in Appendix 1.

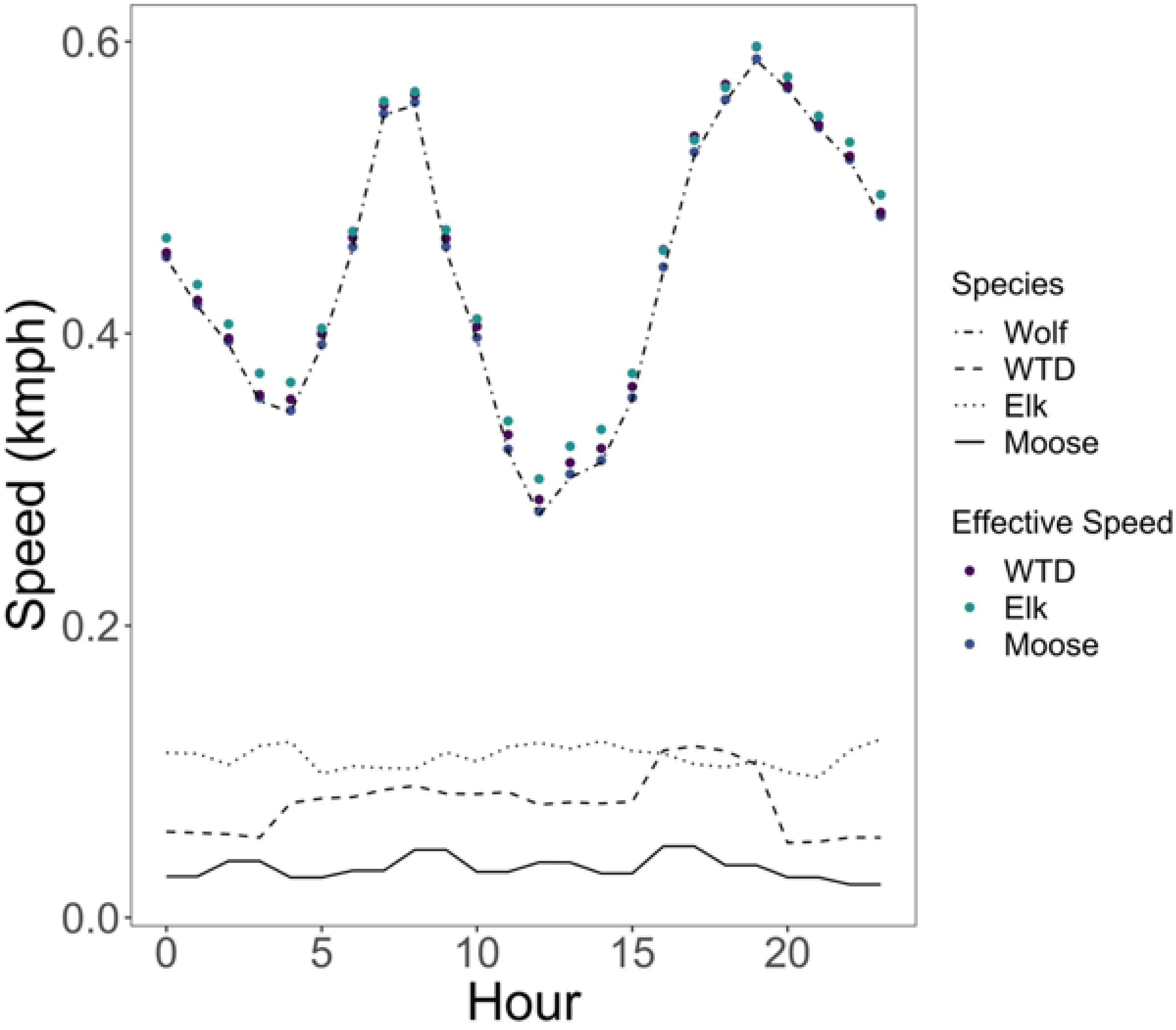

Figure 3.2. Diel speed over 24-time bins of an hour, calculated as an average of step length over interval duration from GPS data. Effective speed (dots, coloured by species included as prey), calculated from $v = \sqrt{v^2{}_{predator} + v^2{}_{prey}}$ for the system, is governed by wolf speed (dot-dash) which is much greater than prey speeds for elk (dotted), deer (dash), and moose (solid). Data in figure is from snow season, snow-free season is presented in Appendix 1.

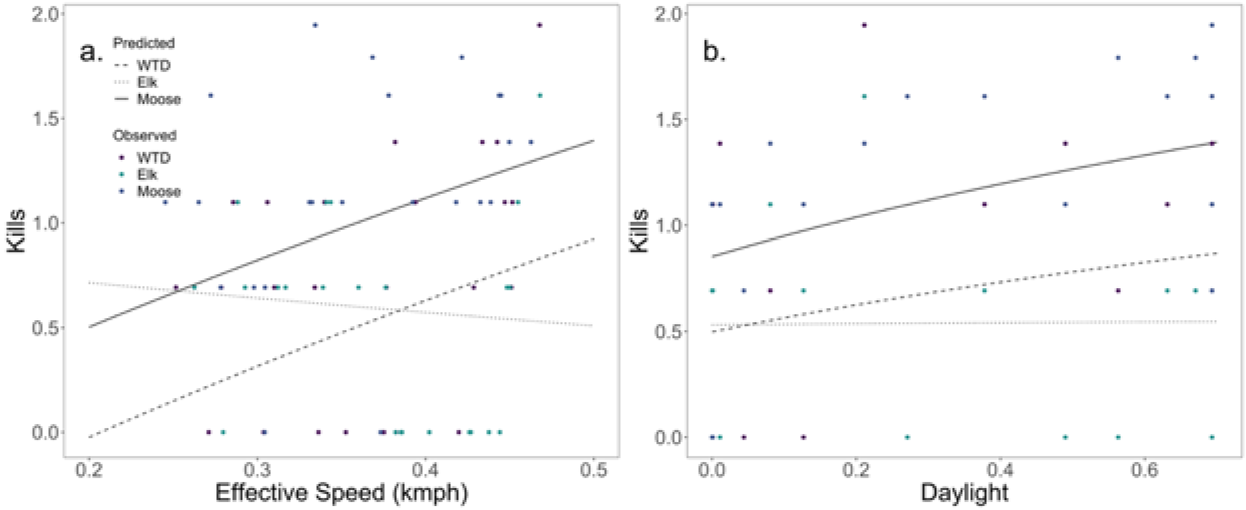

Figure 3.3. Predicted (lines) and observed (points) kills with effective speed and daylight for three ungulate prey white-tailed deer (WTD; dash, purple), elk (dotted, green), and moose (solid, blue). Top performing model for the snow season (Table 1).

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CHAPTER 4: OPTIMAL PREY SWITCHING: PREDATOR FORAGING COSTS PROVIDE A MECHANISM FOR FUNCTIONAL RESPONSES IN MULTI-PREY SYSTEMS

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4.1 ABSTRACT

Foragers must balance the costs and gains inherent in the pursuit of their next meal. Classical functional responses formulations describe consumption rates driven by prey density and are naive to predator foraging costs. Here, we integrated foraging costs into functional responses to add mechanism and precision to foundational ideas. Specifically, using a model system with a single predator and two prey, we express a functional response emerging from variable energy and time costs of each predation phase: searching, attacking, or consuming prey. The utility of our model is explored through a focused example where prey can exert variable influence on predator foraging costs through antipredator traits. Dissimilarity between prey in their foraging costs influence the energy gain rate of the predator through optimal prey switching. We found that a small subset of prey antipredator traits and density conditions generated a stabilizing Type III (sigmoidal) functional response – the pattern often thought to typify a generalist predator switching between prey species. The sigmoid functional response occurred for highly profitable prey only when the costly prey was 1. at a high density and 2. their antipredator traits increased energy or time costs following an encounter. We outline testable predictions regarding foraging costs from our model. We provide guidance for how to apply optimal foraging theory to empirical scenarios where predator foraging costs vary due to prey type, predator type, or environmental conditions. Our framework represents a synergy of foundational and contemporary theory across disciplines, facilitating the discovery of shared principles and context-dependent variation across varied predator-prey systems.

4.2 INTRODUCTION

To understand the flows of mass and energy through ecological communities, foundational ecology theory has structured consumer-resource interactions to be the outcome of density-driven changes in consumption rates, *i.e.* “the functional response’ (Solomon 1949, Holling 1959a, Murdoch 1969). Early formulations of the functional response were developed for a single predator consuming a single prey type of varying density (Holling 1959a, 1959b; Appendix 1). However, this classical density-based approach to framing consumption is limited because: 1) a more direct measure of changes in the flows of mass and energy may better capture the ecological process in question; 2) density-driven interactions overlook the optimization that generalist foragers face in terms of consuming prey that vary in body size, abundance, risk, and other traits. There is a need to articulate a more generalizable framework of consumer-resource interactions that accommodates energetic transfer in diverse, multi-prey food webs that characterize the most common ecological communities in nature (Marleau et al. 2020).

Generalist predators consuming multiple prey types are a common feature of natural systems. Within multi-prey systems, predators demonstrate ‘preference’ for certain prey types. A density-dependent preference is an indicator of prey switching (Murdoch 1969, Oaten and Murdoch 1975). In instances of prey switching, preference relates to lower-than-expected consumption rates at low prey densities and disproportionality high consumption rates at high prey densities. Prey switching can create a Type III functional response (Oaten and Murdoch 1975, Elliott 2004). Often the parameters that generate prey switching pattern lack a mechanistic interpretation (DeLong 2021). One suggested mechanism of prey switching is predator learning or experience (*e.g.* search image; Real 1977, Van Leeuwen et al. 2013). For example, after little egrets (*Egretta garzetta*) experienced a prey capture failure they changed their behaviour to prioritize areas with particular conditions, such as reduced cover and increased prey density (Vijayan et al. 2019). As we will show here, an alternative and arguably simpler mechanism to explain prey switching emerges from predator foraging costs.

Optimizing the balance between costs and gains of foraging manifests as diverse patterns in predator-prey interactions. Predators may modify their hunting behavior in response to injury costs (Berger-Tal et al. 2009, Mukherjee and Heithaus 2013) and the nutritional condition of a predator can promote their risk-taking behavior (Moran et al. 2021). The interaction between predator hunting modes with prey antipredator traits influences prey switching (Elliott 2004). For example, changes to activity patterns and space use may be effective against some predators but increase predation by others (Miller et al. 2014, Fouzai et al. 2019). The environment where predators and prey reside also shapes their interactions; detection and catchability of prey can be promoted or hindered by habitat (Hebblewhite et al. 2005, Ruxton 2009, Stevens and Merilaita 2009, Ford et al. 2014). For example, wolf (*Canis lupus*) home ranges get smaller in landscapes characterized by disturbances that increase wolf mobility (Dickie et al 2022). This pattern of home range shrinkage also arises when prey occur at greater densities. Thus, environmentally induced predator mobility and prey density can have similar effects on predators-prey interactions. Prey switching itself has costs, thereby promoting diet specialization to maintain consumption efficiency (Hooker et al. 2017). Whether diet specialization arises through competition, resource access, or natural enemies, it can be linked to optimal foraging (Araújo et al. 2011). Harmonizing the characteristics of prey, predator, and the environment on an energetic framework of gains and losses offers a generalizable pathway to assess the role of predation in multi-prey systems.

Here, we express a mechanistic functional response model that incorporates optimal foraging behavior to link predator foraging costs with density-dependent consumption rates in a multiprey system. Energy is used to quantify the flow between trophic levels, and frameworks describing this flow provide avenues to integrate ecological theories (Lindeman 1942, Schramski et al. 2015, Marleau et al. 2020). This is an avenue for energetic equivalencies to be calculated and compared across predator-prey systems. A testable and unifying principle emerges from optimal foraging theory: predators should target prey with the greatest energetic gain per unit time. An energetic perspective on the functional response means that consumption rates, energetic gain, and the costs of foraging can be considered in parallel to the effects of prey density per se. Here, we build upon the substantial foundation of existing work completed on functional response (Jeschke et al. 2002, Appendix S1) to generalize consumption rates of prey species that may vary in their density and costs to predators. We developed a model that evaluates the energy budget of predators in a multi-prey system. Our modelling approach is flexible enough to include factors that influence foraging costs of consumers, such as trophic level (*e.g.* plant-herbivore interactions), environmental context (*e.g.* habitat structure), or attributes of the predator (Fig. 1, Table 1).

4.3 MODEL

We quantify the total energetic gain rate (energy acquired per predator per unit time, *e.g.* calories/second or Watts). We define parameters that relate to the behavioral sequence from the searching phase to consumption of a prey item. The energy and time parameters of this model generalize concepts from empirical studies on foraging costs such as hunting mode, spatial variation, and antipredator traits (Fig. 1, Table 1).

After an individual of prey type i is encountered by the predator (Fig. 1), the energy-gain rate is reduced by the cost in effort spent attacking the prey, where $t_{a,i}$ is the attack time per prey unit and $e_{a,i}$ is the energetic cost of attacking (in units of energy per unit time). The probability of killing prey i at the end of the attack, $p_{k,i}$, determines the transition to the consumption phase. Handling time has previously been defined as the time to attack, eat, and digest prey (Holling 1966, Jeschke et al. 2002, Sentis et al. 2013). We separate handling into two phases, the pre-kill attack phase, and the post-kill consumption phase. Consumption encompasses the ingestion and digestion phase that occurs post-kill. If a predator kills the prey, the energy-gain rate may be further reduced due to the energetic cost of consumption $e_{b,i}$ (energy per unit time) and the time taken to consume a prey, $t_{b,i}$. Finally, the predator obtains $E_{n,i}$ (net assimilated energy such as calories or Joules) once the prey is consumed and after accounting for the metabolic costs of assimilation. The potential energy gain (G_i, units of energy) from engaging with an encountered prey of type i is then given by a weighted average of the possibility that the predator was successful at killing the prey (with probability $p_{k,i}$), and the possibility that it failed to do so (with probability $1 - p_{k,i}$):

$$G_i = p_{k,i} \cdot \left(E_{n,i} - t_{a,i} \cdot e_{a,i} - e_{b,i} \cdot t_{b,i}\right) - \left(1 - p_{k,i}\right) \cdot t_{a,i} \cdot e_{a,i} \tag{1}$$

In optimal foraging theory, energy-gain rates are a currency of interest (Charnov 1976), as predators are assumed to maximize their lifetime reproductive success by maximizing this proximate fitness gain rate. The expected net energy-gain rate, g_i, is energy gain, G_i, over time. Energy and time costs are incorporated into the gain rate from prey i:

$$g_i = \frac{G_i}{t_{a,i} + p_{k,i} \cdot t_{b,i}} = \frac{-e_{a,i} \cdot t_{a,i} + p_{k,i} \cdot \left(E_{n,i} - e_{b,i} \cdot t_{b,i}\right)}{t_{a,i} + p_{k,i} \cdot t_{b,i}} \tag{2}$$

where g_i is reduced by both increased energy and time investment and is increased by higher probabilities of killing the prey and the net assimilated energetic value of the prey item.

If only two prey types occur (the simplest multiprey system), the alternative to pursuing and attacking the encountered prey (i) is to forgo it and instead search for a second prey type, j, with an expected net energy-gain rate of:

$$g_{alt}(N_j) = \frac{-e_{s,j}\cdot(N_j\cdot s_j)^{-1} - e_{a,j}\cdot t_{a,j} + p_{k,j}\cdot(E_{n,j} - e_{b,j}\cdot t_{b,j})}{(N_j\cdot s_j)^{-1} + t_{a,j} + p_{k,j}\cdot t_{b,j}} \qquad (3)$$

Following (Avgar et al. 2011), we assume that, on average, the predator encounters an individual of prey species j every $t_{s,j} = (s_j \cdot N_i)^{-1}$ time units, where s_j is the predator's prey-specific search rate (in units of area per time), and (N_j) is the density of prey j (number of prey per unit area). Note that s_j is a function of multiple factors, including the speed of both predator and prey, the predator's perceptual range, and the prey's conspicuousness. The expected energy per time cost of searching $(e_{s,j})$ and the expected time to encounter prey j $(t_{s,j})$, are added to the energy-gain rate as the predator must search before prey j is encountered. All else being equal, the energy-gain rate for this second prey type, $g_{alt}(N_j)$, is always lower than the energy-gain rate, g_i,of the encountered prey i. Differences in costs between the two prey types ($s, t_a, p_k, t_b,$ or E_n; see Fig. 1 and Table 1) may interact with or override the effect of prey abundance (N_j) on energy-gain rate, such that $g_{alt}(N_j) > g_i$.

Optimal foraging theory often considers optimal diet choice, and specifically the probability to engage with prey i once encountered. In our model, the probability of engaging, $p_{e,i}$, is a function of weighing the energy-gain rate of prey i compared to the alternative of continuing to search for the alternate prey j. An optimal forager would have $p_{e,i}$ and $p_{e,j}$ values that maximise its long-term energetic consumption. More specifically, an optimal 'Kelly strategist' should allocate resources to the two alternatives in proportion to their expected gains (Kelly 1956, Baddeley et al. 2019). However, since the uncertainty associated with expected gain from an alternative prey is always greater than the uncertainty associated with expected gain from an encountered prey (due to the added uncertainty around search time), and in accordance with error management theory (Johnson et al. 2013), we model this criteria as a Metropolis-Hastings acceptance ratio (Metropolis et al. 1953, Hastings 1970, Rosenbluth 2003):

$$p_{e,i} = min\left(1, \frac{g_i}{g_{alt}(N_j)}\right) \tag{4}$$

Hence, an optimal predator will always (deterministically) engage with an encountered prey if the expected gain rate from that prey is equal to or larger from the expected gain rate of the alternative prey (which includes costs associated with the addition of the search phase). If the expected gain rate from an encountered prey is lower than the alternative, the predator will engage with the encountered prey with a probability given by the ratio of expected gain rates (*i.e.* stochastically). We assume the predator's fitness and therefore, its decision to engage depend only on its long-term energetic gains. Note, that this acceptance algorithm is piecewise asymmetrical, reflecting the added cost of uncertainty related to forgoing engagement with an encountered prey to search for another. Nevertheless, the currency that our theoretical predators are maximizing is the expected long-term energy acquisition rate.

We can now use the above parametrization to derive Holling's attack rate (a, see Appendix S1), $s \cdot p_e \cdot p_k$, and Holling's handling time (h, see Appendix S1), $t_a + p_k \cdot t_b$. The predator's functional response to prey i (number of prey i individuals consumed by a single predator per unit time) is:

$$f(N_i) = \frac{(s_i \cdot p_{k,i} \cdot p_{e,i}) \cdot N_i}{1 + s_i \cdot p_{e,i} \cdot N_i (t_{a,i} + p_{k,i} \cdot t_{b,i}) + s_j \cdot p_{e,j} \cdot N_j \cdot (t_{a,j} + p_{k,j} \cdot t_{b,j})} \tag{5}$$

Further, the ratio of the harvest rates experienced by prey i relative to prey j (*i.e.* switching equation, Murdoch 1969) is:

$$\frac{f(N_i)}{f(N_j)} = \frac{s_i \cdot p_{e,i} \cdot p_{k,i} \cdot N_i}{s_j \cdot p_{e,j} \cdot p_{k,j} \cdot N_j} \tag{6}$$

Lastly, the predator's total energetic functional response (net energy gain per time) is the energy gain from two prey types summed together:

$$F(N_i, N_j) = \frac{N_i \cdot s_i \cdot p_{e,i} \cdot [p_{k,i} \cdot (E_{n,i} - e_{b,i} \cdot t_{b,i}) - e_{a,i} \cdot t_{a,i}] + N_j \cdot s_j \cdot p_{e,j} \cdot [p_{k,j} \cdot (E_{n,j} - e_{b,j} \cdot t_{b,j}) - e_{a,j} \cdot t_{a,j}] - e_s}{1 + N_i \cdot s_i \cdot p_{e,i} \cdot [t_{a,i} + p_{k,i} \cdot t_{b,i}] + N_j \cdot s_j \cdot p_{e,j} \cdot [t_{a,j} + p_{k,j} \cdot t_{b,j}]} \tag{7}$$

In equations 5-7 we formally express fundamental concepts from consumer-resource theory using simple, pre-established building blocks directly relating to various foraging costs. While we formulate this model for two prey species, the arguments we use could be extended to more diverse multi-prey systems.

4.4 APPLICATION: ANTIPREDATOR TRAITS INDUCE FORAGING COSTS

To present a tangible and testable application of our model, we focus on the influence of antipredator traits in a system with one predator and two prey in which we hold the environment and predator traits constant. Holling (1959) discussed the role that prey traits may play in modifying the functional response, specifically, energetic value (calories), defense mechanisms, and evasion strategies. Antipredator traits refer to prey traits that reduce the probability that prey are detected or captured by a predator (Abrams 1990). Differences in antipredator traits between prey may override the effects of differences in prey density when describing predator consumption rates (Tallian et al. 2017). We found 96% of 28 studies on functional responses in multiprey systems and prey switching identified preference (*i.e.* consumption is greater than expected given prey abundance) in a predator's consumption behavior (see Appendix S2 for reproducible literature survey methods). Empirically-measured departures from predictions of optimal foraging theory can be resolved by considering prey antipredator traits that confer vulnerability and profitability (Sih and Christensen 2001). Vulnerability and profitability are tightly related and are both reduced by antipredator traits. Vulnerability integrates how easily predators can access prey, with the risk of injury or death to a predator caused by the prey's defenses, *i.e.* mechanical, behavioral, and constitutive. Profitability refers to the energetic value of prey to the predator, which we define as the net energy gain of the prey, accounting for energy provided by consuming the prey and the costs incurred during the predation sequence (Fig. 1). Therefore, one prevalent source of energetic costs to the predator are antipredator traits: the behavioral, physical, or physiological characteristics that reduce prey vulnerability and profitability (Fig. 1, Table 1).

4.4.1 PARAMETERS AND SCENARIOS

We focused on informative points in the parameter space of our model to demonstrate how to characterize the effects of dissimilarity in the costs of two prey types consumed by a single predator (Table 2). Baseline parameter values were set to: $p_{k,i} = p_{k,j} = 0.5$, $E_{n,i} = E_{n,j} = 1000\ calories$, $e_{s,i} = e_{s,j} = 1\ calories$, $e_{a,i} = e_{a,j} = 1\ calories$, $e_{b,i} = e_{b,j} = 1\ calories$, $s_i = s_j = 1\ \frac{m^2}{sec}$, $t_{a,i} = t_{a,j} = 1\ sec$, $t_{b,i} = t_{b,j} = 1\ sec$ (see Appendix S3 for an exploration of different baseline parameter values). Based on these baseline values we calculated the maximal energy gain rate possible in this system (*i.e.* when prey density is infinite); $F(N = \infty)$ ($332\frac{1}{3}\ cal/s$), and the prey density that resulted in half this maximum gain rate, $N_{0.5}$ (0.7, see Appendix S3 for these calculations). As a point of comparison, we created two single prey scenarios (Appendix S4): 1. A single prey system where the prey expressed a baseline (weak) antipredator trait and the energetic return for the predator is high ('Single Vulnerable'), and 2. The prey had antipredator traits that result in time or energy costs for the predator ('Single

Costly'). Values were calculated for each trait such that the predator's energetic gain rate at $2 \cdot N_{0.5}$ was reduced to the half-maximum energetic gain rate from vulnerable prey ($F_{traited}(2 \cdot N_{0.5}) = F_{vulnerable}(N_{0.5}) = 166\frac{2}{3}$; Appendix S3). This approach provides a comparison of effectiveness through determining the cost that meets the same endpoint (half maximum) at different rates of change. We constructed a multiprey system in which two prey types (i and j) are identical in all costs and vulnerable to predation ('Similar Prey'), which allowed comparison to a multiprey system where one prey is vulnerable (prey j) and the other (prey i) has increased costs ('Dissimilar Prey').

We calculated consumption rates as both prey per time or energy per time in a system with a single prey type (Appendix S4: Fig. S1) or multiple prey types (Fig. 2). To examine the relationship between consumption rates and density for two prey, we produced a switching plot *sensu* Murdoch (1969; Fig. 3), where the change in relative consumption (costly prey consumed for every vulnerable prey) is compared to the change in relative density (costly: vulnerable). The slope of this relationship defines the predator preference for prey. A slope of 1 indicates no preference, with consumption increasing in proportion with density. As a supplement, we depicted the prey perspective by plotting the per capita predation risk (the instantaneous probability that a prey individual will be consumed by the predator; Appendix S4: Fig. S2). This per capita predation risk is often considered an important driver of non-consumptive effects and is important to consider in the context of its potential to induce antipredator phenotypes. All examples were coded and plotted in R version 4.10, (R Development Core Team 2021) see GitHub repository for code.

4.5 RESULTS AND DISCUSSION

Prey antipredator traits and density interact to generate functional response patterns

Our model specifically incorporated how antipredator traits increase energy or time costs for the predator. We found that foraging costs created different predator functional responses when acting on different phases of the predation sequence. In our model, the functional response of the predator for the costly prey followed a saturating curve (Type II functional response, Fig. 2 a & c). As we increased predator foraging costs of a prey, the consumption rates were reduced. Foraging costs that reduced kill probability, increased attack time or increased consumption time (*i.e.* handling time) had the greatest effect on prey- and energetic-consumption rates in a single prey system (Appendix S4: Fig. S2). Increased energy costs supressed consumption rates in the presence of abundant, alternative, and more vulnerable prey (Fig. 2 a vs c). Out of the costs simulated, costs that decreased the predator's search rate or kill probability of primary costly prey were the most sensitive to the density of the alternative vulnerable prey (Fig. 2 a & c). Costs that reduced the predator's search rate or kill probability acheived the lowest consumption rates when alternative prey density was high compared to the other foraging costs tested (Fig. 2 a vs c). Our theoretical predictions agree with empirical tests of foraging theory where the presence of alternative prey reduced the consumption of primary prey (*e.g.* roe deer-moose-wolf; (Sand et al. 2016). Our mechanistic model indicated that in multiprey systems, a reduction of consumption rates in the presence of alternative prey predominantly occurs for a less vulnerable, more costly prey. However, we should not always expect a predation refuge for a rare prey in multiprey systems through a Type III functional response.

The benefits of scarcity for the prey depend on the density of *and* foraging costs associated with the more abundant prey. In the presence of abundant and costly prey, the functional response for vulnerable prey follows a Type III sigmoid shape, and this pattern held for antipredator traits acting on all phases of predation but search rate (Fig. 2d, see Appendix S4: Fig. S2 for more apparent nonlinearity). Empirical evidence supports our theoretical example: sigmoid responses for wolves consuming vulnerable roe deer emerged with an alternative costly prey, moose (Sand et al. 2016). The predator's functional response (Type II) for vulnerable prey in the presence of scarce and costly prey was indistinguishable from the functional response for a prey in the presence of scarce but 'Similar' alternative prey (Fig. 2 b). Being relatively scarce has potential to be an effective antipredator trait whether the prey is or is not well defended. In conclusion, both theoretical and empirical evidence suggest that predators demonstrate a Type III responses for preferred and vulnerable prey, while having a Type II or I response for other prey types or vulnerable prey in other conditions (Elkinton et al. 2004, Chan et al. 2017). The predation rate (per capita consumption rate) is calculated from the functional response an accordingly was influenced by focal prey density, alternative prey density, and the antipredator trait dissimilarities between them (see Appendix S4).

Predator preference is determined by antipredator trait induced foraging costs, relative density between prey, and the absolute density of prey

Predator preference of prey and prey-switching patterns were generated by our model which incorporates antipredator trait induced foraging costs and density (Fig. 3). Predators consumed prey in proportion to their relative availabilities when the costs were similar (slope is 1, indicating no preference, Fig. 3). Predators preferred vulnerable prey when the alternative prey was costly (Fig. 3a; values less than 1 indicate preference for vulnerable prey). In the 'Dissimilar Prey' scenarios, decreasing the predator's search rate had the greatest influence on predator preference, followed by reducing probability of kill, and increased time or energy to attack or consume (Fig. 3). Examples across systems support that preference is driven by prey vulnerability (foraging costs), and the relative consumption of vulnerable prey increases when they are at higher densities (Sundell et al. 2003, Lai et al. 2011, Tallian et al. 2017).

The predator's prey preference as a function of foraging costs was nonlinearly related to relative and absolute densities of prey. Specifically, predators consume costly prey in proportion to their density only when the costly prey are far more abundant than vulnerable prey (Fig. 3 a). Here we altered both absolute density, which is the sum of the costly and vulnerable prey, and the relative density of the prey in model simulations. The magnitude of predator preference for vulnerable prey increased with absolute prey density even when the relative density of costly to vulnerable is fixed (Fig. 3 b). It is hard to quantify cost and density effects on consumption rates in natural multiprey systems. Yet evidence for this is documented in red knots (*Calidris canutus canutus*) whose response to relative and total prey availabilities was explained by the balance between meeting energetic needs while not exceeding toxicity thresholds (van Gils et al. 2015).

In our modeled scenario, we identified an interactive effect between costs and the relative or absolute prey densities in multiprey systems. The effect of alternative prey density is encompassed in the concept of 'neighborhood effects' in predator-prey interactions. In a savanna system, lion predation depended upon both composition and abundance of other prey species in the local area (*i.e.* the prey neighborhood; Ng'weno et al. 2019). Similarly, a neighborhood effect occurred between streams, the amount of salmon killed by bears in a stream decreased with prey abundance in surrounding streams (Quinn et al. 2017). The development of antipredator traits that create predator foraging costs, *e.g.* plant physical defences (prickles), can be induced due to their alternative prey neighbors increasing predation pressure (Coverdale et al. 2019). Although these empirical examples demonstrated that prey are influenced by the neighbors they keep, their link to energetic flows of predators were not formalized. We hope to reinforce the expectation for future empirical studies that, in addition to environmental context and predator traits, efforts to provide a quantitative link between energetic gains by the predator, prey traits, and density in ‘prey neighbourhood’ studies are likely to form productive lines of inquiry into the mechanisms that underly functional responses.

