

Window of opportunity: examining gray wolf (*Canis lupus*) diets and seasonal patterns of predation on wood bison (*Bison bison athabascae*)

by

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Abstract

Prey selection by predators is a complex process, with acquisition strategies varying between generalists and specialists. However, generalist predators like wolves (*Canis lupus* Linnaeus, 1758), can select prey in response to increases in abundance or vulnerability of the prey, often influenced by environmental conditions. In multi-prey systems that include bison (*Bison bison* Linnaeus, 1758), this is not always the case, as wolves will often select less dangerous prey. To investigate the predator-prey relationship between wolves and a small (~275 – 300 individuals) *Threatened* herd of wood bison (*Bison bison athabascae* Linnaeus, 1758) in northeast Alberta, Canada, I monitored location data from global positioning system (GPS) collars affixed to both species for one year. I evaluated seasonal differences in wolf diet, the effect of temporal variables on relative bison predation risk by wolves, and space use relative to bison for three wolf packs whose territories overlapped with the bison herd's home range. I used wolf GPS collar data to find and investigate wolf location cluster sites for prey remains and collected wolf scat to assess seasonal diets. I used consecutive winter days as a measure of winter duration along with daily measures of temperature and snow depth to assess how relative bison predation risk changes through the winter season. Further, I assessed seasonal differences in wolf movements relative to bison to decipher whether wolves were opportunistically preying on bison or actively selecting for them during times of greater bison vulnerability. Seasonal changes in prey selection from beaver (*Castor canadensis* Kuhl, 1820) in summer (77%) to cervids (white-tailed deer (*Odocoileus virginianus* Zimmerman, 1780) and moose (*Alces alces* Linnaeus, 1758)) in winter (70%) was consistent with other boreal systems. Wolves began preying on wood bison later in winter when snow depths exceeded 30 cm. While wolves were within the bison range, they spent significantly more time in areas highly frequented by bison in late winter relative to early winter. This suggests that wood bison predation risk is higher with longer winter durations

and deeper snow depths that make them more vulnerable, and wolves respond to the vulnerability of this profitable, but rarely obtainable prey source.

Preface

This thesis is the original work of Lindsey Dewart. The objective of this thesis is to investigate the top-down influence of wolf predation on the Ronald Lake wood bison herd in northeast Alberta, Canada. I formed the specific questions, study design and funding proposals, and led on wolf collaring, field data collection, laboratory work, data analysis, and manuscript composition. Scott E. Nielsen and Mark A. Edwards contributed to the concept formation, study design, securement of funds, supported collaring work, data analysis, and thesis edits. Lu N. Carbyn contributed to concept formation and study design.

Dedication

This dissertation is dedicated to my gido, William Peter Triska (1926 – 2011).

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Introduction

Populations are regulated by either limitation in bottom-up food availability (White 1978), top-down forces such as predation (Hairston et al. 1960), or a combination of the two (Sinclair and Norton-Griffiths 1979; Power 1992). Estimating diet is the first step of identifying where, when, and how a species acquires their food resources and determining associated limitations (Robbins 1983; Hunter and Price 1992). Insights into a species diet provides a foundation for understanding behaviours and habitat needs, which are necessary for developing effective strategies for managing populations (Robbins 1983; Sutherland 1998). For carnivores, determining their diet is essential to understanding their role in the ecosystem and their impacts on prey populations (Mills 1996; Klare et al. 2011). Insights into the diets and factors influencing prey selection by predators can improve management plans and inform conservation efforts for prey species (Sinclair et al. 1998; Wittmer et al. 2005; le Roux et al. 2019).

In multi-prey systems, predators are limited to a suite of prey types based on relative prey size, abundance, and vulnerability (Karanth and Sunquist 1995; Patterson et al. 1998; Sand et al. 2016). Prey acquisition strategies vary between generalists, like red fox (*Vulpes vulpes* Linnaeus, 1758) that prey on many different species (Lindstrom 1983; Dell'Arte et al. 2007), and specialists with high fidelity toward a specific prey type (Murdoch 1969; Andersson and Erlinge 1977), such as lynx (*Lynx canadensis* Kerr, 1792) and snowshoe hare (*Lepus americanus*) (Elton and Nicholson 1942) or ermine (*Mustela erminea* Linnaeus, 1758) and meadow vole (*Microtus pennsylvanicus*) (Simms 1979; King and Powell 1990). These prey acquisition strategies are frequently represented by the spatial distribution of predators relative to the spatial availability of their prey sources (Sih 2005). Generalist predators with a more diverse diet, often described as