4.6 SYNTHESIS

Aspirations to identify generalizable processes are limited by our appraisal of the ecologically or energetically important factors. The phenomenon of prey switching can be understood through foraging costs reducing energy flow. We provide evidence that the two main indicators of prey switching, Type III functional response and changes in predator preference, are mediated by dissimilar energy and time costs. Often prey switching is identified in ecological studies by calculating a disproportionate relative consumption rate with relative prey density, *i.e.* preference *sensu* Murdoch (1969). Predators consistently exhibit preference for more profitable prey over the costly alternative prey across the scenarios we tested. However, only a small subset of prey trait and density conditions generated the classic Type III functional response (Holling 1959a), the pattern often thought to typify a generalist predator switching between prey species. Specifically, the sigmoid functional response occurred for profitable prey only when the costly prey was at a high density and their traits increased energy or time costs following encounter. Our model provides a previously lacking mechanism for the parameters that can generate Type III functional responses. The precise requirements identified by our model provide an explanation for the limited observations of the Type III response in real systems (Oksanen et al. 2001). Commonly, changes in relative prey density are thought to explain prey switching, through processes such as search image formation or learned hunting techniques (Real 1977, Van Leeuwen et al. 2013). These cognitive processes are important, but our model suggests that prey switching, and Type III functional response patterns can arise in their absence. We demonstrate these patterns can arise from an optimal predator responding to foraging costs.

Consuming resources is motivated by energetic needs of predators, and accordingly energy provides a means to incorporate foraging costs into calculations of consumption rates. The costs incurred by predators when consuming prey can supersede the energy contained by that prey item. Put simply, energy assimilation rate may be far lower than the energy contained in the prey item. For example, leech (*Whitmania laevis*) predators preferred smaller and vulnerable prey over large and defended prey because ease of capture impacted profitability (Lai et al. 2011). Even an optimal predator cannot fully counteract the costs of a more taxing prey community. A predator in a system with prey that possess intrinsically higher costs will result in lower total energetic gain for the predator population, thereby, structuring food webs via bottom-up processes, *i.e.* ‘donor control’ (Polis and Strong 1996). As such, an energetic, rather than strictly ‘prey item’ perspective should be taken when studying predator-prey interactions. Absolutely, predator-prey population dynamics are a product of the functional and the numerical response, as the energy required through prey consumed over time promotes growth of the predator population (Pettorelli et al. 2011, Serrouya et al. 2015). Biomass, which is one simple way to appreciate energy flow through ecosystems, has been used to establish fundamental and widely applicable laws in predator-prey ecology (Hatton et al. 2015). Calls to consider phenomenon like trophic cascades as fluxes in energy measured as biomass or nutrients, rather than changes in foraging behavior or space use are prevalent (Polis et al. 2000, Bolker et al. 2003, Ford and Goheen 2015, Carmona et al. 2016, Schmitz 2017, Leroux et al. 2020). We echo the recommendations for dissolution of species-specific qualitative descriptions of ecological relationships in favor of quantitative approaches to describe underlying energetic flows of consumer-resource patterns (Marleau et al. 2020). Energy is the currency with which to build our understanding and we have provided a framework in novel functional model that quantifies the energy required for a predator consuming multiple prey.

4.7 FUTURE DIRECTIONS

Our specific model scenarios were created to illustrate the utility of our framework with energy as a currency to understand the effect of foraging costs on functional response and prey switching. This exercise generated expectations for the confluence of prey density and predator foraging costs to be explored with empirical data across systems and trophic levels. Future predator-prey studies should aim to test:

1. *Necessity rejects no prey:* Predators will consume costly prey when alternatives are scarce, as prey become more abundant overall predators can afford to be more discerning on high energy landscapes. Consumers are more willing to take risks when hungry (Blecha et al. 2018), and this includes focusing on prey that are most abundant.
2. *The many outweigh the few:* Abundant costly prey only offers refuge to vulnerable prey types at extreme density dissimilarity. Thus, vulnerable prey populations may be more likely to persist in the presence of an abundant ‘costly’ prey population by experiencing positive density-dependent survival at low densities.
3. *More than a phase:* The patterns resulting from interactions between foraging costs and density depend on which phase of the predation sequence the cost is incurred. We need measures of energy rates to understand this link.

To effectively test these ideas, consumption rates must be sampled at a variety of prey densities across foraging costs. From a data collection perspective, the detection of a sigmoid relationship requires intensive measurement at low and high densities. Though our example focuses on prey-dependent foraging costs emerging from antipredator traits, this general framework can apply to variation in foraging costs due to predator type or environment (Fig. 1, Table 1). Energetic gain rates and the behavior of predators can vary due to internal and external factors. In our model, all single parameters can be expanded into functions that be informed by predator-specific qualities. Instead of single mean values representing energetic costs, the variation in parameters can be modelled as distributions or nonlinear relationships (see Appendix S1: Eq. S9 outlines a density-dependent search rate, Appendix S5: Fig S1 presents alternative formulations of engagement rates). As myriad costs emerging from foraging costs can be included into our model (Table 1), it can be tailored to many empirical systems.

We demonstrate the influence of foraging costs on the functional response but any implications relating to dynamical system behavior should be formally evaluated within a dynamical model (Abrams 2008). We provide a link between multiprey predation rates and the energy consumption of predator. Energetic gain rates are positively related to population growth (Lemon 1991). Our formulation can be incorporated into a dynamical model via prey mortality and predator growth; any discussion of stability can be resolved there. We expect most multiprey systems should be characterized by distinct differences in prey vulnerability because such differences can lead to negative density-dependent survival of the more vulnerable prey, hence greater stability (Fryxell and Lundberg 1994). An organism's traits determine the outcome of their interactions with others (Morales-Castilla et al. 2015). A natural extension of our work is employing the dynamical formulation to consider the evolution of prey antipredator traits that induce foraging costs and how selection is influenced by the presence of alternative prey (Abrams 2000, Schmitz 2017). We recognize that there is likely a cost to the prey expressing antipredator traits to induce foraging costs and the optimality of this action for the prey will depend on the costs to the prey in expressing that trait. More precisely, the reduction in predation rates must exceed the reduction in growth rate of the prey (Peacor et al. 2013).We predict that variation in multiprey systems may decouple or weaken the evolutionary arms race or long-standing eco-evolutionary dynamics of predator-prey interactions.

Optimal foraging allows integration of proximate behavior with ultimate processes but requires the proper appraisal of the costs in resource acquisition. Foraging costs can arise from multiple sources including characteristics of the environment, predators, and prey. In multiprey systems, a predator is faced with a choice between resources comprising different gains and inherent costs. Linking fundamental predator behavioral responses to these currencies allows calculations of equivalencies and trade-offs, leading to tests of generalizable versus context-dependent patterns across diverse systems. Tracking currency dynamics that underlie behavioral responses can forge quantitative links across levels of ecosystem organization.

4.8 ACKNOWLEDGEMENTS

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4.9 AUTHOR'S CONTRIBUTIONS

Development of the conceptual framework was supported by discussions with all coauthors, the model was formalized by CMP and TA. CMP wrote the manuscript which was revised by all coauthors.

Table 4.1. Foraging costs arising from physical, behavioural, and environmental sources, brief definitions, empirical examples, and corresponding parameters in the model.

Foraging Cost	Definition	Empirical Examples	Parameter
Physical			
Body size	The dimensions of an animal, including length, height, mass	Smaller prey (roe deer, moose calves) are more readily killed than larger individuals (Sand et al 2012, 2016)	energy value (E_n) consumption time and/or energy cost (t_b, e_b) attack time and/or energy cost (t_a, e_a)
Toxicity	Containing compounds that harm the predator when prey is consumed	Shorebirds recognize and reject toxic mollusk prey (Kvitek and Bretz 2005) Increased tannins decrease consumption by deer (Bergvall and Leimar 2005)	consumption energy cost (e_b) energy value (E_n)
Crypsis	Avoidance of detection by the predator, can be visual or non-visual: including camouflage, or mimicry	Mimicry can be a special case where the dissimilarity between prey types is integral to the success off that	search rate (s)

		antipredator trait (Johnstone 2002)	
Armor and weaponry	Morphological protection against attack, including integument, shell, spines	Leeches selected for snail species without opercula over more profitable snail species with them (Lai et al. 2011) Plant prickles deter herbivores and increase in susceptible neighborhoods (Coverdale et al. 2019)	consumption time and/or energy cost (t_b, e_b) probability of kill (p_k)
Energetic or nutritional Content	Gain received by the predator when it consumes prey	Often related to body size, but more specific measurements may be important (*e.g.* fat content). Phenology stage (Duparc et al. 2019)	energy value (E_n) Note: predator energy requirements are important context
Internal State	Short- or long-term condition of predator and prey *e.g.* hunger	Consumption of defended prey increased with predator hunger (Kaczmarek et al. 2020).	probability of engagement $(p_e, eqn\ 4)$ could follow different

	versus starvation, disease		functions (*e.g.* taking into account a risk of starvation).
Behavioural			
Sociality	Use of conspecifics to reduce risk or promote resource acquisition	Aggregation, group vigilance of prey (Creel et al. 2014), Cooperative versus solitary hunting	attack time and/or energy cost (t_a, e_a), consumption time and/or energy cost (t_b, e_b)
Aggregation	Spatial or temporal grouping with conspecifics	Dilutes the risk to an individual but can increase detectability. Reproductive synchrony (Ims 1990) or herd formation (Hebblewhite and Pletscher 2002, Fryxell et al. 2007)	search rate (s) attack time cost(t_a) probability of kill (p_k)
Flight response	Escape response to predator encounter	Could be quantified through distance and speed of flight (Sutton and O'dwyer 2018)	attack time and/or energy cost (t_a, e_a) probability of kill (p_k)

Fight response	Aggressive response to predator encounter	Can be quantified through duration and intensity of fighting, typical injury caused	attack time and/or energy cost (t_a, e_a) probability of kill (p_k)
Hunting mode	Suite of behaviours used to acquire prey *e.g.* active, cursorial, sit-and-wait, sit-and-pursue, ambush	Increased activity light avoidance in larva reduced their predation from active fish but predators increased from ambush predators (Miller et al. 2014, Fouzai et al. 2019).	all parameters of the model can vary with hunting mode, influence of antipredator traits or environmental condition will vary
Migration	Large-scale movement from one area to another	Many prey species avoid predation at a broad scale (Fryxell et al. 1988), *e.g.* caribou select seasonal ranges that reduce wolf predation (Rettie and Messier 2000)	search rate (s)

Space use	Use of spatial heterogeneity to influence predator efficiency and effectiveness	Prey use spatial refugia or habitat (Hebblewhite et al. 2005), predators occupy areas of prey vulnerability (Hopcraft et al. 2005, Coon et al. 2020).	search rate (s) attack time and/or energy cost (t_a, e_a) probability of kill (p_k)
Movement rate	Distance travelled over time	Reduced activity decreases encounter rates between squirrel tree frogs (*Hyla squirella*) and their odontate predators (McCoy and Bolker 2008). Kill rate is governed by predator movement rate (Vander Vennen et al. 2016)	search rate (s) attack time and/or energy cost (t_a, e_a)
Environmental			
Temperature	Degree of heat	Predator metabolism has thermal windows of efficiency which	consumption time and/or energy cost (t_b, e_b)

		influences consumption rates (Sentis et al. 2012)	
Snow	Accumulation and condition of snowpack		attack time and/or energy cost ((t_a, e_a))

Table 4.2. Values for scenarios used to determine the effects of cost dissimilarity in multiprey systems. We refer to prey with low time and energy costs (baseline values) as vulnerable. The antipredator costs values from reduce the energetic consumption rate to half maximum values (Appendix S3) in the scenario where there is a single vulnerable prey. We define cost dissimilarity (*Δ*) as the ratio of the costly prey i to the vulnerable prey j.

Term	**Definition**	**Model parameter (units)**	**Scenario values**
Predator energetic gain	Energy assimilated through consuming prey	Energetic gain (energy) Energetic gain rate (energy per time)	G_i , eqn 1 g_i , eqn 2 $g_{alt}(N_j), eqn$ 3
Prey	Consumable individual providing energy to the predator. We describe a single predator with two available prey, i and j	Density (individuals per unit area) Energy content (energy per individual prey)	N_i and N_j vary from 0 to 10 individuals $E_{n,i} = E_{n,j} = 1000$
Search	Leading to the discovery of a prey item	Search rate (area per time)	$\varDelta s = 2, s_i = .5, s_j = 1$
Engage	Attempt to pursue and capture a prey item	Probability of engagement	$p_{e,i}, eqn$ 4
Attack	Pursuing an encountered prey item	Attack energy cost (energy)	$\varDelta e_c = e_{c,i} = 125.6,$ $e_{c,j} = 1$

		Attack time cost (time)	$\Delta t_c = t_{c,i} = 1.745,$ $t_{c,j} = 1$
Kill	Successful capture and subduing of a prey item to be eaten	Probability of kill	$\Delta p_k = 1.4, p_{k,i} = .35,$ $p_{k,j} = .5$
Consume	Energy assimilation of resource to consumer	Consumption energy cost (energy)	$\Delta e_h = e_{h,i} = 250.25,$ $e_{h,j} = 1$
		Consumption time cost (time)	$\Delta t_h = t_{h,i} = 2.5, t_{h,j} = 1$

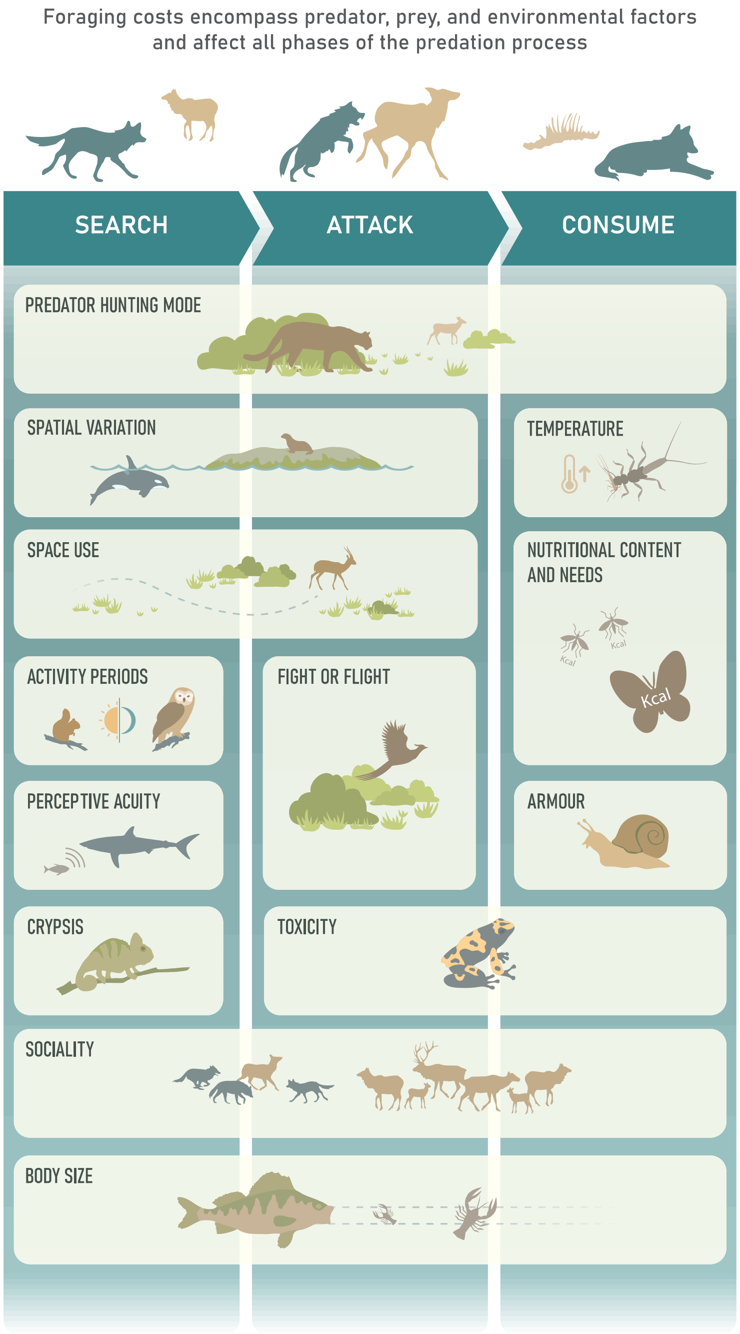

Figure 4.1. Examples of predator foraging costs. The predation sequence is three phases – search, attack, and consume – and the probability of transition from one phase to the next. When a prey type is encountered, a predator can engage or abandon the prey. The decision to engage depends on the potential energy gains and energy or time costs of the prey and the alternative

prey type (described by probability of engagement, p_e Eq. 4). Following a kill (p_k), the predator will enter the consume phase during which the prey is ingested and digested. Foraging costs can occur during any phase of the predation process, from initial searching to consumption (see Table 1). Whereas we highlight time vs energetic costs here, many factors may be manifested as either or both. Figure by Kate Broadley, Fuse Consulting Ltd.

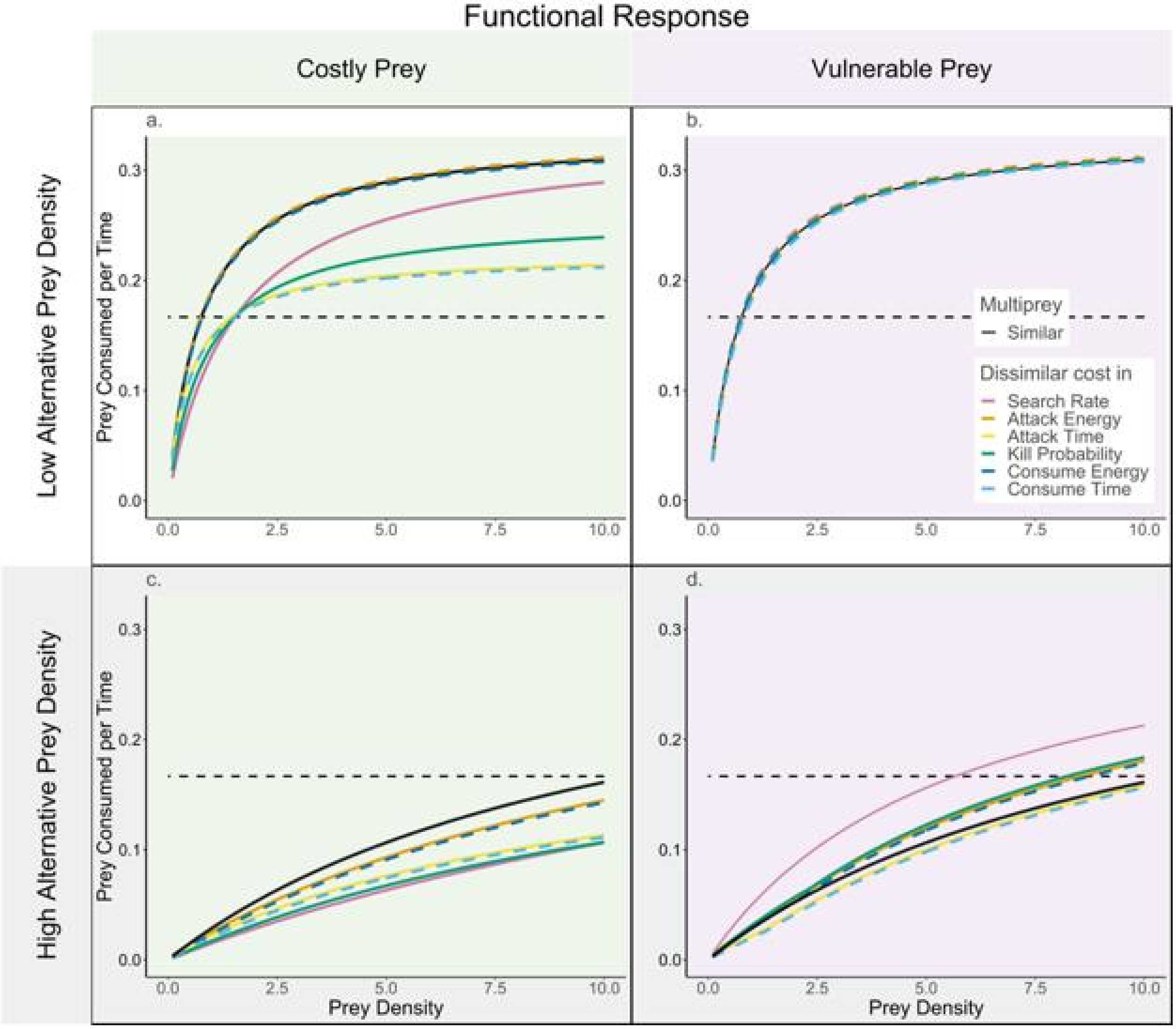

Figure 4.2. The functional response for a single predator in a two-prey system. The black functional response curve in all plots represents the 'Similar Prey' scenario where prey are identical in their foraging costs (baseline values defined in Scenarios section). The coloured lines present 'Dissimilar Prey' scenarios where one prey is vulnerable and the costly prey has elevated foraging costs influencing the search rate, kill probability, time, or energy to attack or consume prey. Functional responses for the predator in relation to the density of costly prey is displayed in light green (left column, a & c) and vulnerable prey in light purple (right column, b & d) when

the alternative prey is at a low (top row with white frame, a & b) or high (bottom row with grey frame, c & d). The grey dashed horizontal line indicates the half maximum consumption rate. Coloured dashed lines indicate there is overlap in the patterns generated from different scenarios.

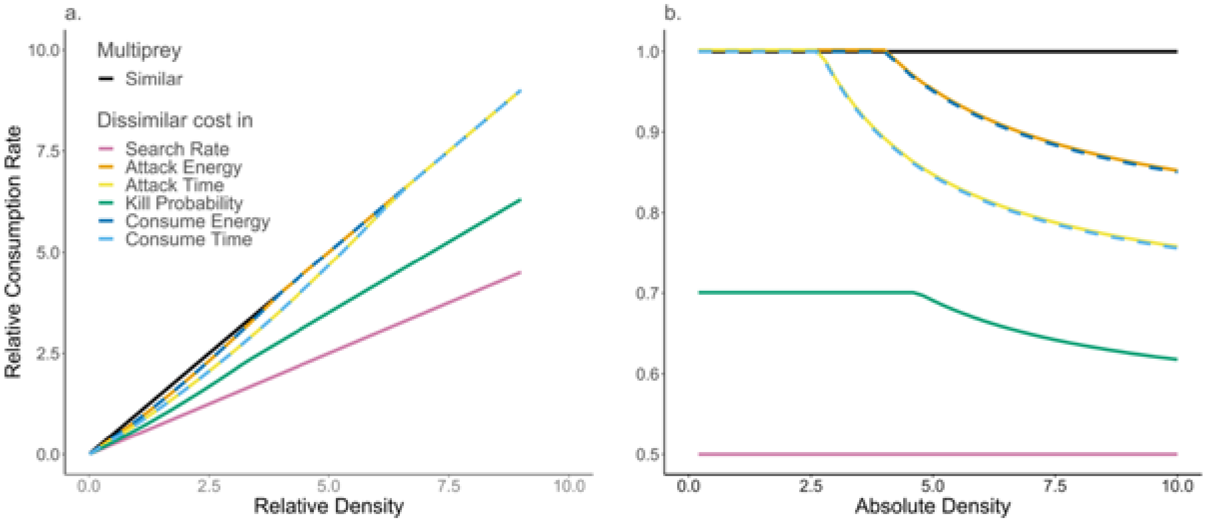

Figure 4.3. Relative consumption rates vary with foraging costs, relative density, and absolute density. Relative measures are determined by the ratio of costly prey to vulnerable prey. The black line with a slope of 1 indicates the predator has no preference and prey are consumed in proportion to their availability (black line is the 'Similar Prey' scenario where prey do not differ and have baseline cost values). The relationships are displayed for 'Dissimilar Prey' scenarios where costly prey increase time or energy costs to the predator at one of the three phases of predation (search, attack, consume). (a) Switching plot *sensu* Murdoch (1969): the response to changes in relative prey density of relative consumption rates (relative measure is the ratio of costly to vulnerable). Relative consumption below the black line indicates a preference for the vulnerable prey. In this example, prey densities are held constant at $N = 10$. (b) The relative consumption rate of costly prey consumed per vulnerable prey is reduced as the absolute density in the system increases. The relative density of costly: vulnerable is held constant (costly prey density is equivalent to vulnerable). Coloured lines with dashes indicate there is overlap in the patterns generated from different scenarios.

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CHAPTER 5:EMPIRICAL EVIDENCE OF PREY SWITCHING IN AN APEX PREDATOR

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5.1 ABSTRACT

For at least 40 years, wolves (Canis lupus) have subsisted predominantly on elk (Cervus elaphus) in Riding Mountain National Park. Then wolves switched to a more dangerous alternative, moose (Alces alces). Generalist predators are ubiquitous but testing mechanisms of population-level prey switching in large vertebrates is rare. While the population density of prey appears to be the simplest factor to explain the composition of predator diets, recent theory has shown that antipredator traits can override density in some cases. We populated a quantitative model with empirical estimates of predator success rates and handling times for moose and elk. We integrated data from long term monitoring at Riding Mountain National Park that tracked changes in wolf diets and prey abundance to test two main predictions. First, predators prefer more vulnerable prey, consuming them disproportionately more than expected by their density (P1: Qualities over quantities). Second, predators exhibit a stronger preference when total prey abundance is high but are less discerning when total prey abundance is low (P2: Necessity rejects no prey). We present a rare example of a population-level switch in diet from elk to moose. However, despite moose being most abundant and most consumed, wolves still maintain their preference for elk over moose. Patterns at both the population and pack scale support our predictions (P1) that predators prefer more vulnerable prey, and (P2) wolves' preference for elk declined as the total prey biomass available declined. We illustrate feasible applications of an optimal foraging model that dissolves species boundaries and places animals on a quantifiable energetic continuum. This work provides insight into factors, such as prey vulnerability and availability, influencing predation behaviour of a free-ranging social carnivore.

5.2 INTRODUCTION

For minimally 40 years, wolves have preferentially consumed elk in Riding Mountain National Park – an intensively monitored predator-multi-prey system (Carbyn 1980, Mech and Boitani 2003). Through prey populations have fluctuated – for example due to disease outbreaks and landscape changes – the diet of wolves has been dominated by elk. Then in 2016 for the first time in the park's history, intensive tracking revealed that moose had become the predominant species consumed by wolves (Figure 1). The observation marked a tipping point in an ecologically important protected system, which sparked curiosity regarding the underlying mechanism behind the switch from elk to moose. The natural history observation is a catalyst for interrogating ideas about prey switching, such that its example transcends systems and can be applied to any generalist predator consuming multiple prey. Namely, quantifying the both vulnerability and availability of prey to accurately model the predator-prey relationships.

In nature, almost all consumers use more than one type of resource. In its broadest sense, an organisms' dietary diversity is essential for survival because not all resources are available in a single prey item. Prey vary in their nutritional content, minerals, proteins, sugars, water, and other key components that provide energy and material for life to persist (Leroux et al. 2020). Dietary diversity brings these resources together into the body of a consumer at the concentrations needed for survival. Dietary diversity can become more nuanced, but no less important, when considering the impact of consuming 'similar' resource types – consider the bison's choice for the stalk or the leaf of grass, or leopard's choice for the old or the young antelope. These choices affect the energetic trade-offs consumers make as well as the impact of resource consumption on the prey, competitors, and predators in the food web (Ford and Goheen 2015). Consequently, our understanding of consumer-resource interactions – the central relationship of ecology – is the emergent outcome of the mechanism affecting a consumers' diet selection, consumption rate, and switching. Prey switching occurs when a predator displays a change in its diet. This change may include temporal or spatial shifts in prey selection, either species, age, sex or condition. Preference is defined as the disproportionate consumption of prey in relation to their relative densities with the other prey type (Murdoch 1969, Oaten and Murdoch 1975). In systems with prey switching, there is a non-linear relationship between relative kill rates and relative densities. The simplest explanation for predator diet is that of prey abundance, but a prey's anti-predator traits is as important as their densities. While diet diversity in consumers is exceedingly common in nature, the chance to test hypotheses with observations of population-level prey switching in large, free-ranging carnivores is rare.

Especially in systems where predators are smaller than their preferred prey, the risk of injury and low success rates for the predator increases the pressure to seek more vulnerable prey over a more common but less vulnerable prey (Mukherjee and Heithaus 2013, Tallian et al. 2017b). Antipredator traits are physical or behavioural defences that reduce prey vulnerability to mortality from predation and can decouple kill rates from prey abundance. These concepts can be further generalized through the concept of predator foraging costs (Berger-Tal et al. 2009). A prey's realized or functional availability to a predator may be less than its abundance for well defended prey (Prokopenko et al. Accepted). Likewise, a prey's realized or functional availability to a predator may be greater than its abundance if it is a highly vulnerable prey. There can be a further context dependency to these dynamics where the relative differences between prey and the composition of prey available to a predator influences consumption rates (Prokopenko et al. Accepted). For example, poorly defended prey living near other poorly defended prey species may be equally vulnerable to predation, but poorly defended prey living near well defended prey could be highly vulnerable to predation.

Wolves consume diverse prey across their range and often exhibit preference for certain species or demographic classes. We use long term data collected in Riding Mountain National Park supplemented with literature of predation parameter estimates to test if prey abundance and vulnerability describes wolf diets over a 40-year period. In Riding Mountain, moose are the riskiest most well defended prey due to their differences in flight responses and size (Paquet 1992, Wikenros et al. 2009) Our main predictions arise from the optimal functional response model that can account for prey vulnerability and antipredator traits through quantifying foraging costs (Prokopenko et al. Accepted). First, predators prefer more vulnerable prey, consuming prey disproportionately more than expected by their density (P1: Qualities over quantities). Following this, wolves will prefer elk, the more vulnerable prey, over moose, the riskier prey. Second, predators exhibit a stronger preference when total prey abundance is high but are less discerning when total prey abundance is low (P2: Necessity rejects no prey). Thus, we expect wolves to exhibit stronger preference for elk when both prey are more abundant.

5.3 STUDY AREA

Riding Mountain National Park is a 3,000 km^2 federally protected area southwestern Manitoba (50°51′50″N 100°02′10″W) that is conspicuous because of the surrounding agriculture-dominated landscape. The maximum elevation is around ~750 m, with average elevation in the core study area being 550 to 650 m, in contrast to the surrounding prairie which is 300 to 550 m. The climate is defined by warm summers (July average temp) and cold winters (January temp). Snowfall can begin as early as October and snowmelt is often only complete by May. Wolves (*Canis lupus*) are the apex predators in this system. In addition to an abundant black bear (*Ursus americanus*) population, other predators include coyote (*Canis latrans*), and lynx (*Lynx canadensis*). Wolves were present in the area until they were locally extirpated around 1900, directly from human caused mortality and indirectly from landscape change and returned in 1930 (Carbyn 1980). Wolf monitoring has occurred within the park since that time, with consistent survey data by pack range being recorded since 1983. Wolves are consistently within 60 to 80 individuals, reaching an exceptional peak of 113 animals in 2012. During the present study the wolf population was approximately 71 individuals.

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*). Population abundance of ungulates in Riding Mountain has been recorded since 1914, following standardized procedures since 1976 (Figure 1). Elk and moose fluctuated from 2000-4000 individuals each for 20 years, with elk typically more abundant than moose. Elk and moose existed at similar abundances of ~4500 individuals for a decade. A significant population decline began in the late 1990's for both species but was more dramatic for elk (Figure 1). As the populations levelled off in 2000, moose became the most abundant ungulate in the park. White-tailed deer have been present in the area with elk, and moose. However, estimating their abundance is difficult do to sightability issues but have been recorded consistently since 2000. The aerial survey estimates over the past 5 years indicate white-tailed deer are fluctuating but increasing in abundance (Figure S1).

5.4 METHODS

We compiled data spanning long-term monitoring from ungulate population surveys, wolf packs, population surveys, and scat or kill studies on wolf diet to determine diet preference in wolves across years and seasons or packs within years (2016-2017).

5.4.1 PREY POPULATIONS

Prey abundance was estimated from geographically referenced visual observations recorded during annual ungulate survey conducted by Parks Canada over a two- or three-day period in January or February when animal sightability is maximized (Vander Wal et al. 2011).We determined annual prey density for all study years, and calculated pack territory prey density for the current study period using annual survey data. The total prey biomass (kg) available, and the biomass density (kg per km^2) was calculated in Riding Mountain and for each pack territory in the current study.

5.4.2 WOLF POPULATION

Annual counts were synthesized from wolf sightings and track counts, sometimes supplemented with aerial surveys. We determined the average population and pack size for each period scat or kills were sampled. We calculated total wolf abundance, population density, pack size, and wolf density in each pack given their territory size (Table S1).

5.4.3 KILL SITE DATA

The studies on wolf diet composition spanned 42 years (14 years of sampling coverage). Early wolf diet studies located kills from ground and aerial observations resulting in 37 kills in Lake Audy and Baldy Lake 1978-1979 and 194 wolf kills in Whitewater Lake from 1982-1986.

2016-2017 GPS Collars

Wolves were collared in Riding Mountain in 2016 (13 individuals in 4 packs) and 2017 (14 individuals in 5 packs). Animals were captured by Bighorn Inc., contracted through Parks Canada, using net gun immobilization via helicopter (Memorial University AUP 16-02-EV). All collars were Iridium-based from the following companies: ATS (1), Lotek (4), Televilt (14), Telonics (6), Sirtrack (2). In 2016, collars took relocations every 2 hours, 8 collars sampled locations on odd hours while 5 collars sampled locations on even hours. The odd and even schedules were distributed between packs with at least one collar following each schedule in a pack.

2016-2017 Cluster Investigations

Continuous and extensive fieldwork investigations determined the timing and location of wolf behaviours, including wolf killed prey. Important areas of wolf activity were indicated by an increased density of GPS locations, i.e., 'clusters'. Clusters were identified in Python from an version of the code presented in Knopff et al. (2009) created by Warren (2008) adapted for wolves (Webb et al. 2008, DeCesare 2012, Irvine et al. 2022). In our study, the inclusion rules were set to a radius of 300m and a time of 96 hours, meaning that if a new location was within those limits from any of the locations currently in the cluster it was added.

A total of 6323 clusters were created from the locations of individuals over the study period. In the field, clusters were categorized into three classes created based on the total number of points in the clusters. Clusters were investigated by following a systematic stratified method to sample across size classes and pack territories. Clusters were most often accessed via snowmobile, quad, horseback, or on foot. Every 2-3 months a helicopter was used to visit sites not accessible from the ground. The geometric centre of the cluster ('centroid') and associated locations were input into a handled GPS unit to direct investigations for physical evidence. We concentrically searched an area around the centroid based on the radius of the cluster and every GPS location of the cluster was searched within a radius of ~15m. On average, clusters were investigated within a mean of 13.8 days of occurring (median = 9 days).

Once clusters were investigated, unique areas were then termed 'sites'. 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, e.g., tracks, disturbed vegetation, hair, blood. In some instances, clusters with carcasses were determined to be a scavenge based on evidence that the animal died due to another cause or if the collared wolf spent too short of a duration are the site to have been responsible for the death of the animal, e.g., 2 hours at a large ungulate kill. When possible, prey species at the site was determined and samples were collected. In the absence of a carcass other evidence from wolves or other species such as tracks, hair, beds, scat, dens were used to determine the behaviour that occurred at the site. For example, beds under a spruce tree containing wolf hair were indicative of a resting site.

A total of 1260 clusters were investigated, which translated to 598 unique sites. Often multiple clusters occurred at each unique site and multiple wolves visited the same site. Aggregate clusters of wolves were defined from spatial and temporal to determine unique kills. The primary behaviour was 'kill' at 181 unique sites (433 clusters designated as kills), probable kills at 24 sites, and scavenge at 46 sites.

5.4.4 SCAT COLLECTION

Wolf scat was collected in four study periods, 1626 samples 1975 -1979 (Carbyn 1980), 1027 samples in 1982- 1984 (Carbyn 1983), 369 samples from 2001-2003 (Sallows 2007), and 296 from 2016 -2018. Samples were collected in three to four seasons allowing for a year-round diet comparison, however there are some slight differences in seasonal designation of months (Supplementary data). Data on prey frequency and biomass was extracted from the publications of previous work and used for subsequent calculation. During the most recent study, we collected scat samples during cluster investigations at sites and opportunistically during the approach.

Diet Composition Measures

We calculated various measures of wolf diet composition by the observations of prey items sampled at an investigated kill sites or in a scat sample. The count of prey in either kills or scat gives a measure of frequency of occurrence or ‘frequency’. We used frequencies were to calculate proportional consumption and biomass contribution. We calculated proportional consumption as a single prey type occurrence out of the total occurrences. Similarly, we calculated biomass contribution to the diet, but scaled by the average weight of prey (Table S2, from Carbyn 1980). For kills and abundance, the biomass conversion is straightforward. However, there is a disproportionate relationship between prey biomass and the amount of scat produced, i.e., smaller species produce more scat per unit weight. A linear conversion can calculate the kg of prey consumed per scat (y) from the average weight of the prey (x): $y = 0.439 + 0.008x$ (Weaver 1993). We then multiplied values of y by the frequency of occurrence, which was then divided by the total biomass consumed to calculate proportion of biomass contributed by each prey to the wolf diet. The same diet index and calculation was used across research periods.

Prey Switching

For the specific instance of a predator consuming two prey (elk: moose), we define preference by comparing the relative consumption of prey to the relative densities of prey available (*sensu* Murdoch 1969). If a predator has no preference, the relationship will have a slope of 1. Values above the line indicate a preference for the prey in the numerator, while below the line will be preference for the prey in the denominator.

First, the preference coefficient, *c*, was decomposed into attack preference, vulnerability, and nourishment (*z, v, m*) in Garrott et al. (2007). The ‘relative nourishment’ calculated as the ratio of handling times, $\frac{t_{h,i}}{t_{h,j}}$. Where handling times are defined as the total time to consume prey.

The vulnerability of prey, *v*, is the component that the optimal prey switching model incorporates through predator foraging costs (Prokopenko et al. Accepted) The time, *t*, expended on prey once encountered is composed of both chase and handling times. Even in situations where the time expended is on consuming the prey, certain prey antipredator traits unrelated to nourishment will increase the time to ingest the prey (e.g., armour, spines, shells). Thus, nourishment, m, in our model can be more specifically described as $\frac{e_{n,i}}{e_{n,j}}$, the ratio of energy content of prey i to prey j, but does not enter the preference description explicitly. Instead, it is included in p_e. The *b* coefficient in contemporary prey switching models (added by Greenwood and Elton 1979) was not explicitly included. However, accelerating or decelerating relative preference with relative density occurs as expected despite this omission. When the *b=1* the slope of the relationship between relative consumption rates and relative density is constant, otherwise non-linear dynamics occur. The density dependence of p_e means it is a dynamic preference relationship, thereby, demonstrating non-linearity with relative density. Here, we present relative consumption rate $\frac{f(N_i)}{f(N_j)}$ described by relative density using the Murdoch equation, the Garrott et al. equation and the Prokopenko et al. equation, respectively.

$$\frac{f(N_i)}{f(N_j)} = \left(c\frac{N_i}{N_j}\right)^b = \left[(z * v * m)\frac{N_i}{N_j}\right]^b = \frac{p_{e,i} \cdot p_{k,i} \cdot N_i}{p_{e,j} \cdot p_{k,j} \cdot N_j}$$

There is diversity in the antipredator traits of ungulates available to wolves in Riding Mountain, but only some direct data that can inform parameter estimates (Carbyn 1980, Paquet 1992). We predicted a prey switch between elk and moose with estimates of success rates and handling times reported in the literature (Table S3). The ratios of elk to moose were calculated in units of prey and in kilograms. We correlated the residual variation in the predictions and observations from relative density to determine the explanatory ability of including prey vulnerability in prey switching equations.

5.5 RESULTS

The study identified the predominant prey for wolves in Riding Mountain were moose (Figure 1). Both kill site and scat data indicated moose contributed over half of the biomass in wolf diets (kill site = 0.65, scat = 0.55). Elk contributed less than half of the biomass (kill site = 0.21, scat = 0.34).

Kill site data estimated a higher proportion of the diet was moose and white-tailed deer (Figure S5) and scat estimated a higher proportion of elk, beaver, and hare in the diet (Figure S5).

Our findings differed from previous studies where elk was the dominant prey consumed (Figure 1). In the study conducted in 2000 to 2003, elk contributed 68% and moose contributed 20% of the prey biomass (Sallows 2007). Within scat samples across the last ~13 years, elk consumed by wolves decreased by 34% and moose consumed by wolves increased by 35%. The three other prey (white-tailed deer, beaver, and hare) remained consistent over the 40 years of wolf studies, each contributing under 10% of the biomass across studies. In the most recent study, packs varied in the prey available in their territories and the prey they consumed (Figure 2). Consuming moose biomass contributed 47 - 80% of kills and 26 - 71% of scat, consuming elk ranged from 19 - 35% of kills and 22 - 59% of scat, for white tailed deer 0 - 26% of kills and 0 - 15% of scat (Figure 2).

Together elk and moose made up over 85% of biomass consumed by wolves. Focusing on these two prey species, the relative of consumption rates and relative density (calculated as elk: moose) are nonlinearly related (Figure 1, Figure 2). The preference for elk has declined over the years as total prey available and the ratio of elk to moose has declined (Figure 1).

The biomass of elk and moose peaked at 813 kg/km^2 in 1978 now is 270 kg/km^2. Although the scale of the relationship of relative consumption and relative density is reduced for packs in 2016 and 2017, most packs preferred elk over moose (Figure 2). The range of total biomass of ungulates in territories is 262 to 1186 kg/km^2 (Figure 2).

Inclusion of prey vulnerability into the prey switching description described more variation than predictions from density alone; the correlation between the residual variation in the observations and the residual variation in predictions was moderate and positive ($R^2 = 0.71$). While the inclusion of prey vulnerability improved our predictions of the observed behaviour, other unaccounted factors could be driving elk preference as our predictions underestimated the preference for elk, except for the most recent study where the preference for is overestimated (Figure S12).

5.6 DISCUSSION

We present a rare example of a population-level switch in diet from elk to moose established across 40 years of research. Moose now make up the greatest proportion of prey consumed by wolves, estimated through kill site investigations and scat analysis. However, despite moose being most abundant and most consumed, wolves still maintain their preference for elk over moose. Elk are consumed disproportionately more than they are available in the environment. Pack-specific differences indicate wolves are consuming moose and preferring elk across a range of local densities. Patterns at both the population and pack scale support our predictions (P1) that predators prefer more vulnerable prey, and (P2) that predator preference increases with total energy, measured in biomass, available in the system. Our work provides insight into factors, such as prey vulnerability and availability, influencing predation behaviour of a free-ranging social carnivore.

Wolves preferred prey that are more vulnerable, elk, over the riskier prey, moose, which supports Prediction 1: *Qualities over quantities*. As expected in prey switching, wolf consumption rates of prey were disproportionate to the density of prey available. Foraging costs shape prey selection by predators and these costs can come from prey themselves, for example injury (Berger-Tal et al. 2009, Mukherjee and Heithaus 2013). Here we view the concept of foraging costs to parallel the concept of prey vulnerability to predation. Vulnerability in this study was assessed between elk and moose through species-level measures of success rates and handling times. However, predators also select for differences in vulnerability between individuals of the same species in a population due to body size, age or condition (Huggard 1993a, Pierce et al. 2000, Hoy et al. 2022). Riding Mountain wolves demonstrated the expected seasonal diet change to include more vulnerable prey when available; e.g. calves and beavers (Figure S8 and S9; Metz et al. 2012, Gable et al. 2018). Predators exploit opportunities by adjusting to changes in prey vulnerability and our descriptions of predation should include this mechanism.

We demonstrate that incorporating just a few foraging costs of prey types to quantify vulnerability (Table S3) can improve predictions of prey consumption over the predictions generated from density alone. Quantifying vulnerability has improved density-dependent descriptions of prey switching in other systems with free-ranging carnivores consuming multiple prey (Garrott et al. 2007). In Yellowstone National Park, wolves maintained a preference for elk, despite increasing bison populations (Tallian et al. 2017b). The findings from both Riding Mountain and Yellowstone support that prey vulnerability drives preference. However, unlike in Yellowstone where preference did not change significantly with changes in prey availability, we found that preference for vulnerable prey declined with relative prey density and the preference for the more dangerous prey increased. Thus, the results from Riding Mountain support the switching hypothesis.

Wolves' preference for elk declined as the total prey biomass available declined, supporting Prediction 2: *Necessity rejects no prey*. The preference for elk was maximized when the total prey biomass was 813 kg per km^2 in the late 1970s. The biomass available in RMNP has consistently declined since the late 90s to 226 kg per km^2 on average during the current study period. The minimum energy requirement of wolves in the wild is estimated to be 3.25 kg per wolf per day to survive and reproduce (Mech and Boitani 2003). The wolves in Riding Mountain National Park (~70 individuals) would need to consume 83,000 kg of prey (28 kg per km^2) annually. Therefore, despite the decline in prey the wolves in RMNP are not energy limited as evaluated by total prey biomass available and metabolic rates. The decline of elk abundance co-occurred with the decline of all prey in the park, but the wolf population has maintained a consistent population size around 70 individuals. A declining population may have individuals in worse condition, with more vulnerable individuals available to predators (Johnson et al. 2017). Alternatively, hungry predators are more likely to take risks in search of food (Blecha et al. 2018, Moran et al. 2021), which may be more common in low resource environments. Further investigation into multiprey systems with variation in relative and total prey availability are required to provide a robust test of this prediction to disentangle the effects of changes in relative abundance and total abundance.

Here we focus on the two dominant prey in a decidedly multi-prey system. Following previous studies, white-tailed deer and beaver were identified as prey in both kills and scat during this study. Both white-tailed deer and beaver are more vulnerable than moose or elk, and thus are likely preferred when available. In support of this, the third ungulate prey, white-tailed deer, contributed 5-10% of diet but were only 1% of the biomass available in the environment. There was pack variation in the consumption of white-tailed deer. For example, white-tailed deer were consumed most by the Lake Audy pack. In this pack the abundance of white-tailed deer and the total available prey was highest. Thus, the general patterns observed for white-tailed deer support the two guiding predictions of this study: (1) where predators will focus on vulnerable prey, (2) especially when they are in a productive area with abundant prey and high biomass availability.

White-tailed deer are emergent prey in many systems. Following moose decline in Minnesota, wolves targeted vulnerable white-tailed deer populations (Barber-Meyer and Mech 2017). Increasing white-tailed deer populations have replaced moose as the primary prey and which generated a numerical response in wolves in northeastern Alberta (Latham et al. 2011). In the northeastern Alberta wolf-multiprey system, there is also seasonal diet shift from white-tailed deer in the winter to beaver in summer (Latham et al. 2013). In Riding Mountain, beaver have contributed ~5% of the diet since the 1970's. When they are seasonally available, small prey provide necessary energy to support predator populations during costly times. Beaver are a substantial food source for wolf pups (Mysłajek et al. 2019) and hare abundance was positively related with wolf birth rate (Borg and Schirokauer 2022). The role of alternative prey in subsidizing predators should not be discounted, despite our focus on switching between primary prey and secondary prey.

Diet composition is estimated using events such as kill sites, scat analysis or gut contents. The series of wolf studies in RMNP have used either kill site investigation or scat analysis. Kill site investigation and scat collection often overlapped in duration, and in the current study we simultaneously collected kills and scat for the same sample population year-round. Our findings are in agreement with a comparative cougar study, that found kills largely agreed with scat data, with a bias for larger prey (Bacon et al. 2011). Both methods were able to identify seasonal variation in diet, with a greater diversity of prey being available from spring to fall. There was a greater preference for moose over elk when estimated through kills sites. In contrast, the contents in scat are represent a more comprehensive diet composition as they include any consumed items, not just prey that were killed. Scavenging behaviours were observed during fieldwork but did not seem to be skewed towards elk compared to the kill estimates (Prokopenko, pers. obs.). However, scavenging can over occur shorter durations of time and our samples derived from in wolf locations and subsequent field investigations may not be representative of these events. Scavenging can provide a subsidy to predator diet (Huggard 1993b, Tallian et al. 2017a). In Yellowstone, wolves scavenged bison more as the population increased, essentially switching feeding behaviour, i.e. hunting to scavenging, instead of just prey species, i.e. elk to bison (Tallian et al. 2017b). Using multiple diet composition techniques can provide insight into diet preferences and behaviour of predators, though the processes generating pattern differences should be further investigated.

After at least decades of elk dominance in the diet of wolves in Riding Mountain, moose have become the dominant prey item. Despite the switching from elk to moose, elk are still consumed at a rate that exceed expectations based on the availability of this prey alone. Wolves follow our expectations of an optimal predator by preferring vulnerable prey, with that preference being sensitive to the relative and total prey availability. Our work shows the value of applying an optimal foraging prism that includes prey vulnerability when describing empirical instances of prey switching. As more evidence emerges, we can gain confidence in predicting predation with changes in communities and landscapes. Prey switching has direct implications for rare species in systems with multiple prey (Jaworski et al. 2013) through apparent competition and incidental predation (Latham et al. 2011, Serrouya et al. 2015). Alternatively, prey switching is suggested to be a predation rate refuge for vulnerable prey at low density (Matter and Mannan 2005) or can stabilize predator-prey systems (Fryxell and Lundberg 1994). Optimal predators are opportunistic and resilient, adapting to variation in environment, for example at the local scale, which then generates population-level patterns at broader temporal scales. It is paramount to identify the dynamics resulting from perturbations to determine how the ecological community will adapt to prey switches of apex predators

5.7 ACKNOWLEDGMENTS

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5.8 AUTHOR’S CONTRIBUTIONS

CMP conceived the original idea for the manuscript. Data was collected and provided by CMP and SZS. CMP conducted the analysis and wrote the manuscript with input and approval from all coauthors.

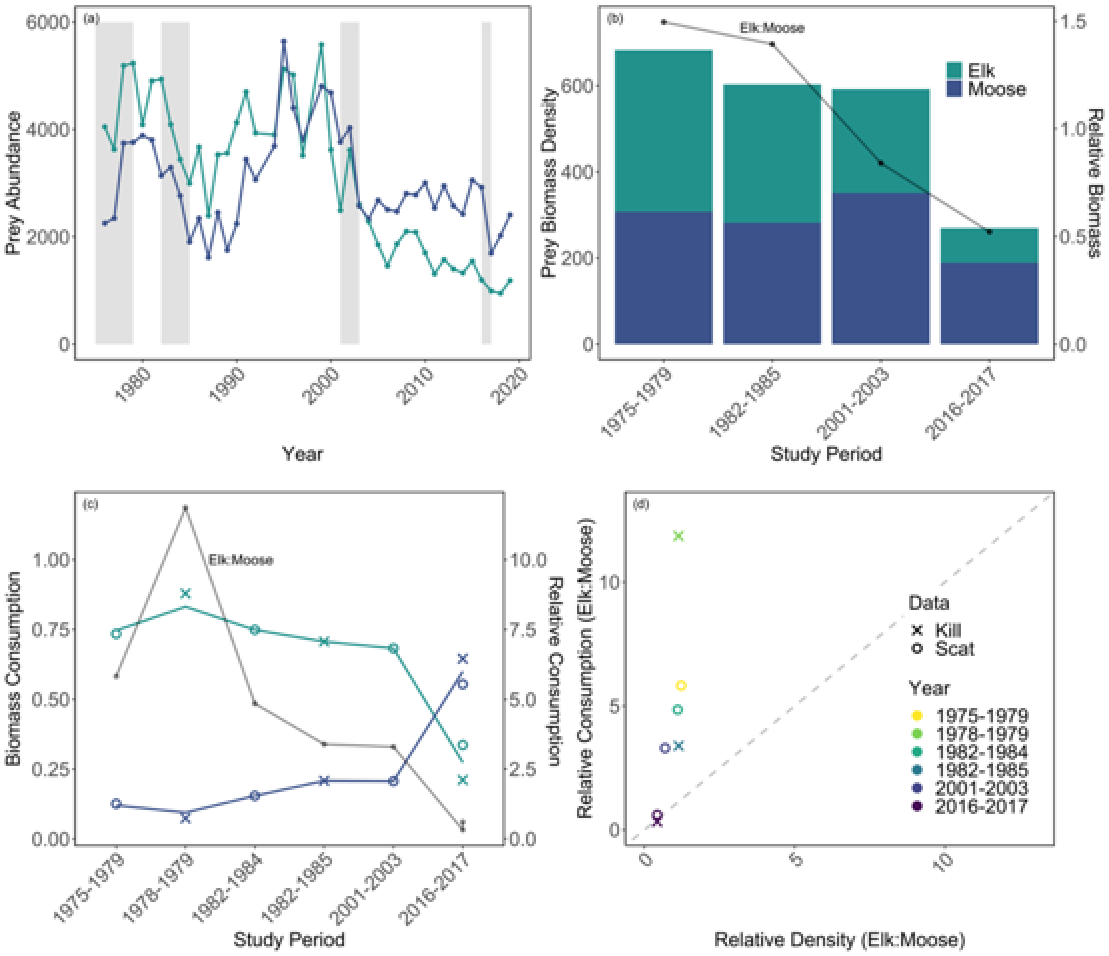

Figure 5.1. (a) Prey abundance and (b) Biomass density (kg/km^2) and (c) biomass consumed by wolves in Riding Mountain National Park for the two dominant prey elk and moose over the last 50 years. Grey vertical bars in panel A indicate wolf diet study sampling periods from 1975 to 2016 and panel B presents the biomass of elk and moose available during those research periods. The black line indicates the ratio of elk to moose for (b) biomass in the park, and (c) biomass consumed by wolves. (d) The relative biomass consumed is plotted against the relative biomass in the environment. The dashed line is a 1:1 relationship between relative consumption rates and relative density, in this instance wolves are consuming prey in proportion to their availability and

have no preference. The top left corner of the plot indicates a preference for elk, while the bottom right corner indicates a preference for moose.

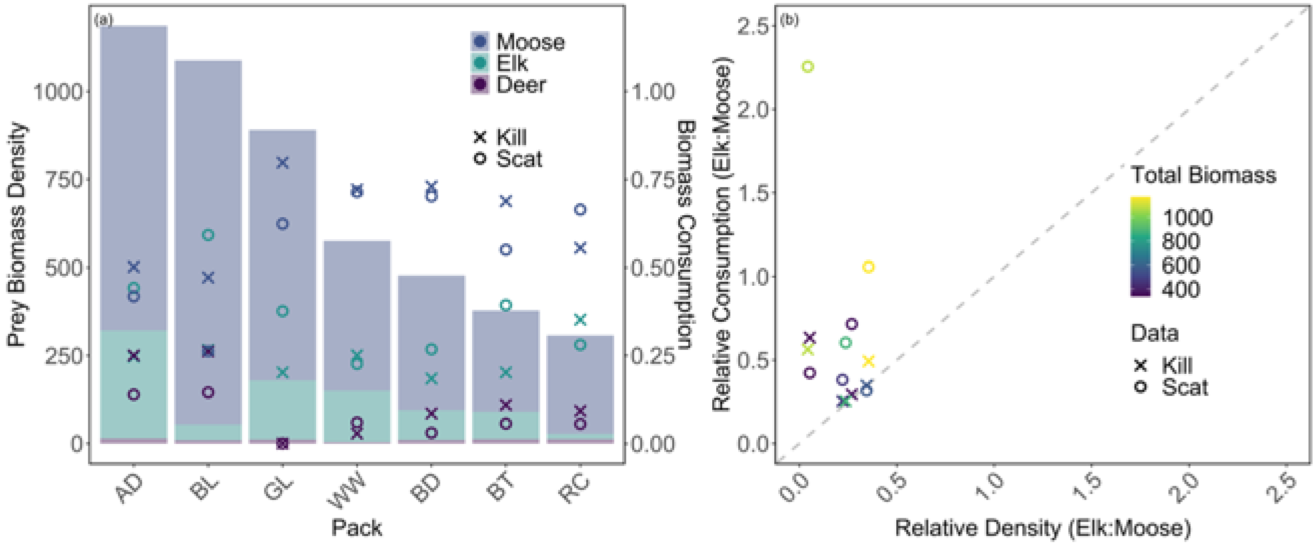

Figure 5.2. (a) The proportion of biomass consumed for packs with the density of prey biomass (kg/km^2) within territories for the 2016 study and (b) the relative biomass consumed against the relative biomass in the environment. The dashed line is a 1:1 relationship between relative consumption rates and relative density, in this instance wolves are consuming prey in proportion to their availability and have no preference. The top left corner of the plot indicates a preference for elk, while the bottom right corner indicates a preference for moose.

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CHAPTER 6: EPILOGUE

Prey switching was apparent in each of the empirical chapters of my thesis and these observations provide support for viewing predator behaviour through an optimal foraging perspective. Switching between elk and moose was observed in predator behaviours across spatial and temporal scales (diel to annual, step to study area), across the hierarchy of organization (individuals, packs, and populations). The ‘ghost of predation past’ is discussed in terms of prey behaviour (Peckarsky and Penton 1988, Des Roches et al. 2022), but the synthesis of findings in this thesis indicate that there is a legacy in predator behaviour as well. Over time, the largest proportion of wolf diet switched from elk to moose, despite a maintained preference for elk in Chapter 5 which contextualizes the results of Chapter 2 and Chapter 3. In Chapter 2, when wolves were searching and satiated, they selected for areas of elk catchability, but hunger resulted in a switch in avoidance for elk catchability and increased selection for moose catchability. In Chapter 3, diel encounter rates for moose increased with light and speed in the winter. Then in summer there was a switch where light and speed described elk kills. The influence of predator foraging costs can describe predator functional responses in multiprey systems (Chapter 4). Throughout my thesis there is evidence that wolves are seeking to maximize energetic gains and reduce potential costs, and that these trade-offs are mediated by prey antipredator traits and predator satiation. My observation of population-level prey switching is novel, but a generalist predator with multiple prey is ubiquitous. The insight into predation processes is broadly applicable and demonstrates the value of long-term research programs to conservation initiatives.

6.1 PREDATORS SEEK SUCCESS

My thesis adds to existing evidence that the vulnerability of prey is an important element in predation. In this study, wolves strongly preferred prey that were easier to kill and posed a lower risk of injury. Here I estimated vulnerability from the literature on wolf-prey interactions and assumed due to body size, fight or flight behaviour, and success rates that elk would be easier to kill than moose.

During this study, a few wolves were found during site investigation that died due to blunt force injuries. Injuries are frequent in predators, estimated to be around ~10% in gray wolves (Berger-Tal et al. 2009). Attacking prey that are more vulnerable can reduce foraging costs associated with injury while increasing probability of capture success. The vulnerability of prey changes over time and predators respond accordingly. In spring, neonates are very vulnerable to predation (Wolf et al. 2021). While in the winter, wolves select for poor condition adults (Woodruff and Jimenez 2019). Therefore, complete descriptions of prey vulnerability to predation will require additional details such as age and condition of prey. The potential to test these ideas in Riding Mountain exists and would be a feasible next step following this study.

My research explored a spatial realization of prey vulnerability through landscape catchability. Catchability relates to how predators select areas that promote encounter and capture of prey (Hopcraft et al. 2005, Balme et al. 2007, Zabihi-Seissan et al. Accepted). In the paucity of preferred vulnerable prey, elk, wolves use the landscape to increase capture success of the more dangerous prey, moose. I defined catchability using elevation, landcover classes, edges to forest and water. However, I did not include snow depth as covariate, but it has been found to influence the ability of wolves to capture prey (Paquet 1991, Huggard 1993). The snow accumulation was ~30cm in 2016 and ~50cm in 2017 (Zabihi-Seissan et al. Accepted). Thus, the variation in weather during this study period and over time could increase capture rates but also movement costs (Droghini and Boutin 2018). To model a wolf space use response to the energetic landscape (Berti et al. 2022, Klappstein et al. 2022) additional covariates that influence costs and gains should be included.