opportunistic predators, use a wider array of habitat types to exploit resources according to their availability (Wimp et al. 2019). Alternatively, specialist predators often target a specific prey type despite their availability relative to other prey types, and exhibit spatial distributions more closely aligned with the habitat of their preferred prey (Sih 2005; Kauffman et al. 2007; Kittle et al. 2017).

The North American grey wolf (*Canis lupus* Linnaeus, 1758) is a widespread carnivore commonly thought of as a generalist predator with a diverse diet that uses a variety of strategies for encountering and capturing their prey. However, in some systems wolves can exhibit more targeted prey selection behaviour and use their territory according to the spatial distribution of their preferred prey (Kauffman et al. 2007; Kittle et al. 2017). Predators may increase encounter rates with a preferred prey by altering their space use patterns to increase spatial overlap with that prey (Sih 2005, Williams & Flaxman 2012, Kittle et al. 2017). Bergman et al. (2006) found that elk (*Cervus canadensis*) and bison (*Bison bison* Linnaeus, 1758) densities had a weak effect on where wolves travelled and made kills, but wolves instead showed strong selection for their prey's preferred habitat. Bergman et al. (2006) also found little evidence that wolf kill sites differed from regular travel routes, suggesting that elk vulnerability influenced where wolves selected to travel.

Wolf prey selection is affected by a variety of factors including prey accessibility (Smith et al. 2000; Jaffe 2001; Shave et al. 2020), density (Garrott et al. 2007; Sand et al. 2016), vulnerability (Peterson and Allen 1974; Becker et al. 2008; Gable and Windels 2018), and injury risk (Tallian et al. 2017). Higher prey vulnerability increases catchability and decreases risk of injury to pack

members (Becker et al. 2008; Mattioli et al. 2011; Metz et al. 2012), making vulnerable prey more enticing for wolves. Injury risk from dangerous prey has been shown to be a key consideration in wolf prey selection. This is particularly relevant for larger prey items such as bison (Jaffe 2001; Becker et al. 2008; Smith et al. 2010), where predation attempts carry significant risks of injury for the predator. In a long-term study in Yellowstone National Park, wolves were shown to actively select for elk despite elk being half as abundant as bison, a phenomenon believed to be driven by the finding that bison were approximately three times more difficult to successfully subdue and kill than elk (Tallian et al. 2017).

Large changes in the relative availability or vulnerability of prey can result in changes in a generalist predator's prey selection behaviour, temporarily exhibiting targeted selection of a given prey type known as prey switching (Holling 1959; Messier 1995; Garrott et al. 2007). Prey abundance and vulnerability to predation can vary both inter and intra seasonally due to prey migration (Hofer and East 1993) or biological factors such as spawning runs (Deacy et al. 2018), birthing pulses (Whittaker and Lindzey 1999), or colour (Mills et al. 2013) and molting phases (Kahlert 2003) that can trigger prey switching behaviour as predators exploit the temporarily available resource. Prey switching can also be initiated by changes in environmental conditions altering prey accessibility, density, vulnerability, and injury risk (Nelson and Mech 1986; Huggard 1993; Szepanski et al. 1999), ultimately leading to complex and dynamic prey selection behaviours. This type of prey switching behaviour can be seen in wolves that kill beavers (*Castor canadensis* Kuhl, 1820) in the boreal forest after the spring thaw makes them available and vulnerable to predation (Voigt et al. 1976; Gable et al. 2016; Dwinnell et al. 2019).