Movement facilitates differential use of space on the landscape and encounters between animals. As predicted by the Ideal Gas Law, encounters increased with speed. This model was aspatial, where movement was measured as speed averages across the diel cycle. However, the ideal gas law assumes a uniform environment and unbiased movement (Hutchinson and Waser 2007). Alternatively, selection is based on the biased space use of animals (Fieberg et al. 2021) where they change their use and movement in response to habitat variation. Though these findings seem to be in opposition, they are complementary in their measure of movement at different spatiotemporal scales. At a course average, wolves are moving faster during the twilight period (300 m/hr faster than mid-day), while across days wolves slow their movement rate (~10 m/hr decrease each day). Movement rates between individuals varied by 300m per hour, but wolf movement rates (200-600m/hr) are much faster than their prey (~100m/hr) (Theuerkauf et al. 2003, Eggermann et al. 2009, Vander Vennen et al. 2016). Thus, at this scale prey are unlikely to outrun predators. However, prey mediate their encounter risk in other ways. For example, elk spend more time in high-risk foraging areas when wolf activity is lower (Kohl et al. 2018). Future work should investigate the prey perspective in these interactions, specifically with the insight of wolves switching between prey species.

Prey switching is suggested to be a predation rate refuge for vulnerable prey at low density (Holling 1959, Berryman et al. 2006). However, observations of this refuge effect is rare (Oaten and Murdoch 1975). At the extremes, vulnerable prey may not be rescued at low densities by switching while invulnerable prey can co-exist with predators and no alternative prey (Matter and Mannan 2005). In this system, despite a declining elk population, the wolf population is supported by alternative prey and numbers have remained consistent over the last decade. Moose are now the primary prey, but white-tailed deer may be increasing in importance in wolf diet. The number of white-tailed deer kills was of similar frequency to elk at the population level. However, the biomass contribution was low for the population and was the dominant prey for only one pack. It is a useful simplification to focus on a single predator and two prey when studying prey switching but the role of additional prey should be investigated. The influence of white-tailed deer should not by fully discounted as they are an alternative and subsidizing prey for wolves in other systems. For example, white-tailed deer are a key alternative prey participating in declining caribou populations (Latham et al. 2013). In addition, non-ungulate prey are important contributions to predator populations which could decouple density-dependence between wolves and ungulates (Borg and Schirokauer 2022). System level switching demarks a '*tipping point*' for ecological change - the implications of which will be realized over generations.

6.2 ECOLOGISTS SEEK STABILITY

In my thesis I focus on encounters, consumption rates, and the functional response of predators to prey density to study prey switching behaviour. The consumptive interactions between a predator and their prey are important but may not govern some systems. For example, Alaskan wolf kill rates of moose did not differ in between high moose and low moose densities, instead there is an equilibrium dynamic between predation and recruitment where wolves are responding numerically to moose (Lake et al. 2013). Predator numerical response is the change in predator density with prey density (Solomon 1949). The total predation rate, i.e. the functional response and numerical response combined, can be density-dependent (regulating – Messier

1994), density-independent (limiting – Gasaway et al. 1983), or inversely-density dependent (depensatory – Serrouya et al. 2015a). There are direct management applications of this ecological theory as it can be used to predict stability and future viability of populations. Indeed, prey individuals removed by predators is a critical measure of predation effects and subsequent management interventions (Alston et al. 2019). Different management actions might have a counterintuitive influence on a vulnerable secondary prey that can be understood through functional and numerical response theory. For example, wolf removal could increase moose populations, the primary prey, and put further pressure on the secondary prey, caribou, while reduction in moose can relieve predation on caribou (Serrouya et al. 2015b). Determining the total response of wolves to prey is a reasonable extension for describing and predicting the effects of predators on prey in Riding Mountain. It should be determined if prey switching is creating a refuge for elk recovery.

Trophic frameworks, as originally outlined by Lotka and Volterra, can be used to identify why populations fluctuate and to evaluate ecosystem stability. Ideally, management decisions can be informed by equilibrium points. Prey switching can lead to negative density-dependent survival of the more vulnerable prey, hence greater stability (Fryxell and Lundberg 1994). Therefore, the findings from this work can be incorporated through prey mortality rates and predator reproductive rates to address questions of stability. These trophic models can help to identify the relative effect of predation on prey compared to other factors, *i.e.* top-down versus bottom-up effects (Peterson et al. 2014). Further, top-down and bottom-up effects interact. For example, there is a trade-off between body condition and antipredator responses (*i.e.* predation-starvation hypothesis). Moose became less responsive to wolves into the winter, with no changes to movement behaviour following wolf encounters in late winter (Oates et al. 2019). The direct and indirect effects of predators and prey are fully contextualized in trophic frameworks

Predator and prey shift over evolutionary time scales as a result of ecological interactions. A dynamical approach could incorporate prey antipredator traits and how selection for these antipredator traits is influenced by the presence of alternative prey (Abrams 2000, Schmitz 2017) particularly in cases of prey switching. There is a trade-off associated with antipredator traits, where the reduction in predation rates must exceed the reduction in growth rate of the prey who express them (Peacor et al. 2013). Further, there is a feedback between predator and prey trait variation (McGhee et al. 2013). A predator switching between prey is an important detail to explore in terms of ecological stability and evolutionary change in predator-prey interactions which should continue to be explored.

While stability is difficult to harness, we can promote resilience by conserving social structures and behavioural variation in predator populations confronting increasing pressures. Social carnivores hunt in groups to counteract risk from large prey and increase their kill rate (Caraco and Wolf 1975, Barber-Meyer et al. 2016). The benefits of sociality may carryover to have positive effects on hunting behaviours that affect prey selection. Indeed, there is growing evidence for cultural transmission of tradition and social learning driving behaviour (Whiten 2021). Foragers can learn diet preferences from conspecifics that last their lifetime (Slagsvold and Wiebe 2011). In our study system, the pack-specific prey preferences may be the result of wolf ‘culture’. Wolves may inherit hunting behaviour from packmates that can be transmitted over generations. For example, the Lake Audy and Baldy Lake packs were tracked in both 1978 then 2016, and 1979 then 2017 respectively. Both packs demonstrated a switch from elk to moose, but Lake Audy continues to consume an exceptional proportion of white-tailed deer compared to other packs. Teasing apart the local environmental conditions, genetic, and social influence within packs would require tracking hunting behaviour and roles of individuals in social units. An experiment on owls suggests that external factors had a greater influence on movement behaviour (Bombieri et al. 2018). The parallelism across chapters support that individual differences in behaviour link to population adaptions (Stuber et al. 2022). There were echoes of inheriting elk preference in space-use behaviour, there was more variation in the response to spatial variation in white-tailed deer catchability, followed by moose, and the most conserved response was for elk. When adult wolves die it can disrupt social structures and removes variation from the population (Borg et al. 2015). The mortality of the wolves in Riding Mountain National Park was high (>68%), caused predominantly by disease and humans, could interrupt these inheritance processes regardless of the mechanism.

Predator selection of vulnerable individuals can regulate disease (Hoy et al. 2022) and disease outbreaks can precipitate trophic cascades (Monk et al. 2022). Due to the outbreak of Bovine Tuberculosis in the Riding Mountain area elk were tested and culled, where older and diseased animals in groups were targeted during these efforts. Future work should investigate the shift in demography, sex ratios, and group sizes that may have occurred during these management interventions. Specifically, if there was a shift in demography of elk compared to moose that would have supported the switch in prey. Recently, the Riding Mountain area has determined that TB is effectively eradicated. There is a potential that in following decades the elk population may resurge and become a predominant prey of wolves once again.

Disease and parasites have been monitored in the wolf population previously and found exposure to Canine Parvovirus and Canine Distemper Virus but only one reported death (Stronen et al. 2011). During the study period of my research, the main cause of wolf mortality (8 deaths, 36% of study animals) was due to Canine Distemper Virus. The space-use behaviour of these diseased individuals was different from other wolves who survived or died of other causes (Turner et al. in review). High mortality rates driven by disease may have accelerated a hunting behaviour change in naïve packs members. Recently, Manitoba has found their first confirmed incidence of Chronic Wasting Disease in a mule deer ~20km from the western edge of the park. Predators can play an important role in removing diseased individuals and supressing disease. Protection for wolves in Riding Mountain would assist in managing disease effects in any trophic levels.

Predation is affected by anthropogenic activity directly and indirectly. Riding Mountain National Park has long been quoted as an 'island of wilderness in a sea of agriculture' (Carbyn 1983, Sallows 2007, Brook 2009). This statement is value-laden, but does highlight a lack of connectivity across southern Manitoba that has prevented dispersal and resulted in genetic differentiation (Stronen et al. 2012). I did not observe successful wolf dispersal in this study, wolves rarely left the park and if they did, they returned to the park or were killed. This agrees with previous research, where no tracked wolves have dispersed to other areas. Human activity on landscapes can create predator shields for prey (Muhly et al. 2011). Alternatively, in Alberta linear features increased speed of all wildlife but are risky to prey and facilitate predators (Dickie et al. 2020). Human activity mediates the top-down effects of carnivores through hunting shared prey (van Beeck Calkoen et al. 2018). Hunters select for prime age and reproductively valuable prey, which contrasts with predators who target vulnerable prey. Further, there are notable differences in timing of human harvest versus the variation in predation pressure that occurs across seasons from predators. The prey selection patterns of humans could result in reproductive suppression from hunter harvest compared to the reproductive compensation that can be supported by predator kills (Wikenros et al. 2016). Wolves experience direct human effects mortality from trapping, poisoning, shooting just outside the park boundary (5 wolves, 20% of study animals). Wolves can be killed outside the park legally by landowners. There were no livestock kills observed in the diet of Riding Mountain National Park wolves during my research either through kills or scat investigations. For many decades wolf diet studies not find evidence of livestock depredation (Meleshenko 1986, Sallows 2007), which supports protection of these behavioural phenotypes. In another system, wolf mortality increased livestock depredation in subsequent years (Wielgus and Peebles 2014). To protect wolves in Algonquin Provincial Park, a buffer area extends past the boundary (Benson et al. 2017). The removal of wolves that take short trips outside of Riding Mountain National Park could disrupt natural predation relationships.

6.3 CONCLUSION: THE STRUGGLE FOR COEXISTENCE

Predators have positive effects on ecosystems and promote coexistence among wildlife (Wallach et al. 2015), but this is put at risk by the challenge of human-carnivore coexistence (Lamb et al. 2020). My thesis documents how wolves have switched prey, which can promote ecosystem stability. It was only because of consistent population monitoring and repeated research studies that I was able to identify this prey switch. Riding Mountain National Park exemplifies the value of long-term research programs. Longterm data allows us to identify environmental and ecological changes occurring over time. In this current period, we are at the cusp of re-evaluating and changing our practices to try to reroute a predicted course of nature and climate. Our management solutions must adapt just as nature adapts to changing circumstances. One piece of this is human-wildlife coexistence, while many current practices and perspectives lack the holistic approach - there is always potential to make the switch.

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SUPPORTING INFORMATION

APPENDIX 1: GLOSSARY

Term	**Definition**
Attack rate	The area where prey are removed by pred per unit time "space clearance rate" (DeLong 2021)
Antipredator trait	A physical or behavioural characteristic of prey that reduces predator consumption efficiency through predator foraging costs
Area-restricted search	A foraging pattern where a predator reduces their movement rate and increases residency time of an area
Prey catchability	Areas that promote capture of prey by predators
Condition	Can have either positive or negative effects on fitness but are not depletable
Consumer	Organisms that eat a resource or prey in whole or in part, also – predator
Equilibria	Points that are attractive
Generalist	A predator that consumes several different prey types, along the diversity spectrum predators can be considered specialists if they focus on a prey type
Habitat	A point in environmental space with resources, risks, conditions (Matthiopoulos et al. 2020).
Handling Time	The time to attack, eat, and digest prey (Holling 1966, Jeschke et al. 2002, Sentis et al. 2013), it may or may not include digestion in some

	formulations. In Chapter 4, I separate handling into two phases, the pre-kill attack phase, and the post-kill consumption phase.
Functional response	The relationship between consumption of prey per predator per unit time with changing prey density (Solomon 1949, Holling 1959)
Movement rate	Distance covered over a time
Numerical response	Predator *numerical response* is the change in predator density with prey density This response can be *demographic* where reproduction or survival is increased from in input of energy into the predator population or *aggregational* were predators use areas of high prey density
Optimal foraging theory	Paradigm for describing and predicting behaviour of consumers also - Optimal diet theory
Predation	When an organism is consumed in part or in entirety which includes herbivory, carnivory, or parasitism.
Preference	Favouring of one prey over an alternative, specifically used to describe the disproportionate consumption of prey compared to an alternative given the relative densities. In the prey switching equation c is the 'preference coefficient' (Murdoch 1969)
Prey switching	Occurs when relative consumption rates and predator preference are disproportionate to density. e.g. consumption rates will be disproportionately low when prey density is low (Murdoch 1969)

	The Type III functional response mathematically depict this pattern (Holling 1959a)
Resource	Benefits the fitness of the consumer, and is depleted so that is cannot be used by another consumer. Can also refer to a consumable organism – prey.
Risk	Negatively effects the fitness of an organism, there is also a density-dependent component to risk. e.g. Predation risk, Mortality risk
Stability	Tendency to return to points, i.e. equilibria, after perturbation
Trait	A physical or behavioural characteristic of an organism.
Total predation rate	Combination of the predator numerical response and functional response. density-dependent (regulating – Messier 1994) density-independent (limiting – Gasaway et al. 1983), or inversely-density dependent (depensatory – Serrouya et al. 2015)
Prey vulnerability	Associated with the risk of being killed by a predator relative to other prey

APPENDIX 2: SUPPORTING INFORMATION FOR CHAPTER 2

A2.S1 INPUT DATA AND ISSA PARAMETERS

Table S1. Summary table of collared wolf ID (bold indicates they were included in the analysis, n = 21), pack ID, used locations (in a strata with 10 available points), tentative gamma shape, scale, kappa shape.

Wolf ID	Pack ID	Collaring Date	Used Locations (Jan–Mar)	Shape	Scale	Kappa
01	Gunn Lake	18/Jan/16	118	0.36132237	2197.12192	0.05475558
02	Whitewater	20/Jan/16	349	0.3962194	2651.77314	0.28421483
03	Baldy Lake	21/Jan/16	314	0.33994584	2483.7291	0.07652301
04	Baldy Lake	19/Jan/16	297	0.29521074	2499.6679	0.12905542
05	Gunn Lake	20/Jan/16	62	0.55817801	1836.46041	0.12612302
06	Whitewater	18/Jan/16	307	0.61605537	1745.5957	0.29198696
07	Baldy Lake	14/Mar/16	47	0.44280656	2586.38024	0.45916766
08	Lone Wolf	26/Jan/16	0			
09	Lone Wolf	27/Jan/16	0			
10	Baldy Lake	27/Jan/16	297	0.47131447	1970.92513	0.12739392
11	Gunn Lake	20/Jan/16	142	0.49732863	1681.45041	0.16125508
12	Whitewater	20/Jan/16	299	0.54819785	1981.95376	0.23867235
13	Gunn Lake	14/Mar/16	0			
14	Lake Audy	14/Feb/17	529	0.35109155	2440.52882	0.07622143

15	Block	13/Feb/17	240	0.40626602	2168.37597	0.14995776
16	Spruce Lake	13/Feb/17	0			
17	Ranch Creek	13/Feb/17	216	0.30702876	2271.3429	0.15828021
18	Ranch Creek	13/Feb/17	203	0.31408058	2348.83172	0.09051765
19	Birdtail Valley	14/Feb/17	298	0.36740815	2642.2791	0.15068368
20	Lake Audy	14/Feb/17	286	0.40987091	2033.40613	0.0092104
21	Spruce Lake	13/Feb/17	0			
22	Birdtail Valley	14/Feb/17	239	0.45398585	2052.52099	0.06714728
23	Spruce Lake	13/Feb/17	0			
24	Block	14/Feb/17	180	0.51934873	1562.19645	0.15046035
25	Block	13/Feb/17	197	0.33823499	2994.93348	0.2313691
26	Birdtail Valley	14/Feb/17	238	0.3571711	2461.43977	0.22878853
27	Lake Audy	14/Feb/17	308	0.44632291	1973.39982	0.03559697

Table S2. Deer catchability model output from a logistic regression analysis (binomial, logit) where kills were designated ‘1’ and available ‘0’ were drawn across wolf territories. Outputs and detailed methods for the moose and elk catchability model are reported in Zabihi-Seissan et al. 2022. Supplementary Material Table S4. Significant values in bold

Term	**Coefficient Estimate**	**Std. Error**	**P-value**
Intercept	-5.1689056	3.7284546	0.16564
ConBog	1.1409895	1.6384719	0.48619
MarshGrass	0.5299321	1.4752452	0.71943
Mixedwood	**2.5498129**	**0.8698398**	**0.00337**
log_BTrail_Dist	-0.1949736	0.1537350	0.20471
log_Road_Dist	0.1500584	0.2891781	0.60382
log_ Trail_Dist	-0.0355165	0.1857109	0.84833
log_Water_Dist	0.2035007	0.3027018	0.50140
log_Edge_Dist	-0.1049687	0.1476021	0.47699
log_Stream_Dist	-0.2620656	0.1446049	0.06994
Ruggedness	-0.0004991	0.1066569	0.99627

Table S3. Model performance was evaluated using the performance package, check_collinearity were determined to have Low Correlation, check_overdispersion reported no dispersion (dispersion ratio = 0.859, Pearson's Chi-Squared = 48938.442, p-value = 1). VIFs for terms in the model are reported in the table.

Term	**VIF**	**Increased SE**	**Tolerance**
log_sl	1.80	1.34	0.56
cos_ta	1.00	1.00	1.00
elk_kill_end	2.48	1.57	0.40
moose_kill_end	1.39	1.18	0.72
deer_kill_end	1.88	1.37	0.53
log_wolf_dist_end	1.67	1.29	0.60
log_park_dist_end	2.45	1.56	0.41
log_sl : tfkill_days	1.80	1.34	0.56
tfkill_days : elk_kill_end	2.25	1.50	0.45
tfkill_days : moose_kill_end	1.45	1.20	0.69
tfkill_days : deer_kill_end	1.64	1.28	0.61
tfkill_days : log_wolf_dist_end	1.84	1.36	0.54
tfkill_days : log_park_dist_end	2.59	1.61	0.39

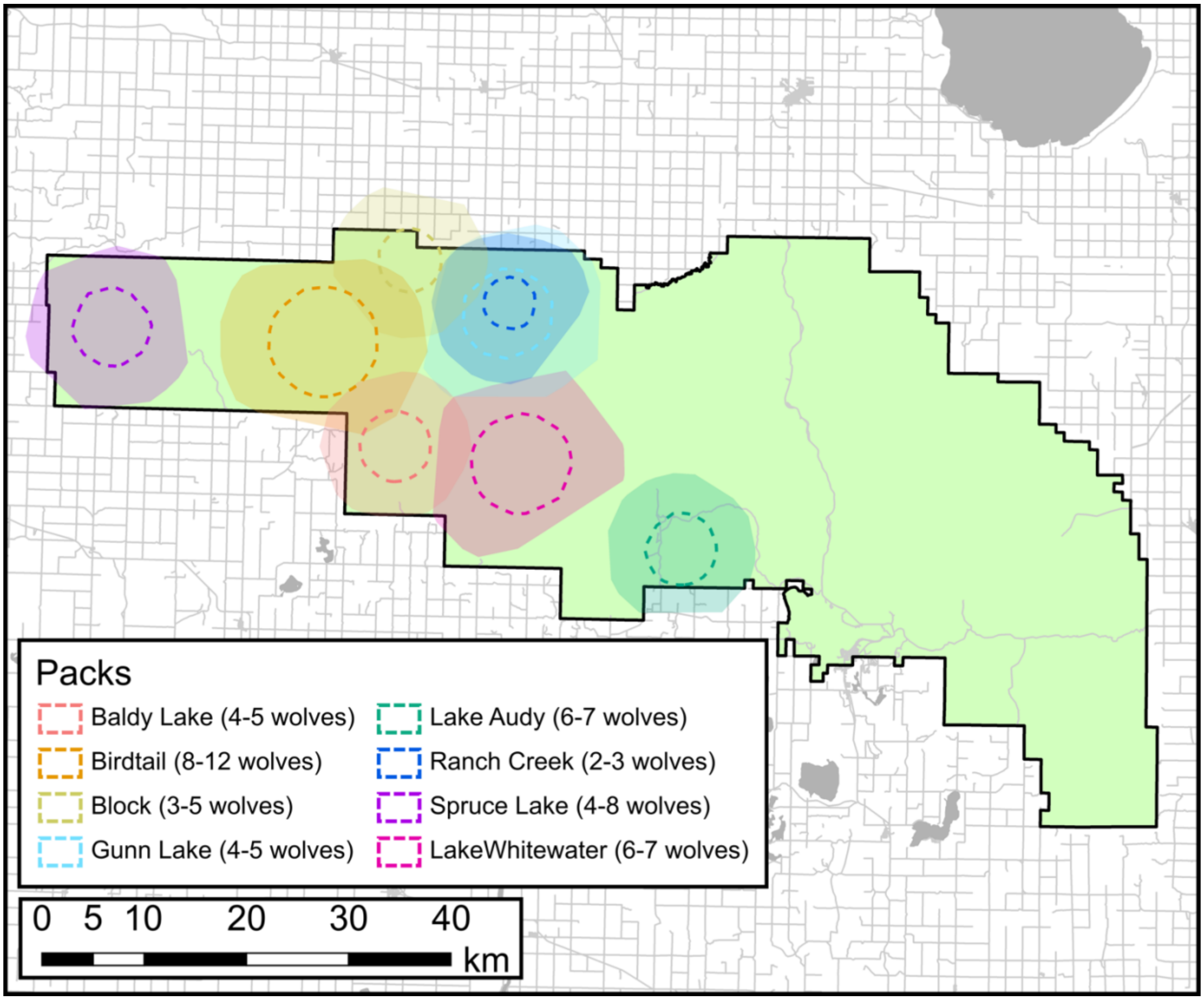


Figure S1. Park map with wolf ranges from collars on the west core area of Riding Mountain National Park. Pack home ranges and estimated number of wolves in each pack based on aerial visual observations and trail camera photos. Shaded areas consist of tradition 95% minimum convex polygon which contain 95% of all wolf GPS points while the dotted lines consist of the core home range (50% minimum convex polygon). The W11 from Gunn Lake 2016 pack and lone wolf W09 established the Ranch Creek pack in 2017.

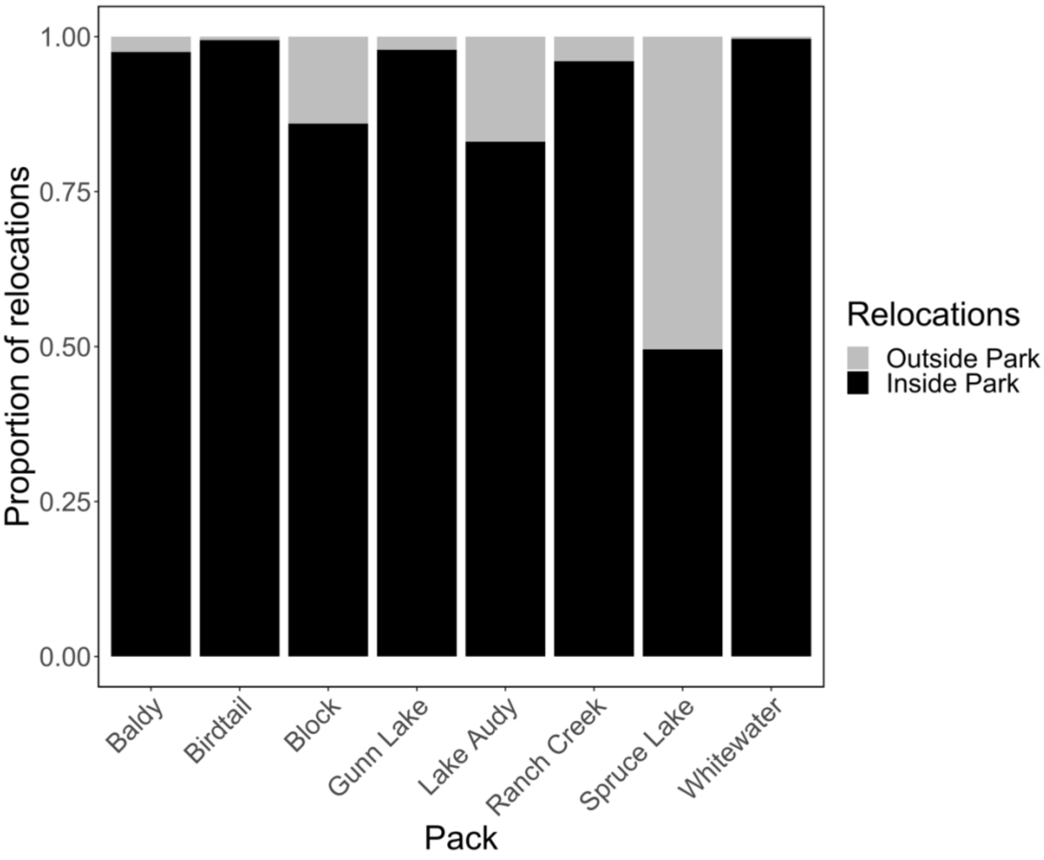


Figure S2. Proportion of locations inside and outside the for all collared wolves by pack 2016-2017.

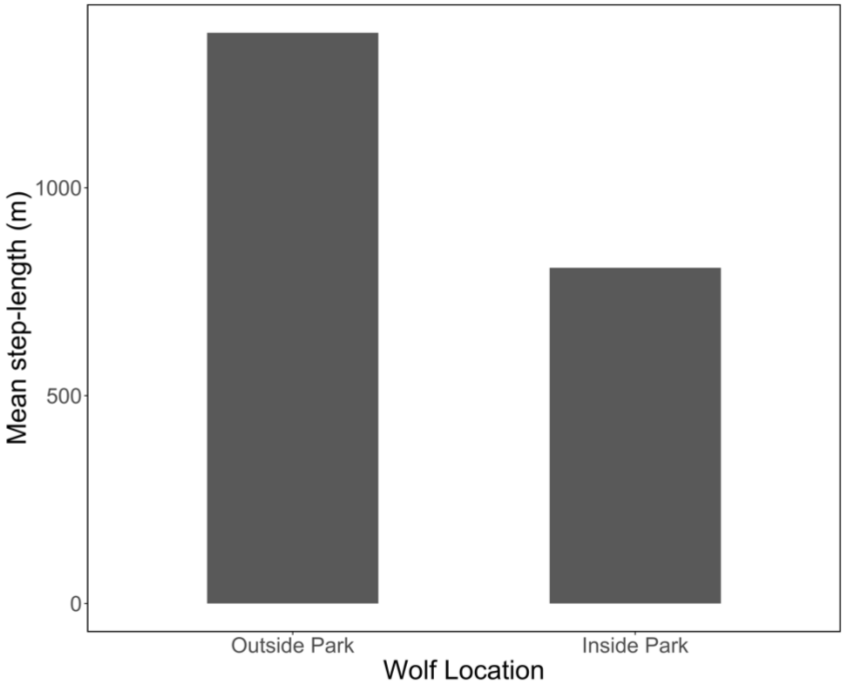
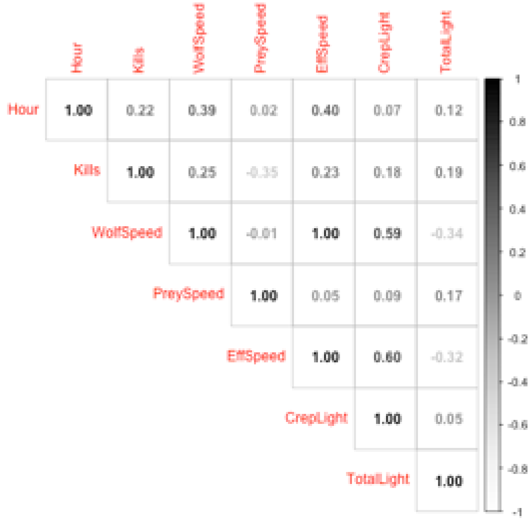


Figure S3. Step lengths of locations inside the park and outside the park for all collared wolves 2016-2017.

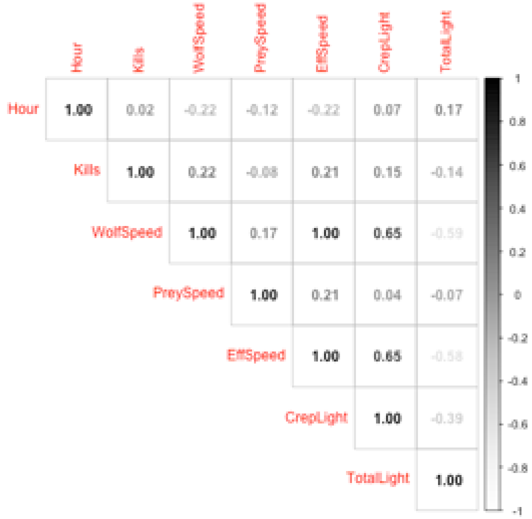
APPENDIX 3: SUPPORTING INFORMATION FOR CHAPTER 3

A3.S1 COVARIATE CORRELATION AND SNOW-FREE SEASON RESULTS



	Hour	Kills	WolfSpeed	PreySpeed	EffSpeed	CrepLight	TotalLight
Hour	1.00	0.22	0.39	0.02	0.40	0.07	0.12
Kills		1.00	0.25	-0.35	0.23	0.18	0.19
WolfSpeed			1.00	-0.01	1.00	0.59	-0.34
PreySpeed				1.00	0.05	0.09	0.17
EffSpeed					1.00	0.60	-0.32
CrepLight						1.00	0.05
TotalLight							1.00

Figure S1. Correlation between covariates for model using data from the snow season.



	Hour	Kills	WolfSpeed	PreySpeed	EffSpeed	CrepLight	TotalLight
Hour	1.00	0.02	-0.22	-0.12	-0.22	0.07	0.17
Kills		1.00	0.22	-0.08	0.21	0.15	-0.14
WolfSpeed			1.00	0.17	1.00	0.65	-0.59
PreySpeed				1.00	0.21	0.04	-0.07
EffSpeed					1.00	0.65	-0.58
CrepLight						1.00	-0.39
TotalLight							1.00

Figure S2. Correlation between covariates for models using data from the snow-free season.

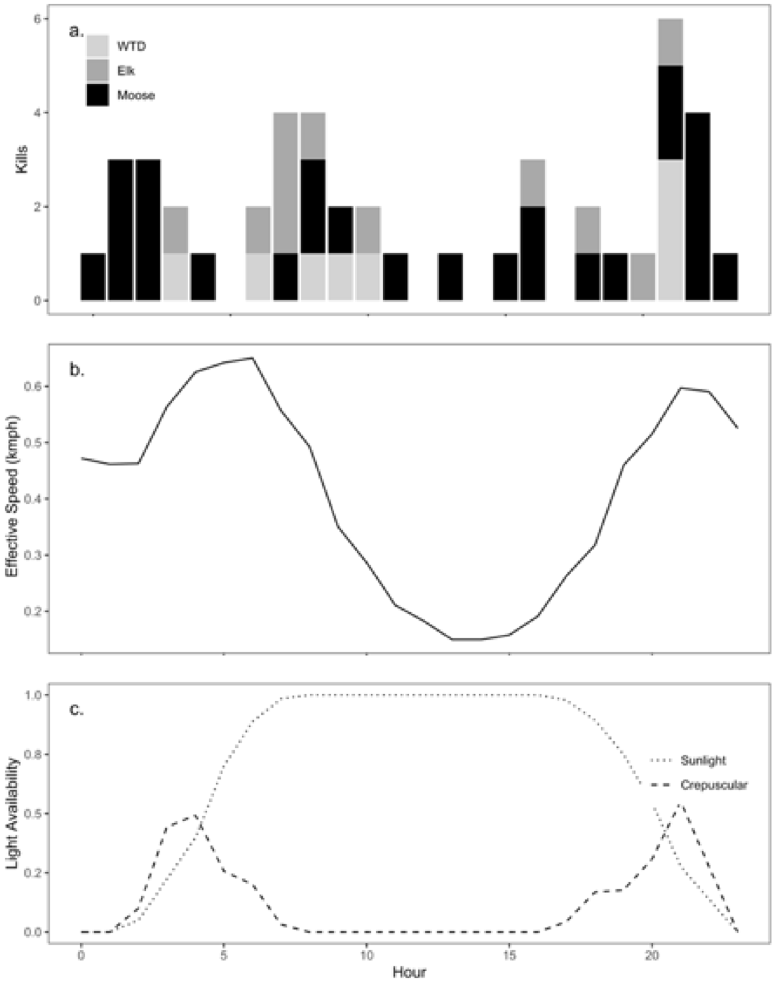


Figure S3. Temporally dynamic covariates used to explain diel variation in a) kill rates are b) effective speed (*v*, calculated from wolves, elk, white tailed deer, and moose) and c) detectability (*D,* which was measured as proportion light availability (L, and crepuscular light (c, purple). Total number of kills per hour are the dependent variable explained by factors interacting with prey species that vary between hours. We identified kill clusters and animal speed from GPS locations, detectability was determined from the proportion of total sunlight and crepuscular light occurring each day and averaged across the year. Data from snow-free season. Compared to Figure 1 of snow season data, the peaks and troughs of the movement rate are more extreme, and the total light period is longer.

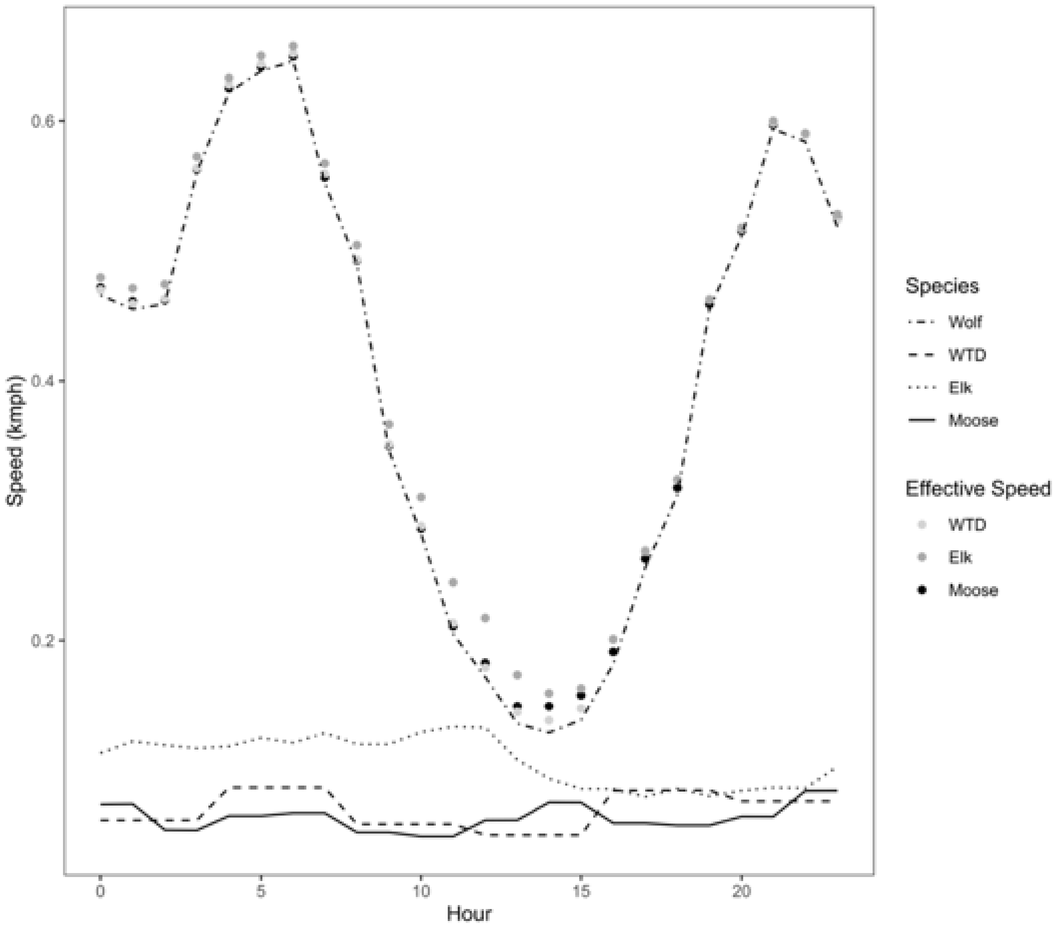


Figure S4. Diel speed over 24-time bins of an hour, calculated as an average of step length over interval duration from GPS data. Effective speed (dots, coloured by species included as prey), calculated from $v = \sqrt{v^2{}_{predator} + v^2{}_{prey}}$ for the system, is governed by wolf speed (dot-dash) which is much greater than prey speeds for elk (dotted), deer (dash), and moose (solid). Data from snow-free season. Compared to the snow season the peaks and troughs of effective speed and wolf speed are more extreme, the movements of prey are slightly elevated.

Table S1. Likelihood and AIC values for three models to empirically test the ideal gas law.

	log Likelihood	AIC
Effective Speed + Total Light + Crepuscular Light		
Snow	**-41.57484 (df=13)**	109.15
Snow-Free	**-31.21387 (df=13)**	88.428
Effective Speed + Total Light		
Snow	-42.16949 (df=10)	**104.34**
Snow-Free	-32.20292 (df=10)	**84.406**
Effective Speed + Crepuscular Light		
Snow	-48.78684 (df=10)	117.57
Snow-Free	-37.713 (df=10)	95.426

Table S2. Output from full model that includes crepuscular light, for snow and snow-free season. The notable change is that the confidence intervals for the Effective Speed: Moose covariate overlaps zero in the snow season.

	Snow			Snow-free		
	estimate	low	high	estimate	low	high
(Intercept)	-1.54	-3.07	-0.01	-0.31	-1.15	0.52
SpeciesElk	2.35	0.12	4.58	-0.44	-1.65	0.77
SpeciesMoose	0.90	-1.25	3.04	1.45	0.26	2.64
log(EffSpeed + 1):SpeciesWTD	**5.65**	**1.52**	**9.79**	0.78	-1.18	2.75
log(EffSpeed + 1):SpeciesElk	-0.74	-5.03	3.55	1.87	-0.17	3.92
log(EffSpeed + 1):SpeciesMoose	4.05	-0.02	8.12	-0.02	-2.01	1.98
SpeciesWTD:log(TotalLight + 1)	**0.82**	**0.12**	**1.53**	0.37	-0.37	1.11
SpeciesElk:log(TotalLight + 1)	0.05	-0.66	0.75	**0.82**	**0.09**	**1.56**
SpeciesMoose:log(TotalLight + 1)	**1.02**	**0.31**	**1.73**	**-0.94**	**-1.68**	**-0.20**
SpeciesWTD:log(CrepLight + 1)	-1.01	-3.00	0.98	0.73	-0.80	2.26
SpeciesElk:log(CrepLight + 1)	-0.13	-2.09	1.84	0.03	-1.49	1.55
SpeciesMoose:log(CrepLight + 1)	-0.04	-2.01	1.93	-0.70	-2.23	0.83

A3.S2 Type II Functional Response Model Example

Kill rates of predators are not solely influenced by encounter rates. A more common pattern is a saturation in predation rates due to limitations from handling time, *i.e.,* time it takes for a predator to add the energy from a prey item to itself (Oksanen et al. 2001). In a system composed of multiple prey, the kill rate of prey species *i* (out of a *j* number of prey types) becomes a Type II functional response (Holling 1959) with the addition of handling time (h)

$$f_i = \frac{Dv_iN_i}{1+D\cdot(v_iN_ih_i \ldots + v_jN_jh_j)} \qquad \text{eqn S1}$$

assuming detectability does not differ between prey species. This is an extension of the encounter rate equation, where the kill rate of prey *i* by the predator now also depends on the detection distance, effective speed and density of the other prey in the system.

Due to the incorporation of handling time, we follow the Taylor (or Maclaurin) series where $\ln(x+1) = x + \frac{x^2}{2} + \frac{x^3}{3} + \cdots$. However, we assumed that $x + 1 = \ e^x$

$$\ln(kill\ rate_i) = \ln(D) + \ln(v_iN_i) - D\cdot(v_1N_1h_1 + v_2N_2h_2 + v_3N_3h_3) \qquad \text{eqn S2}$$

APPENDIX 4: SUPPORTING INFORMATION FOR CHAPTER 4

A4.S1 FUNCTIONAL RESPONSES IN MULTI-PREY SYSTEMS: FOUNDATIONS AND EXPANSIONS

Modelling predator consumption rates across changes in prey density

The functional response describes the change in the consumption rates of an individual predator per unit time with changing prey density (Holling 1959b). In this appendix, we will provide equations to accompany the expanded functional responses model we propose. First. the simplest description of consumption rate, *f(N),* is a linear Type I functional response of the form:

$$f(N) = aN \qquad \text{(Eq. S1)}$$

N is the abundance of prey, and *a* is the attack rate of a predator (also known as the space-clearance rate; in units of area/time (DeLong 2021) which includes the time taken to search, encounter, attack, and subdue a single prey item. With the incorporation of *h*, the time it takes a predator to handle a single captured prey item, a Type II functional response reaches an asymptote.

$$f(N) = \frac{aN}{1+ahN} \qquad \text{(Eq. S2)}$$

A Type III response is described by a sigmoid function arising from the space-clearance rate itself being a function of resource density, $a = aN^q$, where q is the 'space clearance exponent' (Daugaard et al. 2019):

$$f(N) = \frac{aN^{1+q}}{1+ahN^{1+q}} \qquad \text{(Eq. S3)}$$

Values of $q > 0$ (and hence a sigmoidal functional response) are classically thought to arise from predators developing expertise in searching, subduing, consume, or digesting prey as prey abundance increases, but could also arise dues to density-dependent shifts in prey distribution (Fryxell et al. 2007), or, more importantly to our point, prey switching. Note that, the original Type III model (Holling 1959) only considered variation in the density of one prey, while the abundance of the alternate prey was kept constant. Notably, these discrete forms of the functional response can be imagined as existing along a spectrum where the introduction of consume time influences the saturation of the response (Type I versus Type II) and the influence of prey density shifts the relationship of consumption rates with prey density from tending towards Type II to III.

Functional responses in multi-prey systems

(Murdoch 1969c) incorporated the densities of multiple prey with distinct attack and consume times for each prey. A common formulation of a functional response for prey *i*, in a two-prey system with prey *j* is:

$$f(N_x) = \frac{a_i N_i}{1+a_i h_i N_i + a_j h_j N_j} \qquad \text{(Eq. S4)}$$

Switching can be described with the equation created by Murdoch (1969), which was later modified by Greenwood and Elton (1979) and Elliot (2004). The ratio of the consumption rates is compared to a ratio of the prey abundances to calculate the preference term, *c*, and the predators switching behaviour is described by *b,* (Fig. S2)

$$\frac{f(N_i)}{f(N_j)} = \left(c\frac{N_i}{N_j}\right)^b \qquad \text{(Eq. S5)}$$

In addition, prey-specific measures that may impact predator behaviour can be built into this framework. Garrott et al. (2007) decomposed *c* into preference *z*, vulnerability *v*, and nourishment, *m,* (an extended comparison to our model is below) to give

$$\frac{f(N_i)}{f(N_j)} = \left[(z * v * m)\frac{N_i}{N_j}\right]^b \qquad \text{(Eq. S6)}$$

with the functional response

$$f(N_x) = \frac{a_i (z*v*m)^b \left(\frac{N_i}{N_j}\right)^{b-1}}{1+a_i h_i (z*v)^b m^{b+1}\left(\frac{N_i}{N_j}\right)^{b-1} + a_j h_j N_j} \qquad \text{(Eq. S7)}$$

In summary, the functional response provides a framework to test mechanisms that govern the consumption rates of predators in natural conditions where prey density, availability, and defenses differ. From the prey's perspective, the type of functional response has direct implications on predation rates (*i.e.* proportion of prey population consumed per predator per unit time).

Comparing our model with previous Functional Response work

As a point of comparison, the model described in the main text will be expressed in the terms used by Murdoch et. al (1969) and Garrott et al. (2007). First, the switching equation between relative consumption rates, presents the disproportionate relationship originally presented by Murdoch et. al (1969). The parameter *b* was added by Greenwood and Elton (1979) and Elliot (2004), eqn (A1-5) and Fig. S2.

The preference coefficient, *c*, was described by three variables (*z, v, m*) in Garrott et al. (2007).

$$\frac{f(N_i)}{f(N_j)} = \left(c\frac{N_i}{N_j}\right)^b = \left[(z * v * m)\frac{N_i}{N_j}\right]^b \qquad \text{(Eq. S8)}$$

In this model, m, is the 'relative nourishment' calculated as the ratio of time to consume, $\frac{t_{b,i}}{t_{b,j}}$.

However, in our formulation the energetic gain from the two prey and the consume times are included separately, though not necessarily mutually exclusive in real systems. Many situations exist where the nourishment from prey and the time to consume the prey are decoupled, especially when discussing foraging costs induced by antipredator traits aimed at counteracting the energy gained by a predator from successful prey capture. The time expended on prey once encountered is composed time to attack and consume. Even in situations where the time expended is on consuming the prey, certain foraging costs unrelated to nourishment will increase the time to ingest the prey (ex. armour, or spines, shells). Thus, nourishment, m, in our model can be more specifically described as $\frac{e_{n,i}}{e_{n,j}}$ instead, without the consumption time. However, this does not enter the preference description explicitly, it is instead included in p_e. The vulnerability of prey, v, is the component that our model greatly expands upon in the context of time or energy requirements of antipredator trait induced foraging costs. Generally, vulnerability is inversely related to the expression of prey foraging costs. In Garrott et. al 2007, z, is a parameter for predator preference which is not included in our model, because we assume preferences for prey will be explained by foraging costs.

Notably, the b coefficient present in contemporary prey switching models was not explicitly included but accelerating or decelerating relative preference with relative density occurs as expected despite this omission. When the $b=1$ the slope of the relationship between relative consumption rates and relative density is constant, otherwise non-linear dynamics occur. The density-dependence of p_e means it is a dynamic preference relationship, thereby, demonstrating non-linearity with relative density. The density-dependence of p_e is linked to the alternative prey density and not the density of the prey being engaged. The probability of engaging with costly prey decays with the density of the profitable prey (Fig. S3); the speed at which p_e declines and the minimum engagement probability is sensitive to foraging costs of the costly prey. A foraging cost in the form of time investment has a pronounced influence on p_e. The influence of time to attack or consume on p_e outlines that attack rate in our model is in fact a function of total handling time.

A predator may develop a search image based on past experience with prey types, which would influence predator preference (Ishii and Shimada 2010, Van Leeuwen et al. 2013)) In some cases, predators may exhibit a dynamic search rate that changes with the availability of prey due to a more elaborate cognitive mechanism. A density-dependent search rate can be expressed simply as

$$s(N) = s \cdot \frac{N_i}{N_j} \qquad \text{(Eq. S9)}$$

These patterns would differ from the dissimilarity in search rates that are density-independent due to the costly prey *j*, taking a greater time investment, possessing a consistent and non-dynamic reduced rate of discovery.

In summary, our model assumes that both the foraging costs and the predator's hunting strategy (in terms of the underlying decisions rules) are fixed. Neither foraging costs nor predator strategy depend on the density, the relative density, or the composition of prey in the system. Further, the model assumes that the predator keeps track of current densities of all prey species. The model created by Garrott et al. (2007) implicitly assumes that the foraging costs from the traits of prey or the predator hunting strategy are density-dependent. The simple alternative to this model would be a predator that always engages when prey are encountered but that search rate is density dependent, $s(N)$. Biologically this could be due to density-dependent habit use by the prey or a dynamic predator search image. The inclusion of density dependent search image would result in a quadratic term in the functional response. In the model created by Garrott et al (2007) switching occurs even if $c = 1$ when $b \neq 1$. Thus, these two models complement one another, and in natural systems, either, both, or none, may apply. Finally, our model could be extended to include predator density in one of the many established forms (Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975, Arditi and Akcakaya 1990, Akçakaya et al. 1995, Tyutyunov et al. 2008).

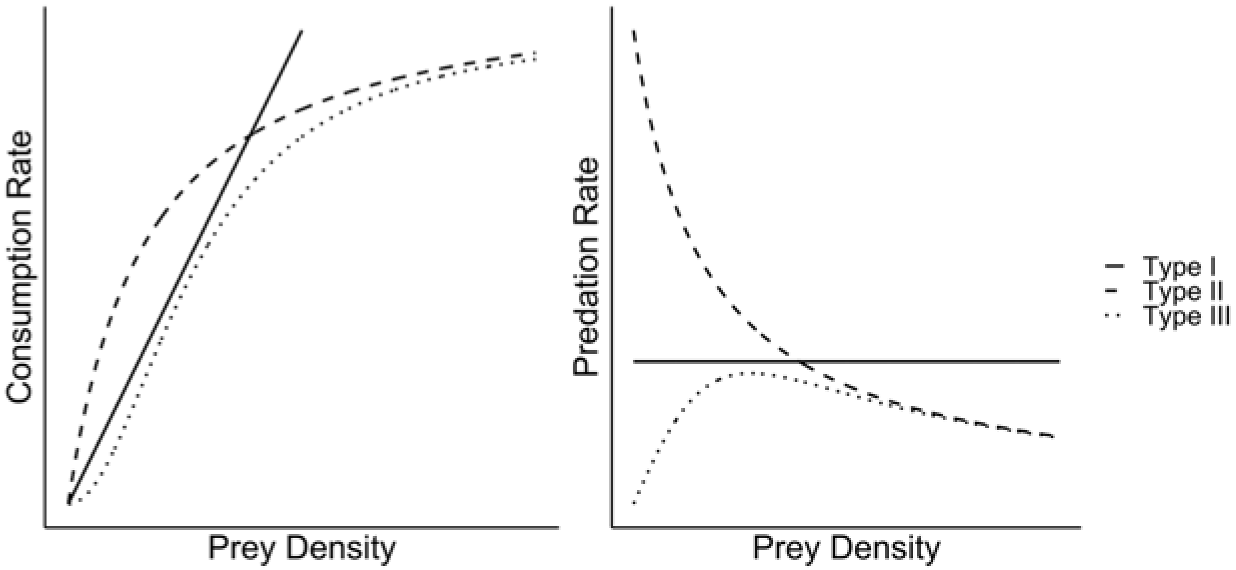


Fig. S1. The three types of functional responses, *f(N)*, as outlined by Holling (1959). The functional response is the relationship of per predator consumption rates with changes in prey density (*N*) for a Type I, Type II, or Type III functional response and the resulting per capita predation rate of prey.

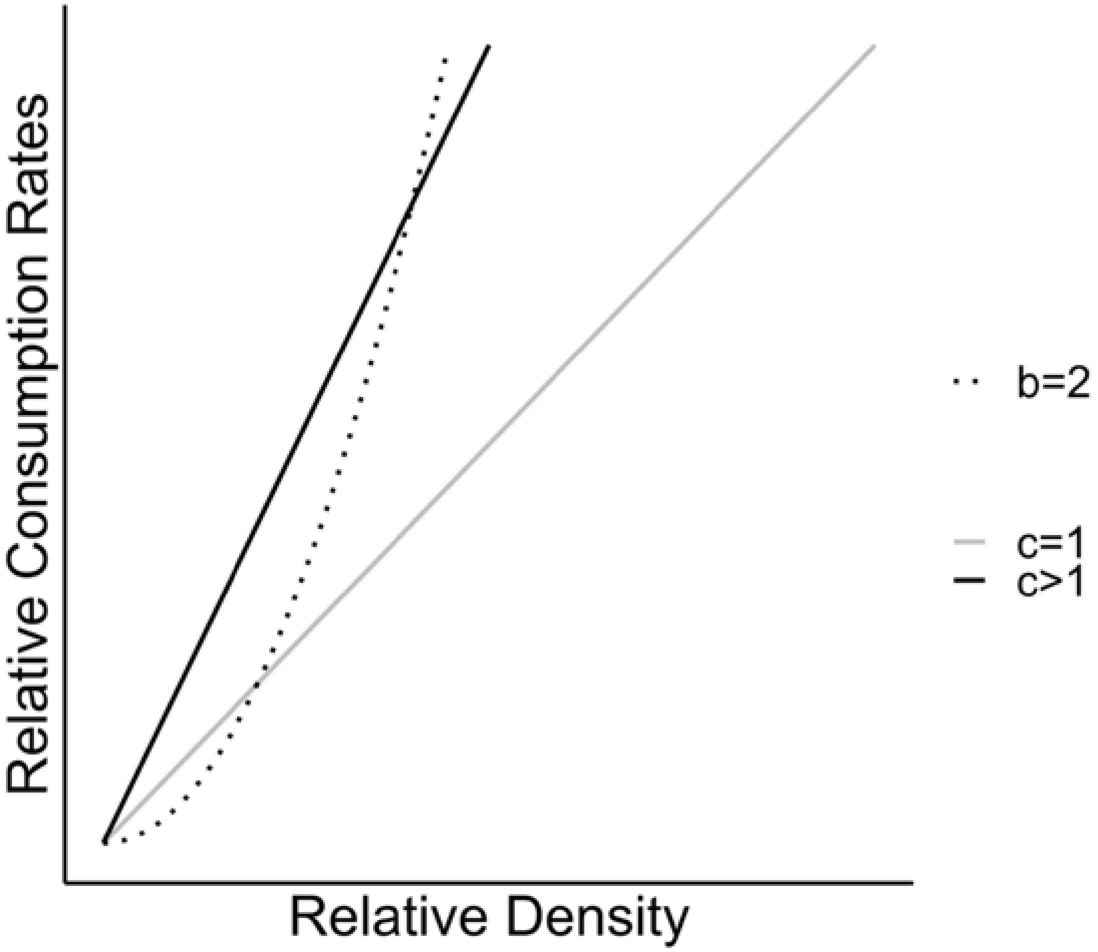


Fig. S2. The preference of a predator, *c*, is determined by comparing the relative proportions of prey consumed to relative density of prey types (see eqn A1-5). A predator with no preference consumes prey proportional to its availability (grey line), when a predator exhibits preference *c* will be greater than 1 (solid black line), finally when *b=2* the preference will demonstrate a non-linear increase as relative density increases.

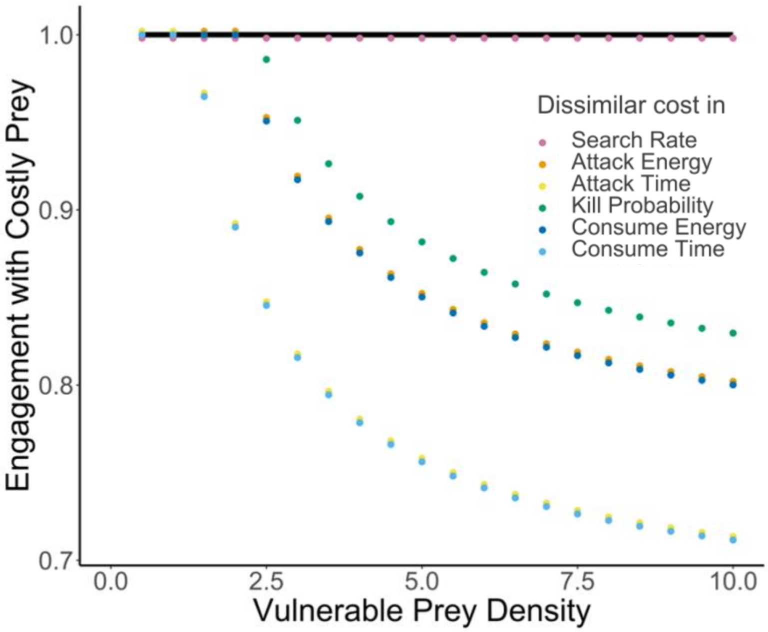


Fig. S3 The probability of engaging with costly prey for scenarios where the foraging cost reduces the engagement of predators with prey by modifying search time, kill probability, attack energy or time, consumption energy or time. When costly prey has increases search time, the predator will always engage once encountered ($p_e = 1$).

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A4.S2 LITERATURE REVIEW: EVIDENCE FOR ANTIPREDATOR TRAIT INDUCED SWITCHING IN MULTI-PREY SYSTEMS

We conducted a literature survey to assess evidence for predators' preferences of prey when prey switching was measured, to determine why predators exhibit preference with a focus on prey traits, and to identify how previous work has distinguished prey types in multi-prey systems. To be reproducible, we searched the literature in a synthetic way. To make this a full metanalysis we suggest future investigation include alternative terms: optimal foraging, foraging costs, resource, consumer, predator preference, diet specialization, and generalist.

Data for the literature survey have been shared on a GitHub repository found at https://github.com/CMProkopenko/optimalswitch

Search Methods

In April 2018, we conducted literature survey through the ISI Web of Science using the following search terms, (= indicates number of papers returned for each search):
TITLE: ("prey switching") (= 43) OR ("kill rate" AND "multi-prey") (= 1) (Note: additional search terms that were used ("frequency-dependent predation") (= 17)

OR TOPIC: ("functional response" AND "multiple prey" AND "switching") OR TOPIC: ("kill rate" AND "multiple prey" AND "switching") OR ("predator" AND "multiple prey" AND "switching") (= 13)

Our literature survey returned 44 studies of prey switching or functional responses in multi-prey systems out of which 28 studies remained following the removal of studies that were not suitable. Specifically, we eliminated theoretical studies that modelled prey switching without empirical data, or experimental studies that artificially altered prey characteristics.

From the 28 studies, we extracted information on the study system and design, and ecological mechanisms discussed in text, with a focus on prey antipredator traits. Observations from both natural systems and experiments were included in survey. Papers that included multiple predator types, study areas, or study periods were considered separate observations of predator behaviour. Prey traits included any aspect of the prey that was mentioned in the paper, often this was in a relative sense where the differences between preferred prey and alternatives were highlighted. Traits mentioned were recorded and the direction of the effect on consumption with an increase in the trait was included. In most cases, the effect on a predator’s preference for a prey type was not tested and instead occurred in a statement, often supported with citations. For example, “[Prey X] was preferred by the predator, because it was more vulnerable and not as mobile”

Questions

What functional responses have been documented in multi-prey systems?

The addition of handling time allows for satiation in the response of consumption to increasing prey density and separates the Type I from Type II responses. Type III functional responses describe a generalist predator consuming disproportionally less prey at low densities (*i.e.*

becoming less effective at low densities or switches between prey types). See Appendix S1 for further discussion of functional response expressions.

Of the literature we surveyed 43% (12/28) of the studies fit functional response curves to their data, although some studies fit multiple functional responses, for a total of 18 functional responses from 12 studies. When functional responses were included, studies fit curves for each predator and prey type; Type II functional responses were the most common form describing predator consumption rate (found in 61% of functional response fits, 11/18 responses in 12 papers testing functional responses), followed by Type III (27%, 5/18), and Type I (11%, 2/18). First, it is important to evaluate density ranges that were used to fit the functional responses of prey because there is likely sampling effect on the type observed. To clarify, most systems follow a Type II response, but at low densities may appear to be a Type I as densities have not increased sufficiently to observe the saturation characteristic of a Type II. Alternatively, if consumption rates are measured at saturation, they may appear unchanging with prey density. Further, it is much more difficult to detect a Type III functional response because it requires many observations at very low densities. These trends can be further complicated when multiple prey types are considered, thus the total consumption rate of a predator should also be described in these studies.