The winter season can be a period of increased ungulate predation risk, particularly in northern climates where ice formation limits wolves' access to beavers. Food resources during winter offer lower nutritional value (Christopherson et al. 1979; Mech et al. 2001), cold temperatures reduce energy reserves (Nelson and Mech 1986), and deep snow increases the energetic cost of mobility (Telfer and Kelsall 1979; Parker et al. 1984). Deep snow can also work to physically impede prey escape from predators, resulting in increased overall predation risk (Nelson and Mech 1986; Huggard 1993; Horne et al. 2019). Further, vulnerability is influenced by the amount of time prey are exposed to winter conditions as seen in white-tailed deer (*Odocoileus virginianus* Zimmerman, 1780) in Michigan and Minnesota where mortality was positively linked to length of winter due to reduced fat reserves (Nelson and Mech 1986; Kautz et al. 2020). Smith et al. (2000) and Metz et al. (2012) had similar findings for bison and elk respectively, where bison and large elk were most frequently killed by wolves in late winter when they are in their poorest nutritional condition.

While ungulate species in general may each be affected by these factors, the relative degree of influence may vary between species and increase the vulnerability of some species over others. For example, moose (*Alces alces* Linnaeus, 1758) that can browse on shrubs above the snow surface may be less impacted by deep snow conditions compared to bison that expend more energy cratering into snow to access forage (Harvey and Fortin 2013). White-tailed deer are known to be vulnerable in cold temperatures due to increased energy expenditures resulting in reduced energy reserves (Kautz et al. 2020). Temperature has not yet been identified as a factor influencing bison vulnerability but it has been shown to affect movement rates (Sheppard et al.

2021). These factors influence relative vulnerability among prey species and may alter variability in seasonal wolf prey selection.

The lower relative vulnerability of bison to predation risk may be influenced by environmental conditions such as snow depth, temperature, and length of winter season. Winter conditions may influence seasonal variation in the predation risk bison experience and ultimately influence temporal variation in the predator-prey dynamics between wolves and bison. These factors may also influence the demographic composition of wolf prey as conditions become more favourable for successful predation events. Many wolf diet studies focus on the winter season and extrapolate winter predation patterns to year-round estimates. Using estimates from one season to represent annual prey selection can lead to misinformed management decisions (Sand et al. 2008), due to the seasonal nature of wolf prey selection.

Wood bison (*B. b. athabascae* Rhoads, 1898) are listed as *Threatened* in Canada, under the *Species at Risk Act*, largely due to genetic introgression by plains bison (*B. b. bison* Linnaeus, 1758) posing a threat to genetic differentiation of the species (Ball et al. 2016), and exposure to diseases such as brucellosis and bovine-tuberculosis (Shury et al. 2015). Studies in the nearby Wood Buffalo National Park (WBNP) and Northwest Territories have found that wolf predation on bison is primarily limited to the winter (Carbyn and Trottier 1987, 1988; O'Donovan et al. 2018), while wolf diets in Prince Albert National Park, Saskatchewan contained more bison in summer than winter (Shave et al. 2020). In similar landscapes without bison, studies found that wolves predominately preyed on moose and deer (Fuller and Keith 1980; Ballard et al. 1987, Latham et al. 2013; Neilson and Boutin 2017; Droghini and Boutin 2018) in winter.

Here I examined seasonal diets of wolves in a multi-prey system overlapping the Ronald Lake wood bison herd in northeast Alberta, Canada, with specific interest in identifying factors affecting the predation of bison and evidence of prey switching. The Ronald Lake bison herd (RLBH) is a small (~275 – 300 individuals; T. Hegel personal communication September 19, 2023) population of wood bison designated as *Threatened* under the Alberta Wildlife Act due to its small size, disease free status, and genetic distinctness from other herds (Shury et al. 2015; Ball et al. 2016). The herd is culturally significant to regional Indigenous communities and is ecologically significant to the landscape, resulting in management concerns around possible effects of nearby oilsands exploration and extraction activities. The nature of the predator-prey dynamics between wolves and bison is unknown for the Ronald Lake population and may be influential in affecting population trends in this small herd and wood bison recovery.

I hypothesized that wolves exhibit prey switching based on relative prey vulnerability. I expected wolves' primary prey to be beaver in summer and moose in winter, supplemented by bison during times of heightened vulnerability in late winter when bison energy reserves are lowest and when deep snow increases energy costs of movement. Further, I hypothesized that wolf predation on bison is regulated by specific winter conditions such as snow depth, temperature, and accumulated winter days, which likely represents the combined effects of snow depth, nutritional deficits and other factors that may be influencing bison vulnerability through the winter. I predicted bison predation events would be negatively related to winter temperature, but positively related to snow depth and accumulated winter day. Finally, I hypothesized that intra-seasonal change in relative prey vulnerability would influence wolf space use within their territories. Specifically, I predicted that wolf occurrence would shift towards bison habitat in late

winter relative to early winter, suggesting targeted prey selection and prey-switching behaviour during a time of heightened bison vulnerability.