Do predators exhibit a trait-mediated preference for prey?

96% of studies identified preference in a predator's consumption behaviour, *i.e.* the diet composition or consumption rates were disproportionate to the density of the prey relative to the other prey types considered. When discussing a predator's preference, prey vulnerability was mentioned in 57% (17/28), and prey traits were mentioned in 75% (22/28) of the studies. There was variation in the traits mentioned in the studies surveyed and the suggested influence of these traits on the predator remarkably only 3% (1/28) directly tested the effect of these traits. Body size was the most discussed trait in the literature, which included length, weight, and biomass; however, if energy content was explicitly mentioned it was considered separately, as energy content can refer to more than just the biomass of prey consumed by predator (*e.g.* fat content). Prey vulnerability was often mentioned as the key influence on switching but was rarely quantified in field systems.

Conclusion

This survey revealed that predators exhibit disproportionate consumption in most multi-prey systems, *i.e.* switching or preference. Instead of evaluating prey switching by fitting a Type III functional response across prey densities, predator behaviour in multi-prey systems was often summarized through the prey switching equation (Appendix S1) or similar measures that compare and relate the consumption of prey to relative densities. Future work on multi-prey functional responses and prey switching should measure multiple traits using replicable methods. Specifically, the explicit inclusion of prey and predator densities will allow for future robust metanalyses. Finally, testing competing hypotheses about which prey traits influence functional responses and how the functional response is affected will certainly result in the expansion of predator-prey theory.

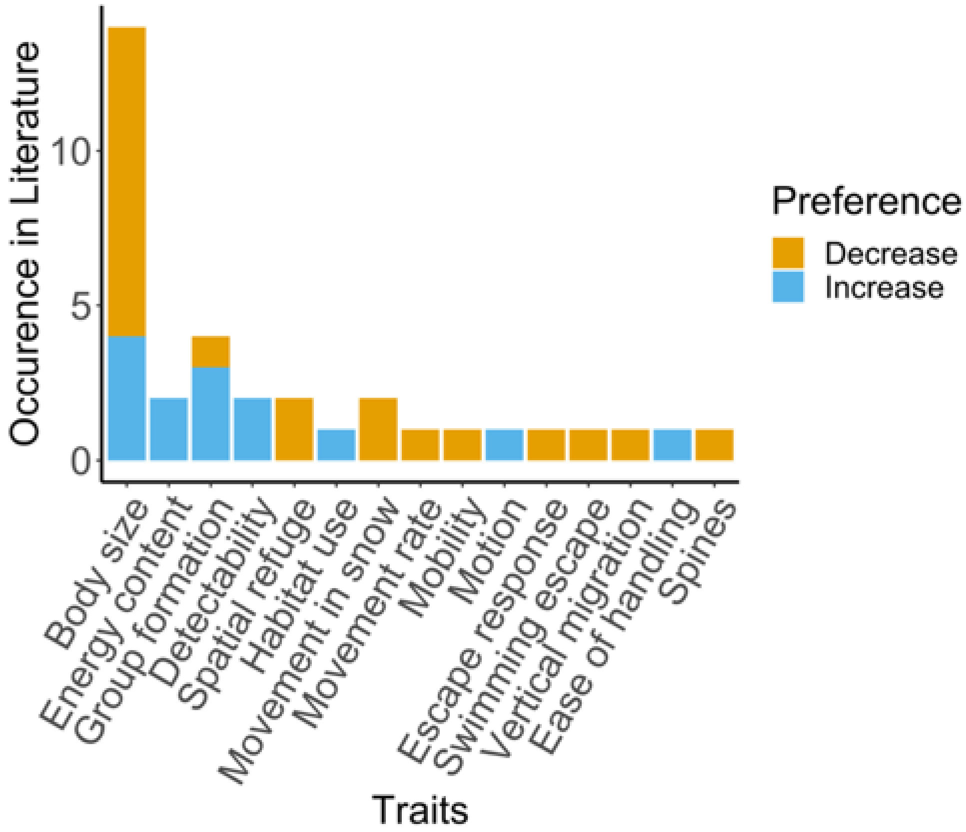

Fig. S1. Prey traits that influenced a predator's consumption preference for prey (n = 28 multi-prey functional response studies) and the effect of an increase in the expression of this trait type on the predator preference for that prey type. For example, in 29% of studies that discussed effects of prey body size on the predator's consumption rate (n = 14), predators preferred larger prey, while predators preferred smaller prey in 71% of studies that examined this effect.

A4.S3 Calculations of Baseline Values for Simulation

First, we determine the half maximum consumption in a single prey system where the costs are set to baseline values: $p_{k,i} = p_{k,j} = 0.5$, $E_{n,i} = E_{n,j} = 1000\, J$, $e_{s,i} = e_{s,j} = 1\, W$ $e_{a,i} = e_{a,j} = 1\, W$, $e_{b,i} = e_{b,j} = 1\, W$, $s_i = s_j = 1\, \frac{m^2}{sec}$, $t_{a,i} = t_{a,j} = 1\, sec$, $t_{b,i} = t_{b,j} = 1\, sec$.

The maximum net energy gain rate in such a system is reached when $N \to \infty$ (see Eq. 7 in the main text):

$$\boldsymbol{F_{max}} = \lim_{N\to\infty} \left(\frac{N \cdot s \cdot p_e \cdot [-e_a \cdot t_a + p_k \cdot (E_n - e_b \cdot t_b)] - e_s}{1 + N \cdot s \cdot p_e \cdot [t_a + p_k \cdot t_b]} \right) = \frac{-e_a \cdot t_a + p_k \cdot (E_n - e_b \cdot t_b)}{t_a + p_k \cdot t_b} \qquad \text{(Eq. S1)}$$

Using baseline values:

$$\boldsymbol{F_{max}} = \frac{-1 + 0.5 \cdot (1000 - 1 \cdot 1)}{1 + 0.5 \cdot 1} = \boldsymbol{332\frac{1}{3}\, W}$$

We will now calculate the prey population density that results in half-maximum predator energy gain rate:

$$\frac{\boldsymbol{N_{0.5}} \cdot s \cdot [-e_a \cdot t_a + p_k \cdot (E_n - e_b \cdot t_b)] - e_s}{1 + \boldsymbol{N_{0.5}} \cdot s \cdot [t_a + p_k \cdot t_b]} = 0.5 \cdot F_{max} \qquad \text{(Eq. S2)}$$

$$\downarrow$$

$$\boldsymbol{N_{0.5}} = \frac{0.5 \cdot F_{max} + e_s}{s \cdot [p_k \cdot (E_n - e_b \cdot t_b - 0.5 \cdot F_{max} \cdot t_b) - t_a \cdot (e_a + 0.5 \cdot F_{max})]} \qquad \text{(Eq. S3)}$$

$$\downarrow$$

$$\boldsymbol{N_{0.5} = 0.670679\, \frac{prey}{m^2}}$$

We will now double this prey density and determine the cost value that reduces the predator’s gain rate to half maximum, assuming everything else being equal. In other words, we are looking for the magnitude of increase in costs, that would result in the prey being consumed at the half-maximum rate, even though they are twice as abundant. The expressions determine the values of costs that result in particular consumption rates if all other parameter values are known. These expressions were used in defining dissimilarity values for scenarios in text and our sensitivity test in this Appendix.

Search energy expenditure rate

$$\frac{2 \cdot N_{0.5} \cdot s \cdot [-e_a \cdot t_a + p_k \cdot (E_n - e_b \cdot t_b)] - \boldsymbol{e_{s,0.5}}}{1 + 2 \cdot N_{0.5} \cdot s \cdot (t_a + p_k \cdot t_b)} = 0.5 \cdot F_{max}$$

$$\downarrow$$

$$\boldsymbol{e_{s,0.5}} = 2 \cdot N_{0.5} \cdot s \cdot [-e_a \cdot a + p_k \cdot (E_n - e_b \cdot t_b)] - 0.5 \cdot F_{max} \cdot [1 + 2 \cdot N_{0.5} \cdot s \cdot (t_a + p_k \cdot t_b)] \tag{Eq. S4}$$

$$\boldsymbol{e_{s,0.5} = 168.169\ W}$$

Search rate

$$\frac{2 \cdot N_{0.5} \cdot \boldsymbol{s_{0.5}} \cdot [-e_a \cdot t_a + p_k \cdot (E_n - e_b \cdot t_b)] - e_s}{1 + 2 \cdot N_{0.5} \cdot \boldsymbol{s_{0.5}} \cdot (t_a + p_k \cdot t_b)} = 0.5 \cdot F_{max}$$

$$\downarrow$$

$$\boldsymbol{s_{0.5}} = \frac{0.5 \cdot F_{max} + e_s}{s \cdot 2 \cdot N_{0.5} \cdot [p_k \cdot (E_n - e_b \cdot t_b - 0.5 \cdot F_{max} \cdot t_b) - t_a \cdot (e_b + 0.5 \cdot F_{max})]} \tag{Eq. S5}$$

$$\boldsymbol{s_{0.5} = 0.5\ \frac{m^2}{sec}}$$

Attack time

$$\frac{2 \cdot N_{0.5} \cdot s \cdot [-e_a \cdot \boldsymbol{t_{a,0.5}} + p_k \cdot (E_n - e_b \cdot t_b)] - e_s}{1 + 2 \cdot N_{0.5} \cdot s \cdot (\boldsymbol{t_{a,0.5}} + p_k \cdot t_b)} = 0.5 \cdot F_{max}$$

$$\downarrow$$

$$\boldsymbol{t_{a,0.5}} = \frac{p_k \cdot (E_n - e_b \cdot t_b)}{e_a + 0.5 \cdot F_{max}} - \frac{0.5 \cdot F_{max} \cdot (1 + 2 \cdot N_{0.5} \cdot s \cdot p_k \cdot t_b) + e_s}{2 \cdot N_{0.5} \cdot s \cdot (e_a + 0.5 \cdot F_{max})} \qquad \text{(Eq. S6)}$$

$$\boldsymbol{t_{a,0.5} = 1.7455\ sec}$$

Attack energy expenditure rate

$$\frac{2 \cdot N_{0.5} \cdot s \cdot \left[-\boldsymbol{e_{a,0.5}} \cdot t_a + p_k \cdot (E_n - e_b \cdot t_b)\right] - e_s}{1 + 2 \cdot N_{0.5} \cdot s \cdot (t_a + p_k \cdot t_b)} = 0.5 \cdot F_{max}$$

$$\downarrow$$

$$\boldsymbol{e_{a,0.5}} = \frac{p_k \cdot (E_n - e_b \cdot t_b)}{t_a} - \frac{\frac{1}{2} \cdot F_{max} \cdot [1 + 2 \cdot N_{0.5} \cdot s \cdot (t_a + p_k \cdot t_b)] + e_s}{2 \cdot N_{0.5} \cdot s \cdot t_a} \text{(Eq. S7)}$$

$$\boldsymbol{e_{a,0.5} = 125.625\ W}$$

Probability of kill

$$\frac{2 \cdot N_{0.5} \cdot s \cdot \left[-e_a \cdot t_a + \boldsymbol{p_{k,0.5}} \cdot (E_n - e_b \cdot t_b)\right] - e_s}{1 + 2 \cdot N_{0.5} \cdot s \cdot \left(t_a + \boldsymbol{p_{k,0.5}} \cdot t_b\right)} = 0.5 \cdot F_{max}$$

$$\downarrow$$

$$\boldsymbol{p_{k,0.5}} = \frac{t_a \cdot (e_a + 0.5 \cdot F_{max}) + \frac{e_s + 0.5 \cdot F_{max}}{2 \cdot N_{0.5} \cdot s}}{E_n - t_b \cdot (e_b + 0.5 \cdot F_{max})} \qquad \text{(Eq. S8)}$$

$$\boldsymbol{p_{k,0.5} = 0.35036}$$

Energy content

$$\frac{2 \cdot N_{0.5} \cdot s \cdot \left[-e_a \cdot t_a + p_k \cdot \left(\boldsymbol{E_{n,0.5}} - e_b \cdot t_b\right)\right] - e_s}{1 + 2 \cdot N_{0.5} \cdot s \cdot (t_a + p_k \cdot t_b)} = 0.5 \cdot F_{max}$$

$$\downarrow$$

$$\boldsymbol{E_{n,0.5}} = \frac{t_a \cdot (e_a + 0.5 \cdot F_{max})}{p_k} + t_b \cdot (e_b + 0.5 \cdot F_{max}) + \frac{e_s + 0.5 \cdot F_{max}}{2 \cdot N_{0.5} \cdot s \cdot p_k} \qquad \text{(Eq. S9)}$$

$$\boldsymbol{E_{n,0.5} = 750.75\ J}$$

Consume energy expenditure rate

$$\frac{2 \cdot N_{0.5} \cdot s \cdot \left[-e_a \cdot t_a + p_k \cdot \left(E_n - \boldsymbol{e_{b,0.5}} \cdot t_b\right)\right] - e_s}{1 + 2 \cdot N_{0.5} \cdot s \cdot (t_a + p_k \cdot t_b)} = 0.5 \cdot F_{max}$$

$$\downarrow$$

$$\boldsymbol{e_{b,0.5}} = \frac{E_n}{t_b} - \frac{t_a \cdot (e_a + 0.5 \cdot F_{max})}{p_k \cdot t_b} - \frac{e_s + 0.5 \cdot F_{max}}{2 \cdot N_{0.5} \cdot s \cdot p_k \cdot t_b} - 0.5 \cdot F_{max} \quad \text{(Eq. S10)}$$

$$\boldsymbol{e_{h,0.5} = 250.25\ W}$$

Consume time

$$\frac{2 \cdot N_{0.5} \cdot s \cdot \left[-e_a \cdot t_a + p_k \cdot \left(E_n - e_b \cdot \boldsymbol{t_{b,0.5}}\right)\right] - e_s}{1 + 2 \cdot N_{0.5} \cdot s \cdot \left(t_a + p_k \cdot \boldsymbol{t_{b,0.5}}\right)} = 0.5 \cdot F_{max}$$

$$\downarrow$$

$$\boldsymbol{t_{b,0.5}} = \frac{E_n}{e_b + 0.5 \cdot F_{max}} - \frac{t_a \cdot (e_a + 0.5 \cdot F_{max})}{p_k \cdot (e_b + 0.5 \cdot F_{max})} - \frac{e_s + 0.5 \cdot F_{max}}{2 \cdot N_{0.5} \cdot s \cdot p_k \cdot (e_b + 0.5 \cdot F_{max})} \quad \text{(Eq. S11)}$$

$$\boldsymbol{t_{b,0.5} = 2.49103\ sec}$$

Sensitivity of patterns to baseline values

We tested the sensitivity of the qualitative patterns emerging from the scenarios described in the main text to variation in the baseline values selected for the foraging cost parameter values. We completed 14 iterations of the above process to determine the cost values that result in half-maximum consumption rate when prey density value is $2 \cdot N_{0.5}$ when the baselines values of all 7 parameters are shifted (Table S1). In each iteration, a single parameter was selected to either be reduced by 50% or increased by an order of magnitude, except for the probability of kill which was increased to 1. We focused on modifying attack time and attack energy as these costs occur regardless of successful killing of prey and produced interesting results that were highlighted in our results and discussion. We modified attack time and energy to then calculate the dissimilarity values of all parameters (Table S2). From the plots of the functional responses and predation rates we see the results do not qualitatively differ from those described in the main text (functional response and predation rates when attack time = 10 are presented in Fig S1 and S2 respectively, attack time = 0.5 in Figs S3 and S4, attack energy = 10 in Figs S.5 and S6, attack energy = 0.5 in Figs S7 and S8). The relative effect of the attack phase is modified by these changes, but the changes in consumption rates and predation rates observed and the Type III functional response generated in panel d of each figure remain consistent.

Table S1. The half-maximum consumption rate $(F_{0.5})$, the density that results in the half-maximum consumption rate $(N_{0.5})$, when baseline parameter values varied. A single parameter was selected to either be reduced by 50% or increased by an order of magnitude, except for the probability of kill which was increased to 1. Values highlighted in grey are the baseline values used in the main text. Bold values indicate the highest and lowest values generated during this exercise, which both occurred when attack time was varied.

Parameters	Value	$F_{0.5}$	$N_{0.5}$
Search Energy, e_s	0.5	166.1667	0.670679
	1	166.1667	0.670679
	10	166.1667	0.670679
Search Rate, s	0.1	166.1667	0.670679
	1	166.1667	0.670679
	1.5	166.1667	0.670679
Attack Energy, e_a	0.5	**166.3333**	**0.6706747**
	1	166.1667	0.670679
	10	**163.1667**	**0.6707525**
Attack time, t_a	0.5	**249.5**	**1.004008**
	1	166.1667	0.670679
	10	**23.30952**	**0.0993239**
Probability of Kill, p_k	0.25	99.5	0.8080402
	0.5	166.1667	0.670679
	1	249.5	0.502004
Energy Content, E_n	500	82.83333	0.674715
	1000	166.1667	0.670679
	10000	1666.167	0.6670668
Consume Energy, e_b	0.5	166.25	0.6706767
	1	166.1667	0.670679

	10	164.6667	0.6707152
Consume Time, t_b	0.5	199.5	0.80401
	1	166.1667	0.670679
	10	41.16667	0.1707152

Table S2. We determined the dissimilarity values that resulted in the half-maximum consumption rate ($F_{0.5}$) when attack time was either reduced by or increased by an order of magnitude resulting in two additional scenarios. Values highlighted in grey are the baseline values used in the main text.

Parameter	Value	$F_{0.5}$	Parameters	Dissimilarity Values
t_a	10	23.30952	Search Energy, e_s	25.30953
			Search Rate, s	0.5
			Attack Energy, e_a	13.2375
			Attack time, t_a	15.03404
			Probability of Kill, p_k	0.374576
			Energy Content, E_n	755.25
			Consume Energy, e_b	245.75
			Consume Time, t_b	11.06807
	1	166.1667	Search Energy, e_s	168.1667
			Search Rate, s	0.5
			Attack Energy, e_a	125.625
			Attack time, t_a	1.745513
			Probability of Kill, p_k	0.3503602
			Energy Content, E_n	750.75
			Consume Energy, e_b	250.25
			Consume Time, t_b	2.491026
	0.5	249.5	Search Energy, e_s	251.5
			Search Rate, s	0.5
			Attack Energy, e_a	250.5
			Attack time, t_a	0.998004
			Probability of Kill, p_k	0.3335557
			Energy Content, E_n	750.5
			Consume Energy, e_b	250.5
			Consume Time, t_b	1.996008
e_a	10		Search Energy, e_s	165.1667
			Search Rate, s	0.5
			Attack Energy, e_a	132.375
			Attack time, t_a	1.706689
			Probability of Kill, p_k	0.3535892
			Energy Content, E_n	755.25
			Consume Energy, e_b	245.75
			Consume Time, t_b	2.490863

1	Search Energy, e_s	168.1667
	Search Rate, s	0.5
	Attack Energy, e_a	125.625
	Attack time, t_a	1.745513
	Probability of Kill, p_k	0.3503602
	Energy Content, E_n	750.75
	Consume Energy, e_b	250.25
	Consume Time, t_b	2.491026
0.5	Search Energy, e_s	168.3333
	Search Rate, s	0.5
	Attack Energy, e_a	125.25
	Attack time, t_a	1.747752
	Probability of Kill, p_k	0.3501801
	Energy Content, E_n	750.5
	Consume Energy, e_b	250.5
	Consume Time, t_b	2.491036

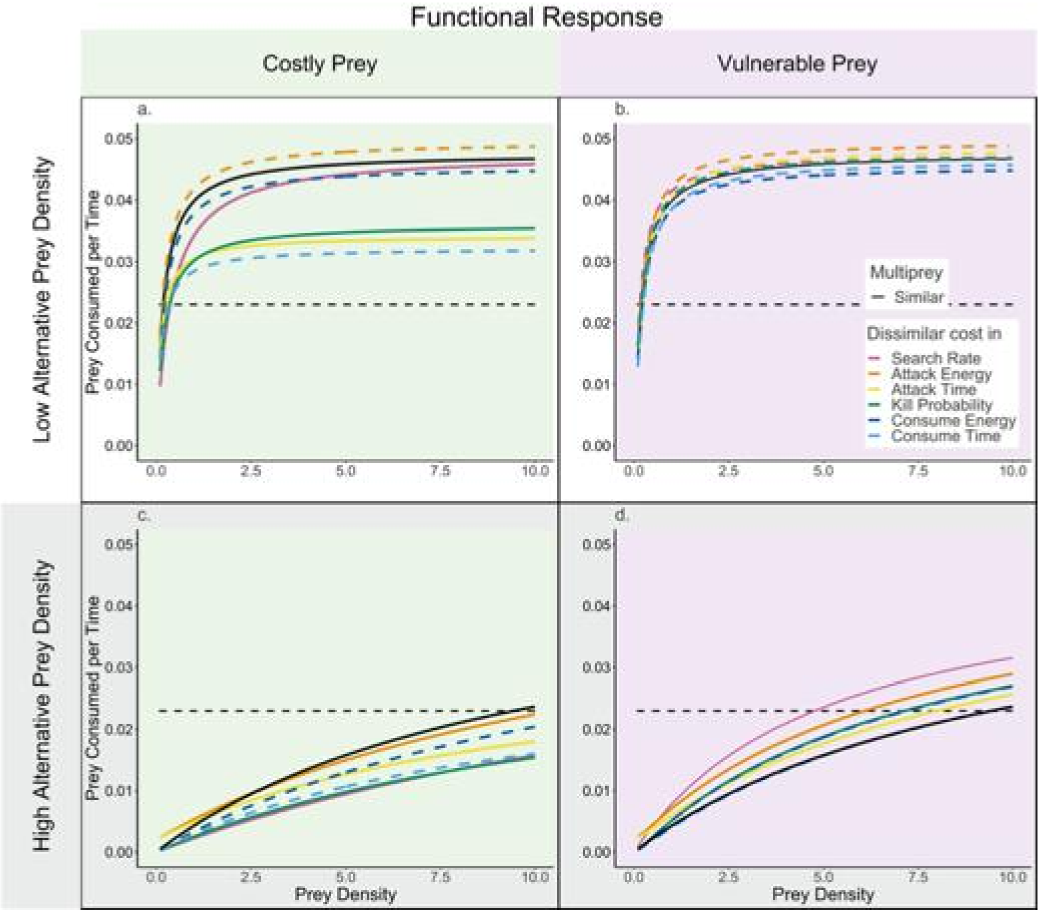

Fig S1. The functional response for a single predator in a two-prey system. The black functional response curve in all plots represents the 'Similar Prey' scenario where prey are identical in their foraging costs (baseline value of **attack time is 10 sec; see Table S1 and Table S2,** all other values are held constant with original baseline scenario). The coloured lines present 'Dissimilar Prey' scenarios where one prey is vulnerable and one is costly. Functional responses for the predator in relation to the density of costly prey is displayed in light green (left column, a & c) and vulnerable prey in light purple (right column, b & d) when the alternative prey is at a low density (top row with white frame, a & b) or high density (bottom row with grey frame, c & d). The grey dashed horizontal line indicates the half maximum consumption rate. Coloured dashed lines indicate there is overlap in the patterns generated from different scenarios.

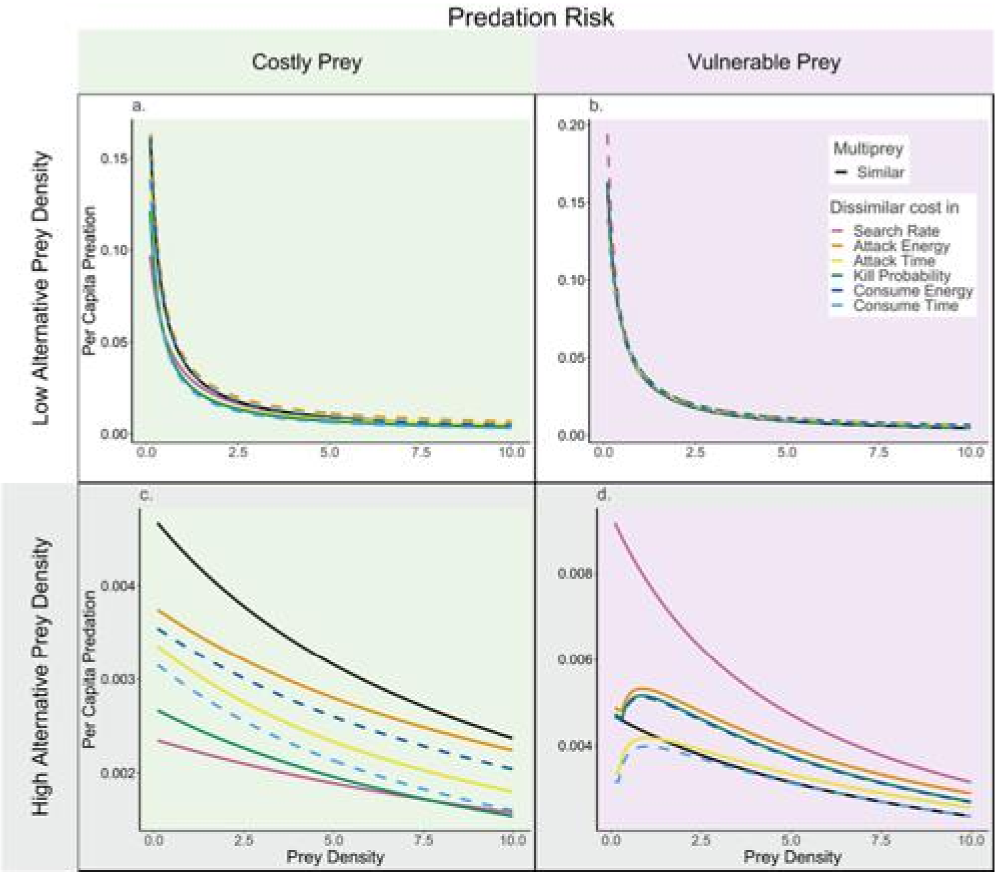

Fig S2. Predation risk as function of prey density. The black curves in all plots presents a scenario where prey are identical in their foraging costs (‘Similar Prey’ baseline values, **attack time is 10 sec; see Table S1 and S2**). The coloured lines are the ‘Dissimilar Prey’ scenarios where one prey is vulnerable and one is costly. Per capita predation risk for costly prey is displayed in light green (left column, a & c) and vulnerable prey in light purple (right column, b & d) when the alternative prey is at a low density (top row with white frame, a & b) or high density (bottom row with grey frame, c and d). The grey dashed horizontal line indicates the half maximum consumption rate. Coloured dashed lines indicate there is overlap in the patterns generated from different scenarios.

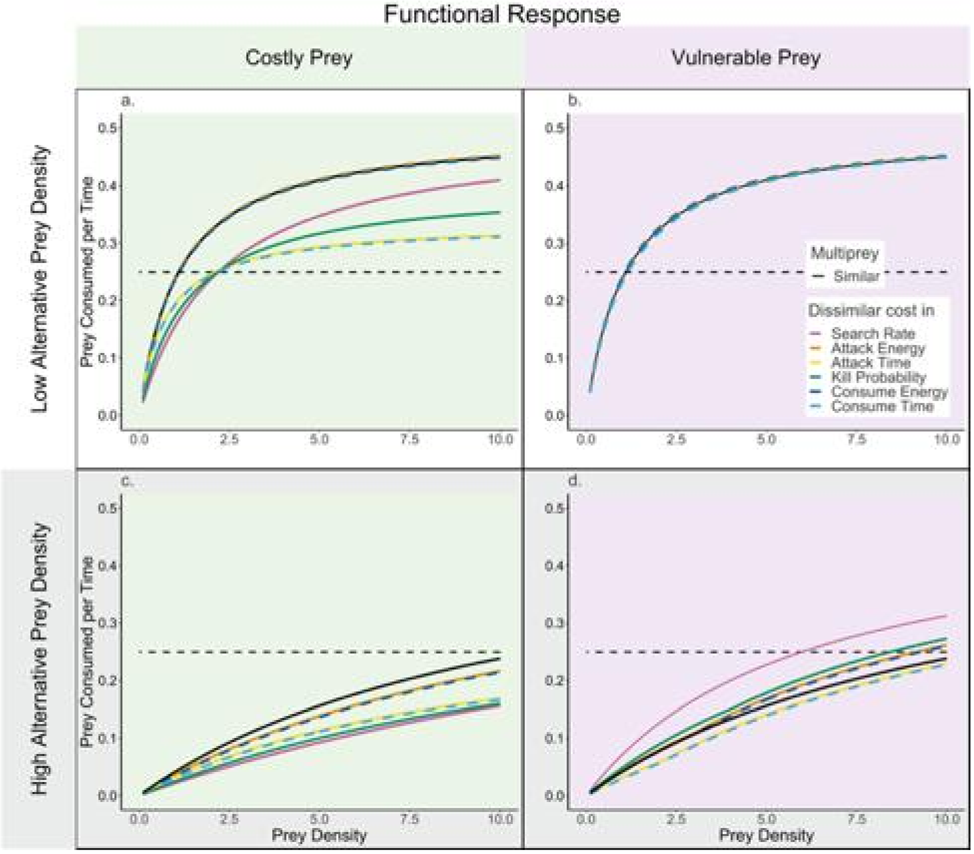

Fig S3. The functional response for a single predator in a two-prey system. The black functional response curve in all plots represents the 'Similar Prey' scenario where prey are identical in their foraging costs (baseline value of **attack time is 0.5 sec**; **see Table S1 and Table S2,** all other values are held constant with original baseline scenario). The coloured lines present 'Dissimilar Prey' scenarios where one prey is vulnerable and one is costly. Functional responses for the predator in relation to the density of costly prey is displayed in light green (left column, a & c) and vulnerable prey in light purple (right column, b & d) when the alternative prey is at a low density (top row with white frame, a & b) or high density (bottom row with grey frame, c & d). The grey dashed horizontal line indicates the half maximum consumption rate. Coloured dashed lines indicate there is overlap in the patterns generated from different scenarios.