Methods

Study area

The Ronald Lake wood bison herd home range is located on the northern fringe of the Athabasca oilsands within the Boreal Plains ecoregion of northeast Alberta, Canada, and is characterized by warm short summers (mean July temperature: 16.6°C) and long, cold winters (mean January temperature: -19.8°C; Natural Regions Committee 2006). Elevation within the study area ranges between 209 and 795 m above sea level, includes the Athabasca River in the east, a portion of the Birch Mountains to the west, and a large south-to-north orientated esker that is frequently used by wildlife. The landscape is characterized by upland forests and a variety of wetlands that support traditional wolf prey such as moose, wood bison, white-tailed deer, beaver, muskrat (*Ondatra zibethicus*), snowshoe hare, multiple species of grouse and waterfowl.

Upland deciduous forests consist of trembling aspen (*Populus tremuloides* (Michx)), balsam poplar (*P. balsamifera* (L.)) or mixed-wood stands, while upland coniferous forests consist of jack pine (*Pinus banksiana* (Lamb)) in the east, and white spruce (*Picea glauca* (Moench (Voss)) in the west. Wetlands are scattered across the area, with the highest density in the centre of the study area around Ronald Lake, and include marshes, swamps, and to a lesser extent fens and bogs dominated by graminoids, shrubs, or trees. Wildfire is the most common natural disturbance, with a portion of the study area previously burned by the 2011 stand-replacing Richardson fire that burned 700,000 ha of northeast Alberta including the east parts of the study

area. The dominant anthropogenic disturbances are energy exploration and forest harvest operations with their associated seismic lines, well pads, cut blocks and temporary roads, mainly concentrated in the southern parts of the study area. The herd's home range currently has few anthropogenic access points that are difficult to travel due to water levels in summer and snow depth in winter.

Snow, temperature, and season definition

Daily snow measures were recorded from four snow stations (Appendix 3) distributed across the bison herd's home range and averaged for a daily landscape level measure. The stations consisted of a remote trail camera set to take one photo of two snow gauges per day (Shephard et al. 2021). To estimate one representative daily snow depth, measures were averaged between the two gauges at each station, as well as among stations (Shephard et al. 2021). Daily temperature measures were averaged between the two closest weather stations to the study area (Aurora and Mildred Lake, AB), approximately 90-km from Ronald Lake (Alberta Agriculture and Forestry 2020).

I defined the seasons using data from the snow stations. The summer season was defined by absence of snow cover (April 2019 – October 2019), and winter by continuous snow cover (November 2019 – April 2020). Winter day was used to represent the length of the winter season (i.e., winter day), with day one being the first 24 hour period of continuous snow cover on 1 November 2019.

Wolf capture

Wolf capture sessions were conducted in the winter and fall of 2019 and in the winter of 2020 to fit Global Positioning System (GPS) collars on a minimum of two wolves per pack to monitor their movements. The purpose of collaring two wolves per pack was to increase the likelihood of acquiring pack data throughout the study in case a wolf died or lost its collar. Wolves were captured using aerial net-gunning and ground trapping, following the Government of Alberta's canid capture, handling, immobilization and release protocol No. 009. Aerial net-gunning was conducted using a MD500D helicopter with four-barrel netguns using .308 blank cartridges. I set 15 #4 EZ grip foothold traps using various scent lures at one-to-three-kilometer distance intervals along linear disturbances for ground trapping. I fit wolves with Vectronics Vertex Lite GPS radio collars (Vectronic Aerospace, Berlin, Germany; University of Alberta Animal Care Protocol # AUP00002913; Government of Alberta Animal Care # 21-064, 20-216), set to acquire a GPS location every four hours in winter (November – April) and every two hours in summer (May – October). Collars were set to the two-hour location interval in summer to aid in the identification of kill events featuring smaller, more quickly consumed prey. Each captured wolf was ear-tagged to aid in identification and collars were equipped with drop-off mechanisms set to release two years after deployment.