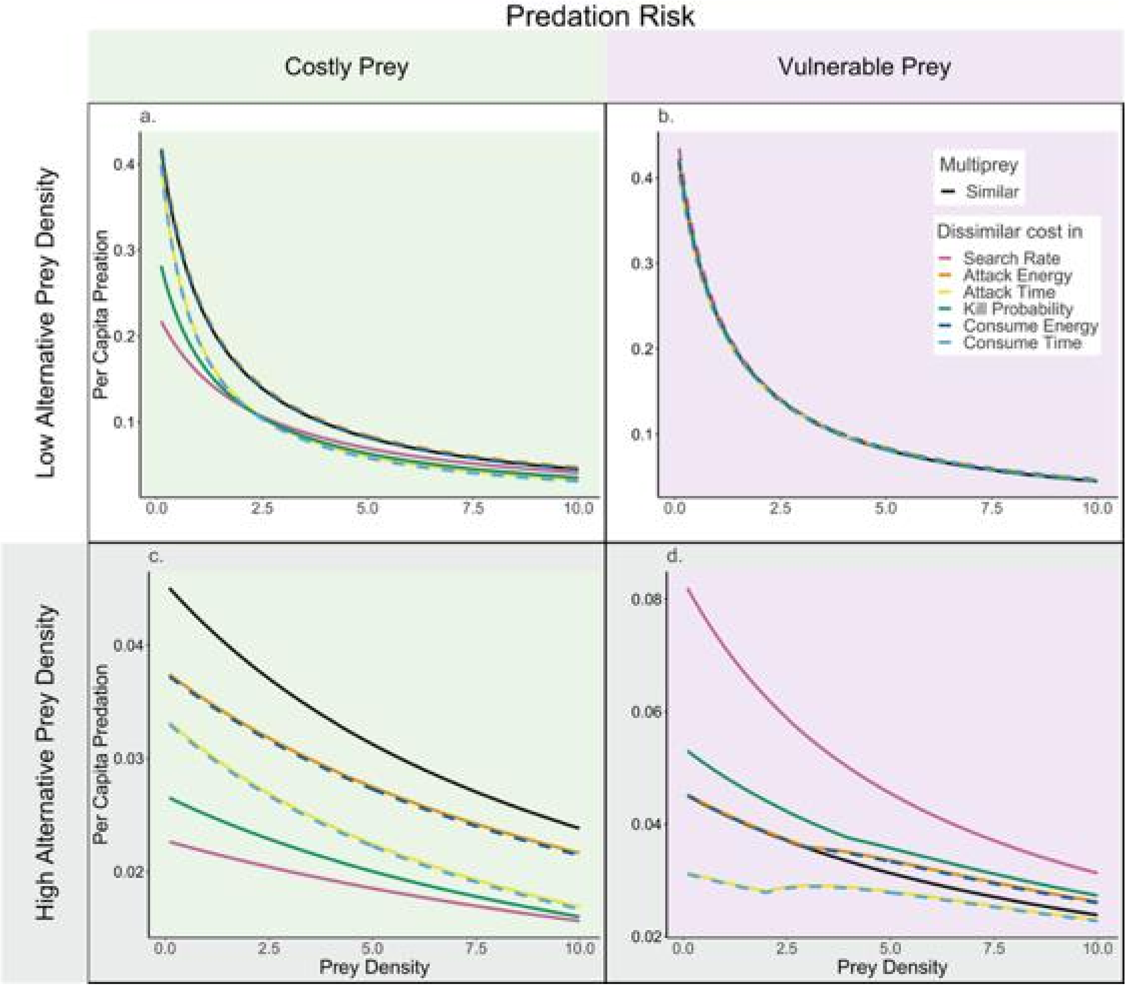

Fig S4. Predation risk as function of prey density. The black curve in all plots presents a scenario where prey are identical in their foraging costs (‘Similar Prey’ baseline values, **attack time is 0.5 sec; see Table S1 and S2**). The coloured lines are the ‘Dissimilar Prey’ scenarios where one prey is vulnerable and one is costly. Per capita predation risk for costly prey is displayed in light green (left column, a & c) and vulnerable prey in light purple (right column, b & d) when the alternative prey is at a low density (top row with white frame, a & b) or high density (bottom row with grey frame, c & d). The grey dashed horizontal line indicates the half maximum consumption rate. Coloured dashed lines indicate there is overlap in the patterns.

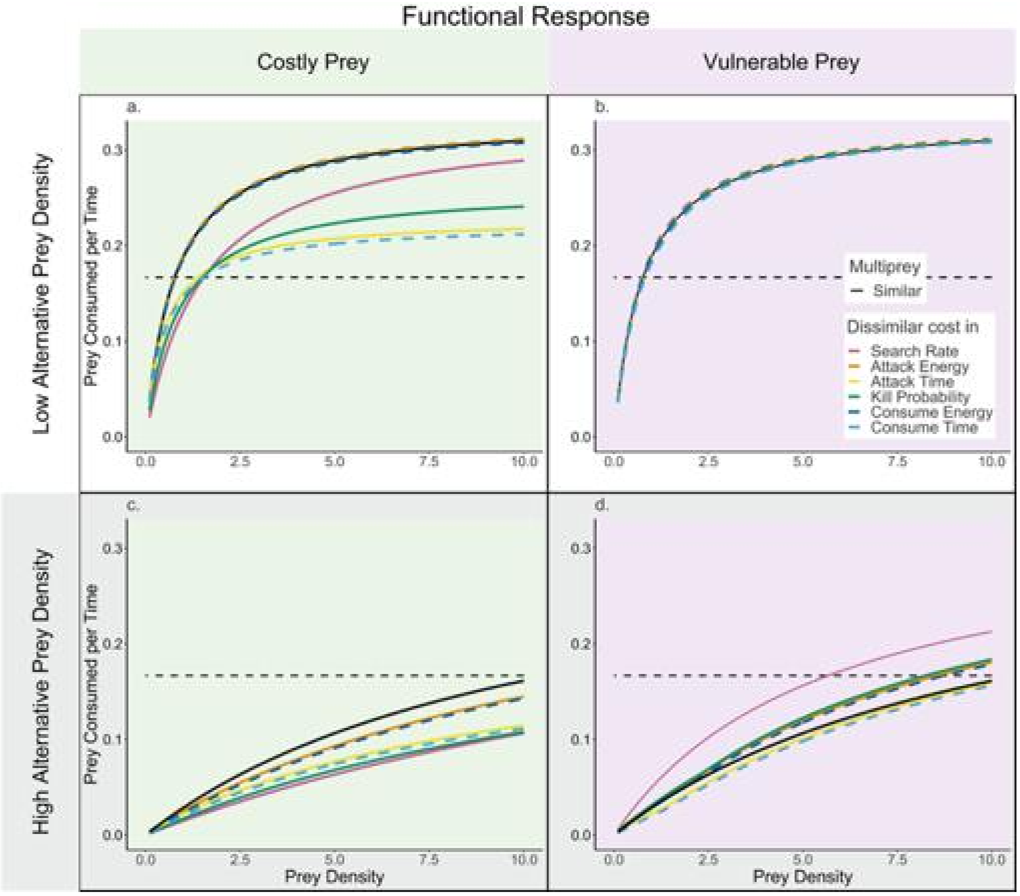

Fig S5. The functional response for a single predator in a two-prey system. The black functional response curve in all plots represents the 'Similar Prey' scenario where prey are identical in their foraging costs (baseline value of **attack energy expenditure rate is 10; see Table S1 and Table S2**). The coloured lines present 'Dissimilar Prey' scenarios where one prey is vulnerable and one is costly. Functional responses for the predator in relation to the density of costly prey is displayed in light green (left column, a & c) and vulnerable prey in light purple (right column, b & d) when the alternative prey is at a low density (top row with white frame, a & b) or high density (bottom row with grey frame, c & d). The grey dashed horizontal line indicates the half maximum consumption rate. Coloured dashed lines indicate there is overlap in the patterns generated from different scenarios.

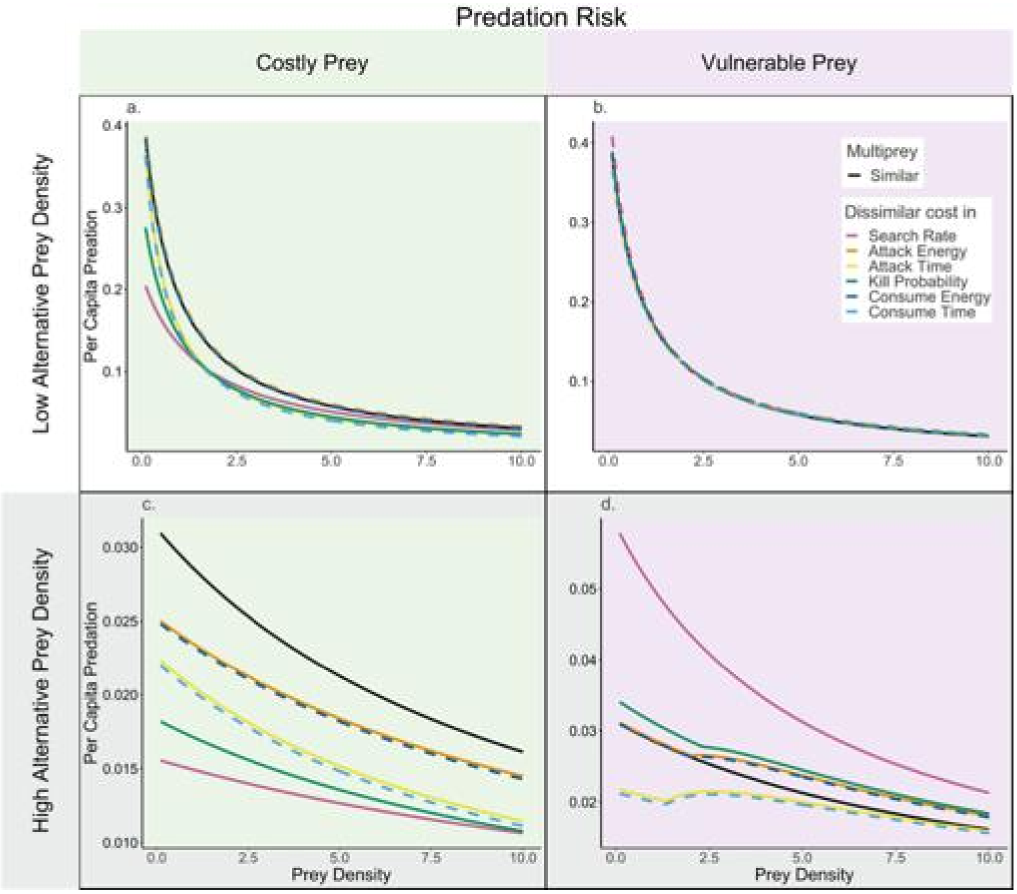

Fig S6. The functional response for a single predator in a two-prey system. The black functional response curve in all plots represents the ‘Similar Prey’ scenario where prey are identical in their costs (baseline value of **attack energy expenditure rate is 10 ; see Table S1 and Table S2,** all other values are held constant with original baseline scenario). The coloured lines present ‘Dissimilar Prey’ scenarios where one prey is vulnerable and the costly prey has elevated costs in either search rate, attack energy, attack time, kill probability, consume time, or consume energy. Functional responses for the predator in relation to the density of costly prey is displayed in light green (left column, a & c) and vulnerable prey in light purple (right column, b & d) when the alternative prey is at a low (top row with white frame, a & b) or high (bottom row with grey frame, c & d). The grey dashed horizontal line indicates the half maximum consumption rate. Coloured dashed lines indicate there is overlap in the patterns generated from different scenarios.

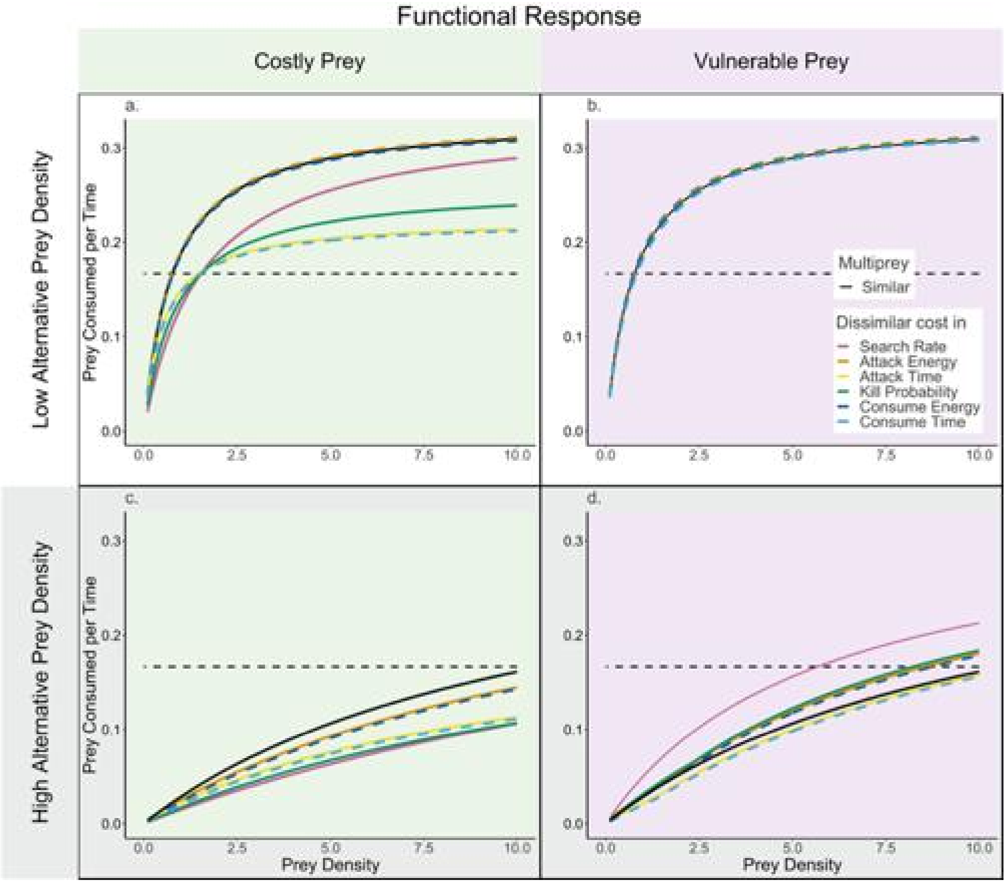

Fig S7. The functional response for a single predator in a two-prey system. The black functional response curve in all plots represents the 'Similar Prey' scenario where prey are identical in their foraging costs (baseline value of **attack energy expenditure rate is 0.5**; **see Table S1 and Table S2,** all other values are held constant with original baseline scenario). The coloured lines present 'Dissimilar Prey' scenarios where one prey is vulnerable and one is costly. Functional responses for the predator in relation to the density of costly prey is displayed in light green (left column, a & c) and vulnerable prey in light purple (right column, b & d) when the alternative prey is at a low density (top row with white frame, a & b) or high density (bottom row with grey frame, c & d). The grey dashed horizontal line indicates the half maximum consumption rate. Coloured dashed lines indicate there is overlap in the patterns generated from different scenarios.

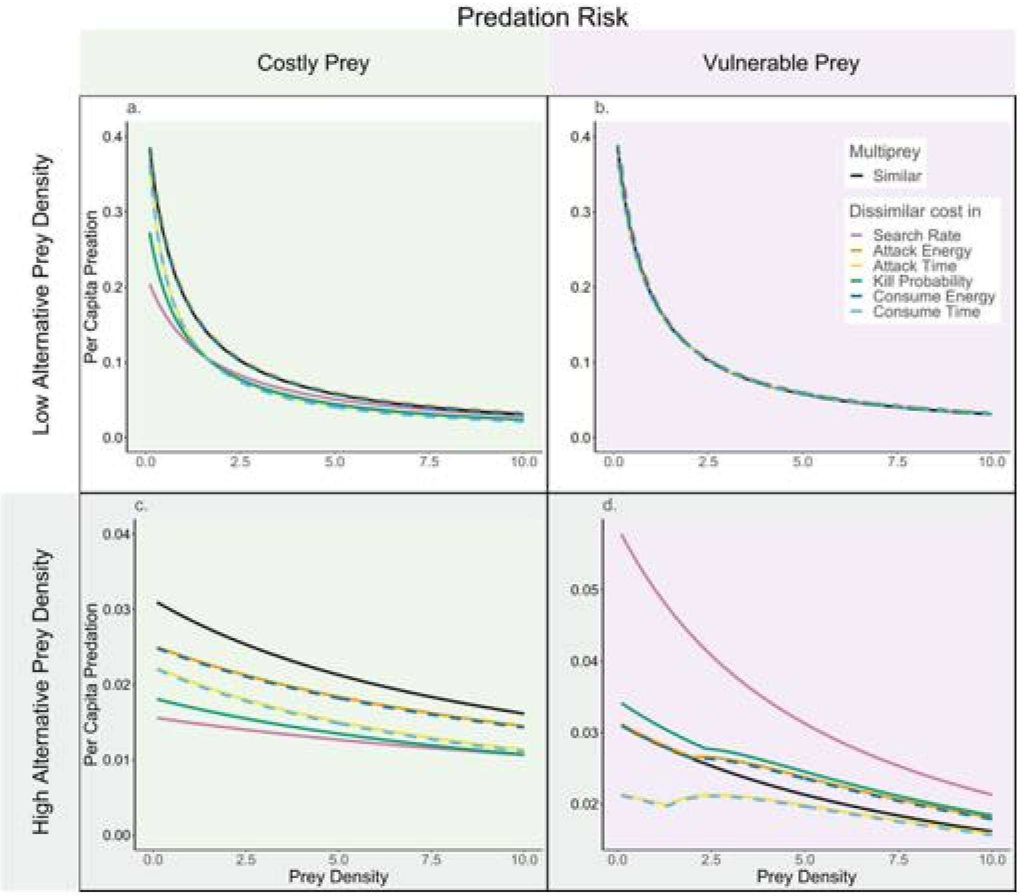

Fig S8 The functional response for a single predator in a two-prey system. The black functional response curve in all plots represents the 'Similar Prey' scenario where prey are identical in their foraging costs (baseline value of **attack energy expenditure rate is 0.5 ; see Table S1 and Table S2,** all other values are held constant with original baseline scenario). The coloured lines present 'Dissimilar Prey' scenarios where one prey is vulnerable and one is costly. Functional responses for the predator in relation to the density of costly prey is displayed in light green (left column, a & c) and vulnerable prey in light purple (right column, b & d) when the alternative prey is at a low density (top row with white frame, a & b) or high density (bottom row with grey frame, c & d). The grey dashed horizontal line indicates the half maximum consumption rate. Coloured dashed lines indicate there is overlap in the patterns generated from different scenarios.

A4.S4 Single Prey System Results And Multiprey System Predation Rates

Foraging costs reduce energy and prey consumed by the predator over time

In a single prey system, as prey become more costly to the predator, the predator's energetic consumption rate is reduced (Fig. S1). Our results suggest the most effective reduction of energy gain rate a prey can create (*i.e.* the smallest change in the baseline required for a 100% increase in $N_{0.5}$) occurs when antipredator traits induced foraging costs reduce the kill probability. In addition, increased attack and consumption time, and decreased search rate also reduced energy gain rates effectively. Finally, energy to attack or consume had the lowest magnitude of the effect (Fig. S1 b). Increased time to attack and consume (*i.e.* handling time) has the greatest effect on prey- and energetic-consumption rates in a single prey system where the prey has developed antipredator trait induced foraging costs, 'Single Costly' scenario (Fig. S1 c & d). Prey may benefit from becoming more costly even when they are the sole resource available to their predator, but the magnitude of these benefits depends on the phase of the predation sequence that these costs are most strongly influencing. In real systems, prey's net benefits will depend on the associated fitness cost creating foraging costs (*e.g.* a prey may become more costly to the predator at the expanse of expending more energy or acquiring less). Such costs, often termed 'non-consumptive effect', are beyond the scope of the current investigation (we refer the keen reader to the burgeoning literature about this topic, *e.g.* (Preisser et al. 2007, Abrams 2008, Peacor et al. 2013a).

Through this Single Prey model, we compared two related response variables: the number of prey consumed over time, and energy consumed over time. Prey individuals are just one of the units in which energy is packaged, and this approach can be used to quantify the transfer of energy between predator and prey. Prey individuals lost per unit time is often a critical measure of predator prey interactions and related management interventions (Alston et al. 2019a)). However, we demonstrate prey numbers and energy transfers may not always be correlated. We observed that energy consumption rates decline during attack and consumption, but the number of prey consumed over time do not decrease (Fig. S1c). Underlying the trade-off between ‘single large’ and ‘several small’ foraging strategies by predators is the energy provided by prey to predators includes the costs of successfully capturing prey. This provides a plausible explanation to the observed dominance of smaller prey in the diet of wild dogs – even when larger prey are available and abundant (Woodroffe et al. 2007). As we expand to multiprey systems, we should keep in mind our findings in single prey system, particularly the importance of considering prey consumption rates in energetic units.

MULTIPREY SYSTEM

Predation risk is influenced by focal prey density, alternative prey density, and the foraging cost dissimilarities between them

The predation risk experienced by an individual prey is an important component of fitness, and therefore evolutionary, demographic and behavioral process (Peacor and Werner 2001, Groenewoud et al. 2016, Prugh et al. 2019). From the prey’s perspective, the per capita predation risk decays with increasing prey density so long as predator density and efficiency is constant (Fig. S2). This generates the predation risk dilution effect that is the impetus for prey aggregation and predator swamping associated with synchronous births (Lehtonen and Jaatinen 2016). Our findings of predation risk patterns follow those observed for the functional responses; both are modified by variations in prey cost and prey density. The presence of an alternative prey reduces predation risk for both prey species if they are similar in costs (Fig. S2). Among dissimilar prey, predation risk is reduced for costly prey, especially if the alternative prey is both more vulnerable and abundant. Naturally, predation risk is higher for more vulnerable prey compared to costly prey and risk decreases with decreasing vulnerability (vulnerability can be age-dependent and species-specific; (Lingle et al. 2008).

Arising from the Type III functional response for vulnerable prey when costly prey is abundant, we see an acceleration in predation risk of vulnerable prey with increasing density of vulnerable prey. Thus, we demonstrate emerging prey-switching patterns driven by optimal foraging decisions (Fig. S2 d). Compared to the ‘Similar Prey’ scenario, the predation risk for vulnerable prey is elevated when the costly prey increases predator search rate, *e.g,* by being camouflaged. In contrast, we show vulnerable prey benefit from an increase in the time required to consume costly prey. Therefore, predation rates depend on the costs and densities of all prey present. The effect of cost dissimilarity between prey on predation rates was documented in a Kenyan savanna system, where lions preference for prey body size (Hayward and Kerley 2005) corresponded with the predation rates of prey. For example, buffalo, zebra, and hartebeest exist on a continuum from most costly and least vulnerable to least costly and most vulnerable. The buffalo were shown to experience reduced predation when zebra were present, but zebra acted to increase hartebeest predation (Ng’weno et al. 2019a).

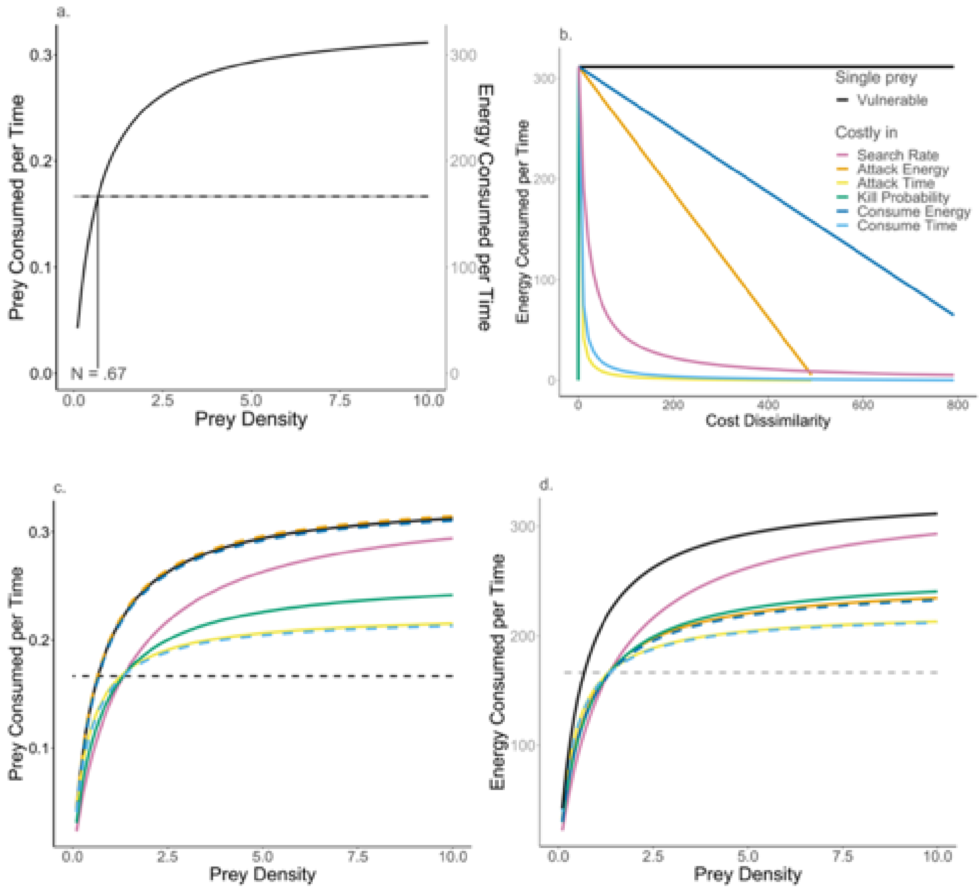

Fig. S1. Consumption rates of a predator consuming a single prey species expressed in units of prey over time or energy over time. The 'Single Vulnerable' scenario sets an important baseline for comparison to other single and multiprey examples (a). A prey is considered vulnerable to predation when there is not an increase in the time or energy investment from basal values. The grey dashed horizontal line indicates the halfway mark of the maximum consumption rate. In the 'Single Costly' scenarios. As costs increase, the amount of energy a predator can consume over time is reduced (b). 'Cost dissimilarity' is the relative change in time or energy cost compared to the baseline cost values. The intersection of these relationships with the grey dashed horizontal line indicate the cost value that reduces the consumption rate to half its maximum value when prey density is doubled (Appendix S3). These cost values are used to display the functional response of a predator consuming a single prey in units of prey (c) or energy (d). Coloured dashed lines indicate there is overlap in the patterns generated from different scenarios

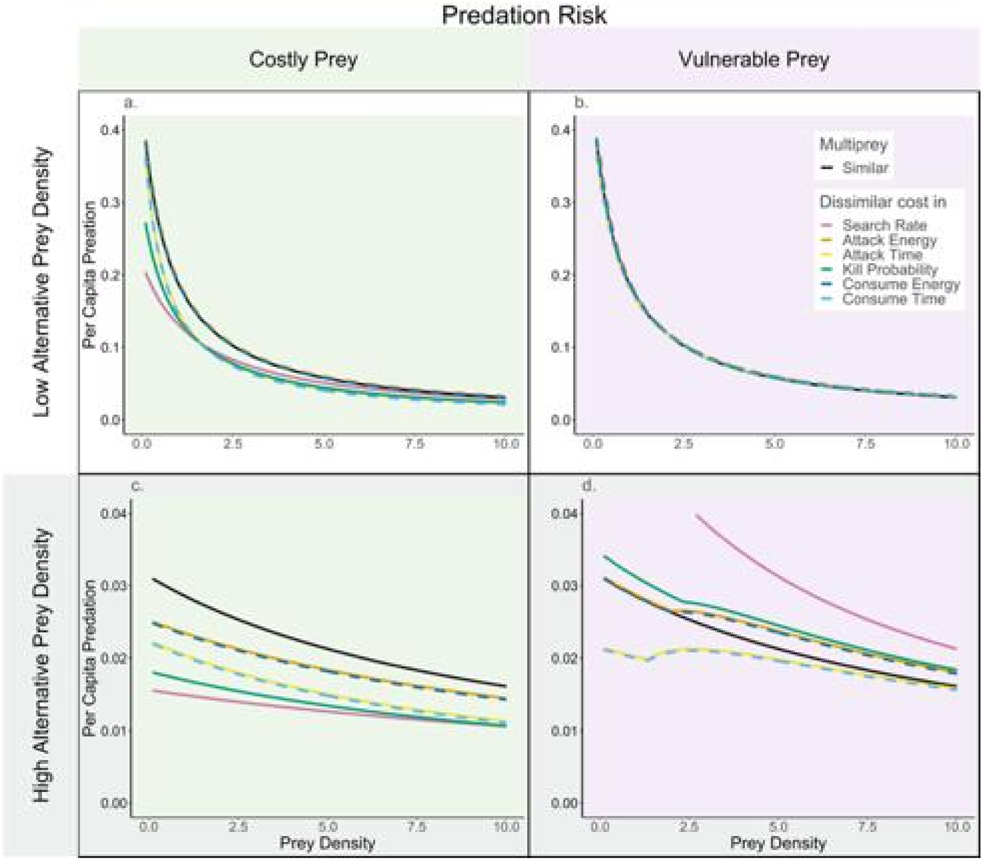

Fig. S2. Predation risk as function of prey density. The black curve in all plots presents a scenario where prey are identical in their costs (‘Similar Prey’ baseline values). The coloured lines are the ‘Dissimilar Prey’ scenarios where one prey is vulnerable and the costly prey has elevated costs incurred at one phase: search rate, attack energy, attack time, kill probability, consumption time, or consumption energy. Per capita predation risk for costly prey is displayed in light green (left column, a & c) and vulnerable prey in light purple (right column, b & d) when the alternative prey is at a low (top row with white frame, a & b) or high (bottom row with grey frame, c and d). The grey dashed horizontal line indicates the half maximum consumption rate. Coloured dashed lines indicate there is overlap in the patterns generated from different scenarios.

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A4.S5 ADDITIONAL ENERGETIC FUNCTIONAL RESPONSE FIGURES

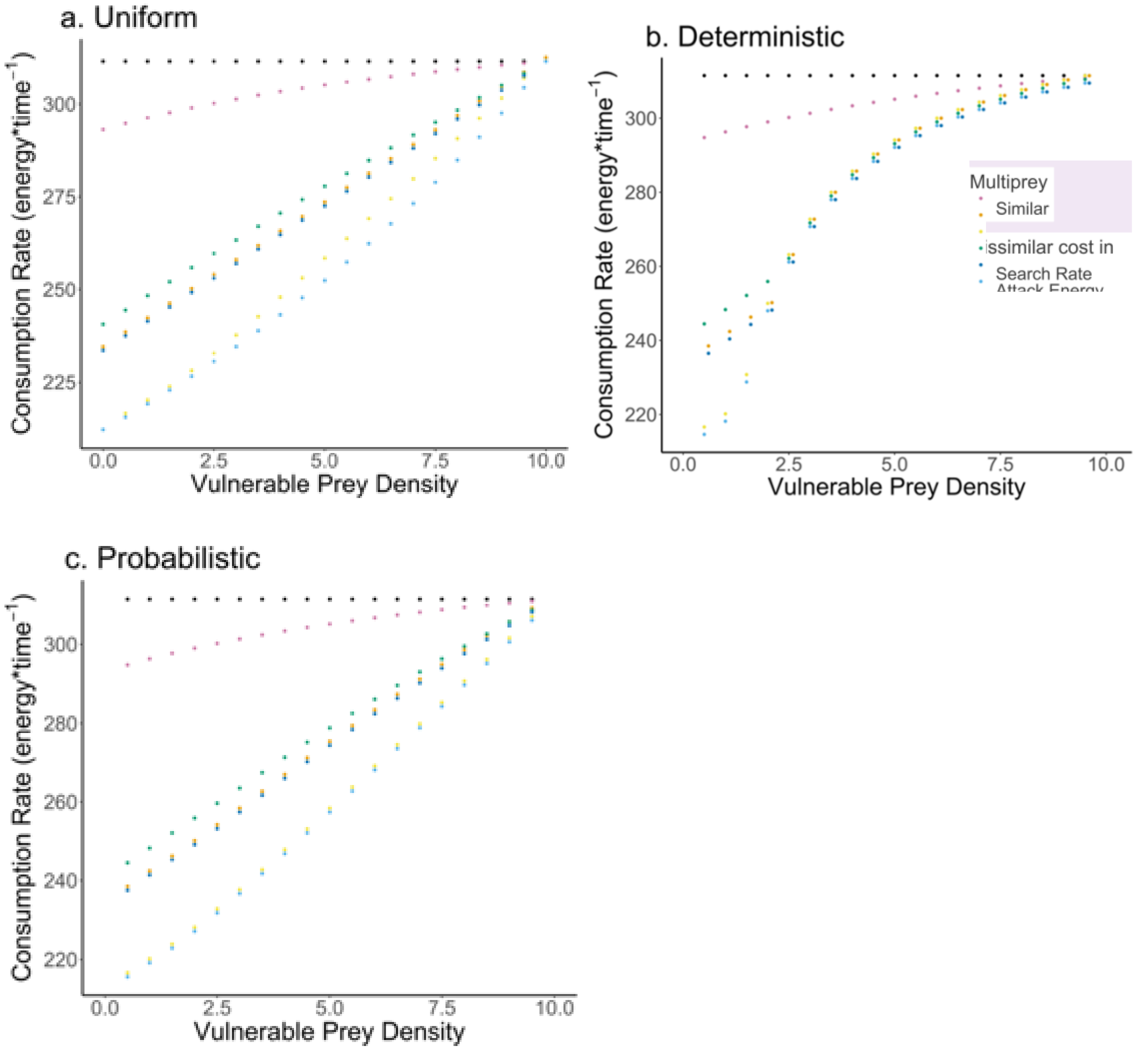

Fig. S1 Comparison of total energetic consumption rates from both prey of the predator when probability of engagement is a) uniform at 1, meaning a predator always engages with the encountered prey, b) deterministic where a predator engages only if the expected gain rate is maximized and abandons otherwise, and c) probabilistic, where a predator always engages with the most profitable prey but abandons following a probability described by the relative gain rates, given by eqn 4. Energetic consumption when prey density is kept at 10 and the composition of two types changes, as vulnerable prey increases costly prey decreases. The black dots represent a scenario where the prey types do not differ in their costs.

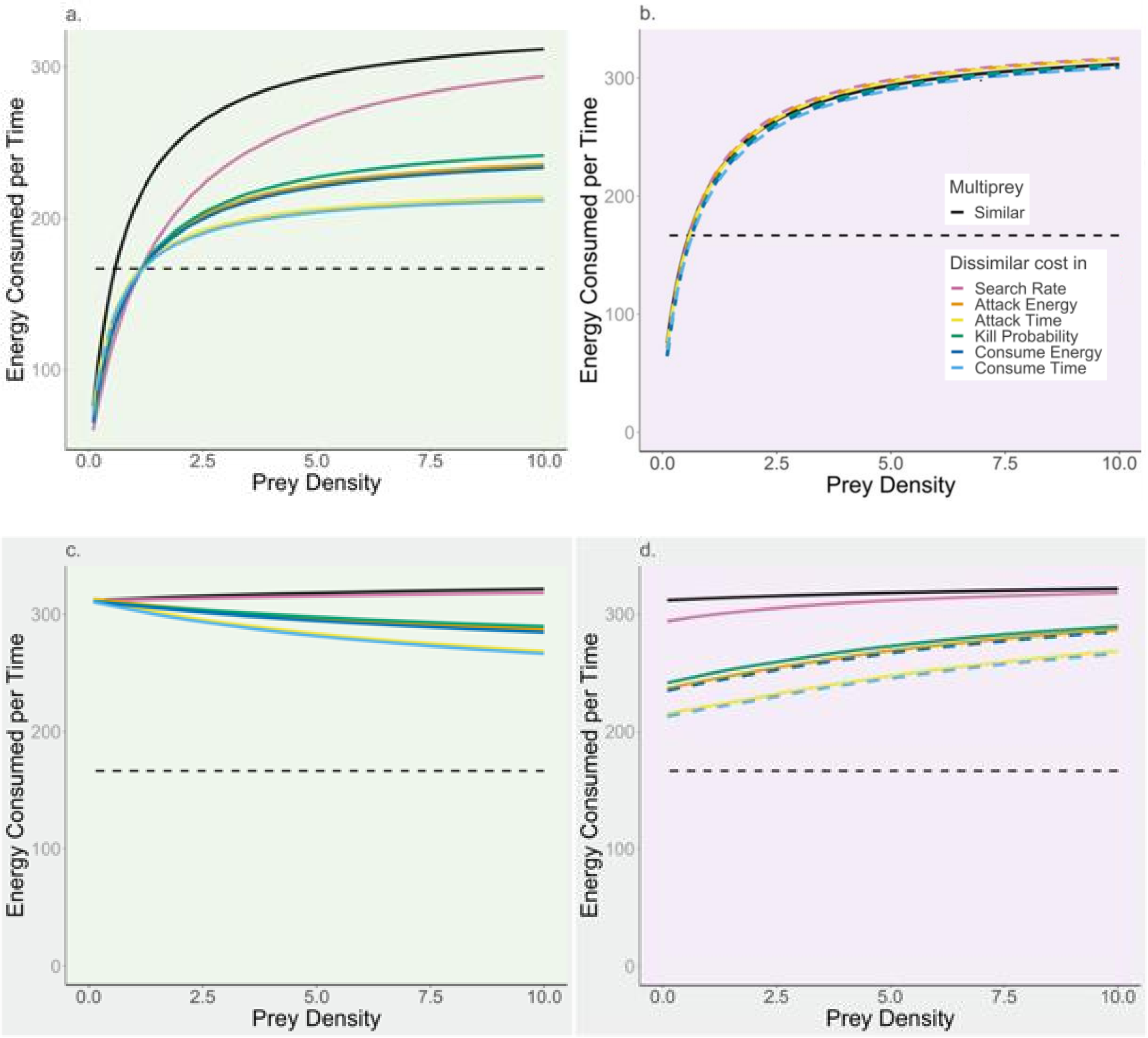

Fig. S2 – The energetic functional response for a single predator in a two-prey system (energy per unit time presentation of Fig. 2 in the main text). The black curve in all plots presents a scenario where prey are identical in their foraging costs (baseline values). The coloured lines present scenarios where one prey is vulnerable and is costly. Energetic functional responses for the predator in relation to the density of costly prey is displayed in light green (left column, a and c) and vulnerable prey in light purple (right column, b and d) when the alternative prey is at a low density (top row with white frame, a and b) or high density (bottom row with grey frame, c and d). The grey dashed horizontal line indicates the half maximum consumption rate. Coloured dashed lines indicate there is overlap in the patterns generated from different scenarios.

APPENDIX 5: SUPPORTING INFORMATION FOR CHAPTER 5

A5. S1 WILDLIFE SURVEYS, WOLF DIET, AND MODEL PREDICTIONS

Table S1. Prey abundance, wolf number, area for study periods and packs. Pack territories were the 100% convex polygons from January-March.

	Elk Abundance	**Moose Abundance**	**Wolf Abundance**	**Area (km^2)**
Study Period				
1978-1979	5210	3752	66	2974
1982-1985	4524	3025	66	2974
1982-1984	3866	2775	59	2974
2001-2003	4156	3065.333333	59	2974
2016-2017	2904.24888	3455.124545	66	2974
Packs				
AD	266	612	5	213.6
BD	52	192.25	10	151.6
BL	34.25	649	4	189.4
BT	99	300.75	7	314.9
GL	263.75	907.5	5	385.7
RC	20	305.75	2	287.8
WW	154.75	367	7	261.0

Table S2. Biomass values for prey from Carbyn 1980.

Prey	**Weight (kg)**
Elk	247
Moose	302
Deer	64
Elk calf	30
Moose calf	58
Deer fawn	20
Beaver	12.5
Hare	1.5

Table S3. Wolf predation estimates from the literature and our study to inform model parameters in the optimal prey switching model. Estimates of probability of kill and handling time. Bolded and highlighted values were used in the predictive model.

Prey	Location	Kill Rate	Attack Rate	Probability of Engagement	Probability of Kill (% success)	Handling Time	Citation
Elk	YNP	.61 elk/day/wolf				16.39 days/wolf/elk	(Smith et al. 2004)
	Banff	0.6 - 0.17 elk/day/pack					(Hebblewhite and Pletscher 2002)
	YNP				**21**		(Mech et al. 2001)
	RMNP					**3.8 days/pack/elk**	
Moose	IRNP		0.00067 - 0.0127 attacks/day				(Jost et al. 2005)

Yukon	0.045 moose/day/ wolf			2.9 days /moose 2.6 days/calf-moose (winter)	(Hayes et al. 2000)
Denali, AK			**19-38**		(Mech 2003)
RMNP				**6.5 days/pack/ moose**	

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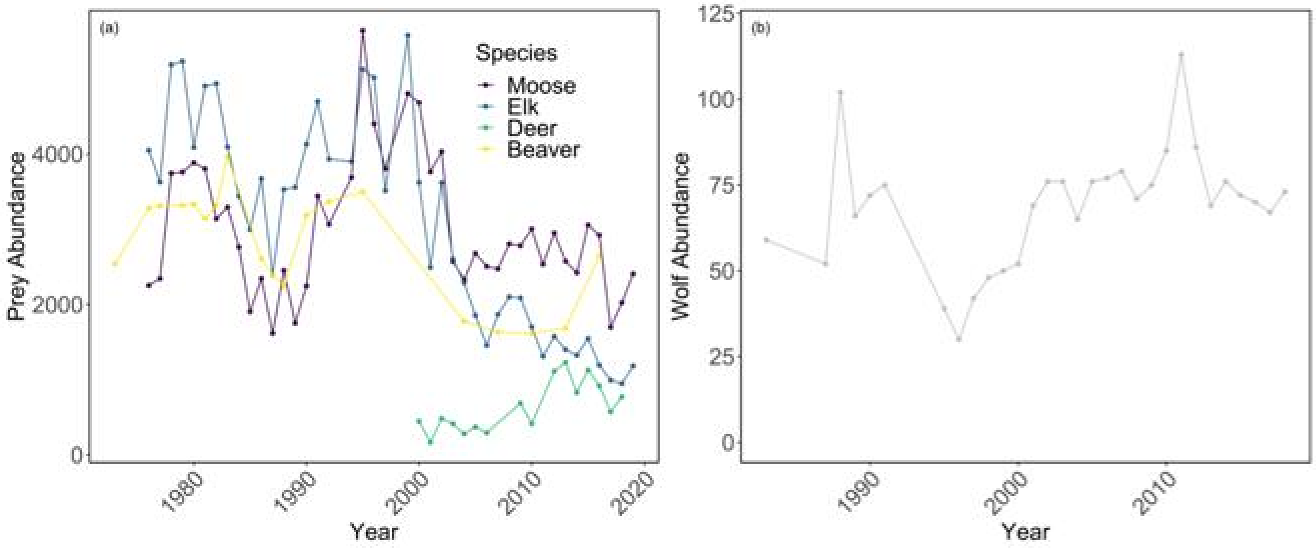

FigureS1. (a) Prey abundance and (b) wolf abundance in Riding Mountain National Park.

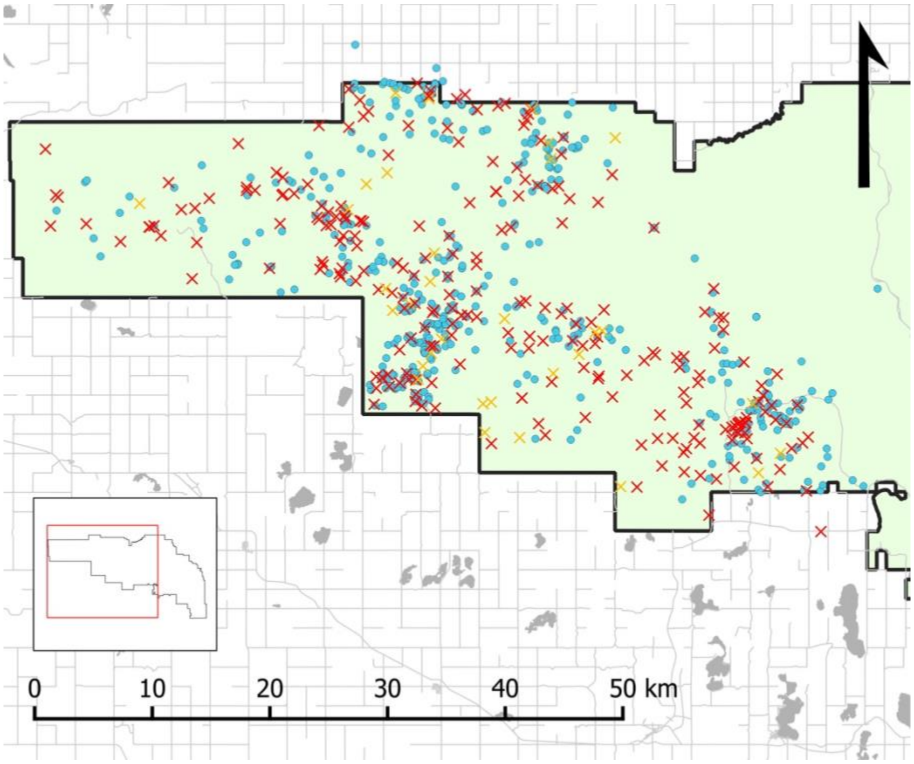

Figure S2. Site investigation locations from the 2016 - 2017 study period in Riding Mountain National Park and the spatial range of sites by each pack. Scat was collected whenever present at the site, including kill sites denoted by red 'X', probable kill in orange, all others sites are blue dots.

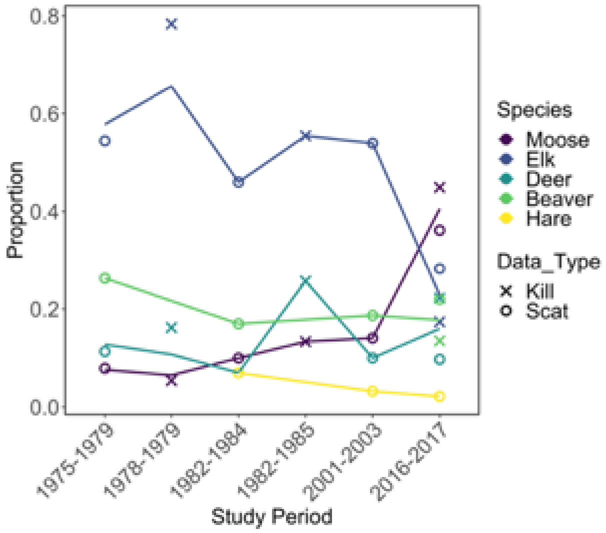

Figure S3. Proportion of prey in wolf diet assessed through kill site investigation or scat analysis across studies conducted in Riding Mountain National Park beginning in 1975 until the most recent study in 2016-17.

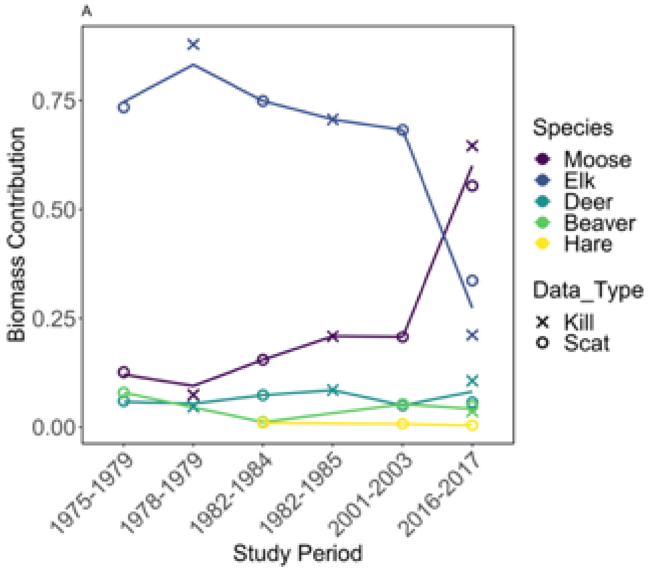

Figure S4. Biomass contribution of prey in wolf diet assessed through kill site investigation or scat analysis across studies conducted in Riding Mountain National Park beginning in 1975 until the most recent study in 2016.

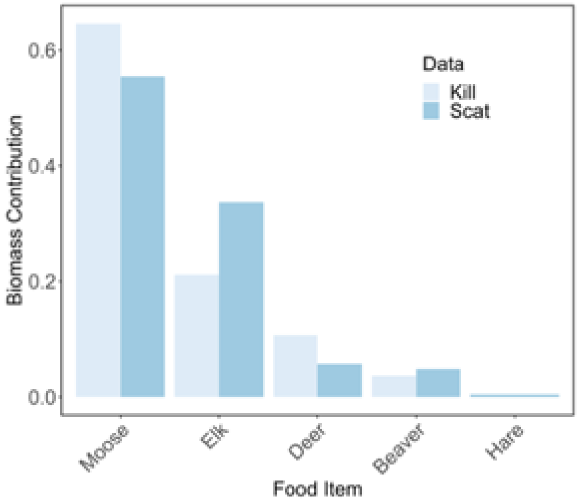

Figure S5. Biomass contribution for the top 5 prey species as determined from kill site investigation and scat sample analysis in the most recent wolf study conducted from January 2016 to January 2018.

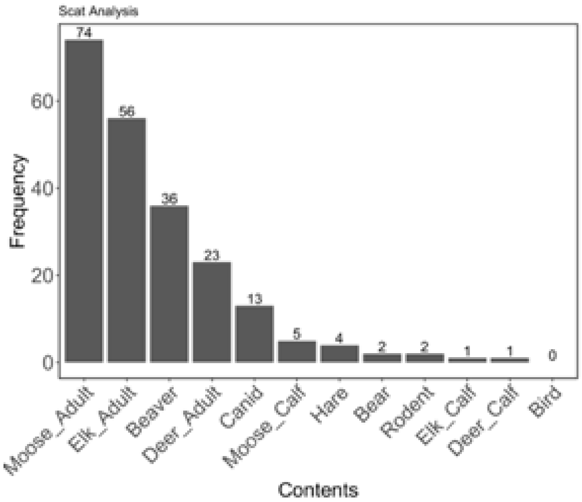

Figure S6. Frequency of occurrence of all contents observed in scat collected in the 2016-2017 study period. For the analysis in the main text data was reduced to not include canids (as it does not represent consumed food contents), group by species level (adults and calves), and only include one scat sample per site (the observation of bird was removed in this rule).

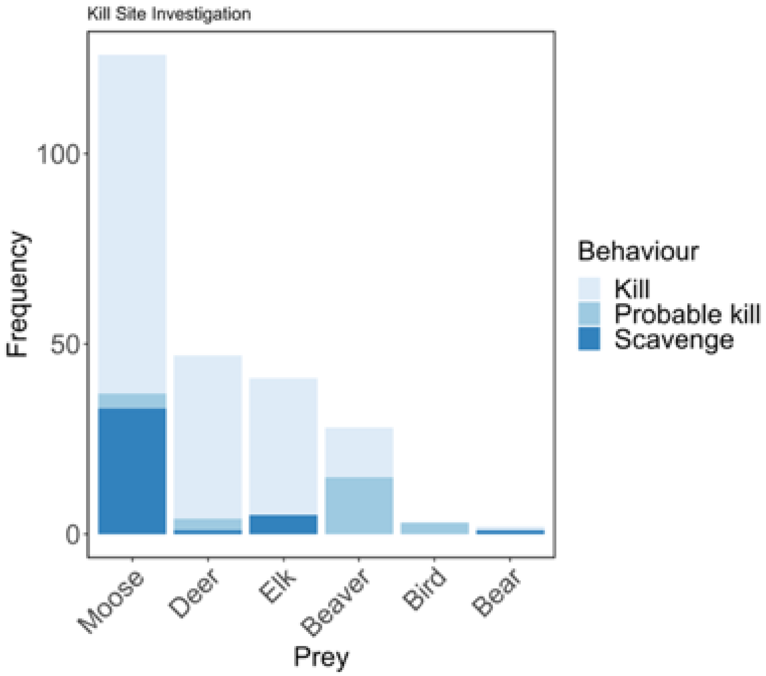

Figure S7. Frequency of prey occurring at sites investigated from January 2016 to January 2018. Kills were designated as sites with clear evidence, probable kill had prey and wolf sign, but minimal carcass evidence, scavenges were carcasses with wolf sign but lacked evidence of wolves being responsible for the mortality. Kills and probable kills were included in the main text figures and analysis as small prey were underrepresented in the 'Kill' designation.

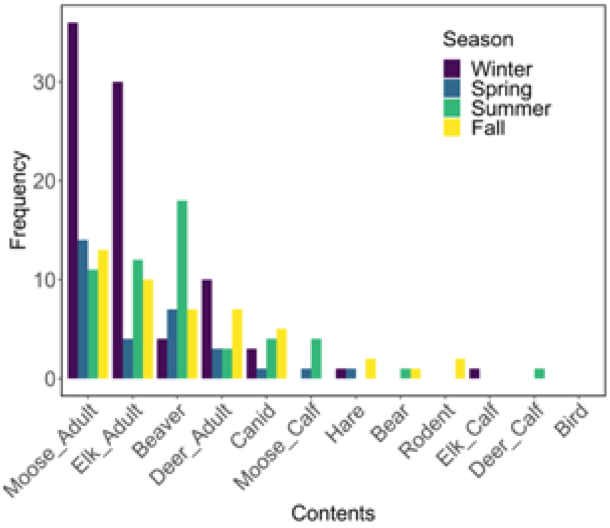

Figure S8. Frequency of occurrence of all contents in scat by season, using only one scat per site, and displaying adults and calves separately to display seasonal differences. Species' age classes were grouped for analyses in the main text. Season designations were Winter: January to March, Spring: April to June, Summer: July to September, Fall: October to December.

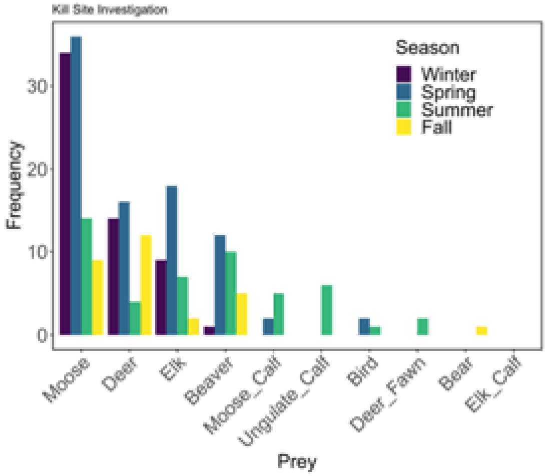

Figure S9. Frequency of occurrence of all prey at kill sites and probable kill sites, adults and calves plotted separately to display seasonal differences. Species' age classes were grouped for analyses in the main text. Season designations were Winter: January to March, Spring: April to June, Summer: July to September, Fall: October to December.

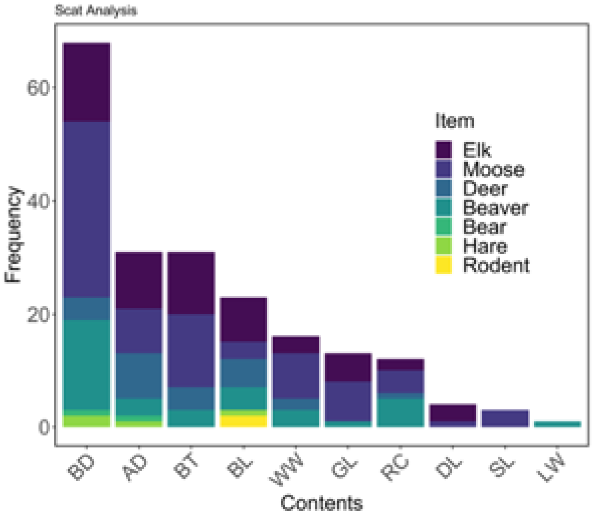

Figure S10. Frequency scat collected per pack by contents for the reduced data, grouped by species level, and with only one scat per site. Packs with under 10 samples were removed from the main text analysis: Deep Lake (DL), Spruce Lake (SL), and Lone Wolf (LW).

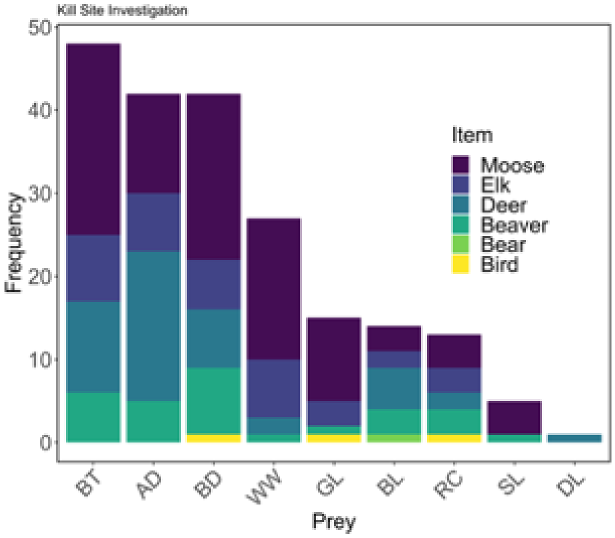

Figure S11. Frequency of prey occurring at kills and probable kills for each wolf pack studied in 2016-17. Packs with under 10 sites were removed from the main text analysis: Deep Lake (DL) and Spruce Lake (SL).

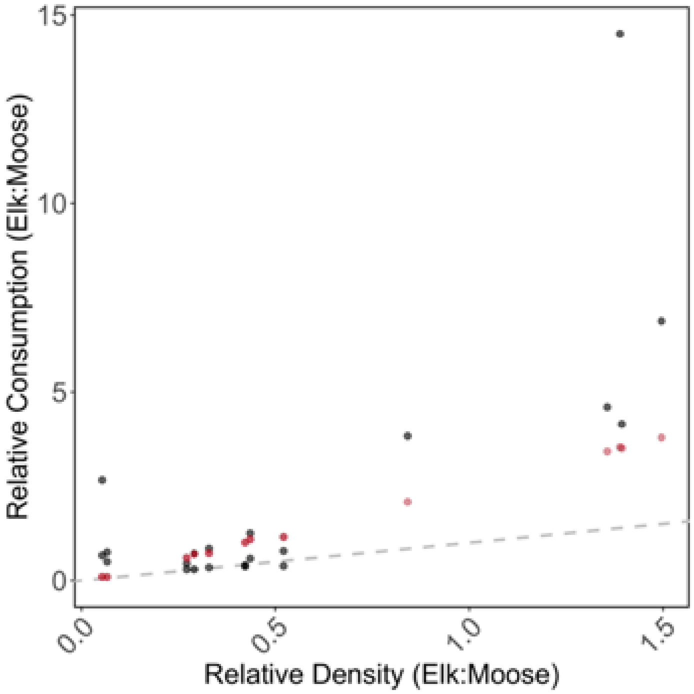

Figure S12. The relative consumption of elk to moose compared to the relative density. Observed consumption rates determined through wolf studies conducted in Riding Mountain National Park from 1975 to 2017 are in black, the predicted consumption rates using the optimal prey switching model are in red. The dashed line is a 1:1 relationship between relative consumption rates and relative density, in this instance wolves are consuming prey in proportion to their availability and have no preference. The top left corner of the plot indicates a preference for elk, while the bottom right corner indicates a preference for moose. The correlation between observations and predictions is 0.71.