Wolf and bison monitoring

I deployed ten remote trail cameras along travel routes to confirm the number of wolves within each pack. Alberta Environment and Protected Areas deployed GPS collars on female bison over multiple years to gather location data. I used GPS collar data from April 2019 – April 2020 from 16 female bison to define the bison herd's home range using bivariate normal kernel density utilization distributions for the associated time period (R package *adehabitat* version 0.4.20,

Calenge 2006). Wolf GPS locations within the same time-period were used to define wolf pack territories using the same methodology. The study area encompassed the combined wolf pack territories that overlapped and extended beyond the Ronald Lake bison herd home range.

I plotted wolf GPS locations in ArcMap 10.3.1, to monitor their movements throughout the year to identify predation sites. Following the methodology of Webb et al. (2008), I subset the location data by selecting any incidences with two or more GPS locations within a 200-m radius. I classified sites based on the number of hours the wolves spent within that 200-m radius (referred to as handling time) and calculated the number of times they exited and returned within the 200-m radius (Anderson and Lindzey 2003; Webb et al. 2008). Location clusters were ranked by relative likelihood of representing a predation site based on the continuous time spent at the site and number of returns to each cluster site (Appendices 1 & 2). The sites with the longest continuous times (> ten hours) or multiple returns for visitation represented a higher likelihood of being a predation or scavenging site or a site with scat samples and were prioritized for investigation in the field. Summer cluster sites with continuous times less than ten hours were selected randomly for field visits. Prior to field visits I examined all prioritized and randomly selected sites individually to identify the site centre point as the densest cluster of all consecutive locations within the 200-m radius.

Once arrived at the centre point of each cluster site, crews of two systematically searched for prey remains and wolf scat within a 50-m radius along transects spaced 5-m apart (Sand et al. 2008; Knopff et al. 2009). A site was determined a predation site if prey remains were found along with evidence that the prey was killed by wolves, such as recent age of remains, signs of

struggle, chase sequence, disarticulated carcass, blood, tracks, and scat (Elbroch 2003; Peterson and Ciucci 2003; Webb et al. 2008). A site was determined a scavenge site if there was evidence that the animal was not killed by wolves, such as age of remains, a hunter kill, or an intact carcass (Appendix 4). If no prey remains were found, the site was classified as a bedding site. Den and rendezvous sites were identified by excessive time spent, repeated returns by wolves to one location and confirmed by pup scat in the field.

Crews collected prey remains (i.e. hair, feathers, bones) and wolf scats greater than 30-mm in diameter (Weaver and Fritts 1979) opportunistically and at cluster sites. Scat samples were not collected from winter clusters with a carcass present, but were collected when no prey remains were detected at the site. For ungulate prey, skulls, mandibles, and other bones were examined to determine species, sex, and age, respectively. Prey skulls were examined for antlers, horns, or pedicles to determine sex. When mandibles were found, the ungulate prey item was classified as calf (< 1 year), yearling (1 – 2 years) or adult (> 2 years) using diastema length, tooth eruption, and wear (Stelfox 1993).

Laboratory diet sampling

Wolf scats were collected with gloves in the field and were frozen, thawed, and autoclaved to eliminate potential for transmission of zoonotic diseases (Otranto and Deplazes 2019; Tse et al. 2019). Remains were separated from fecal matter through sieves of varying sizes to ensure remains of different sizes were not lost (Appendices 5 & 6). Remains found were washed, dried, and spread onto a tray with labeled edges in centimeters for use as a coordinate system for the point frame method. The point frame method uses a blind placement of a set of pins to select individual hairs to randomly select a subsample of prey items from each scat sample (Ciucci et

al. 2004). I used a random number generator to select coordinates along each axis on the pan to ensure a true random subsample was taken. Following the methodology of Ciucci et al. (2004), one sponge with pins was placed at the randomly selected axis on the tray, and the closest prey hair to each of the pin heads was selected for the subsample of hairs. I considered a sample insufficient if it did not consist of at least 12 hairs, as this number has been tested to represent 94% accuracy in scats that contained two prey items (Chenaux-Ibrahim 2015).

I created slide mounts with negative impressions of prey hair samples by pressing hair into clear nail polish spread between slides. Prey hairs were identified to family using a compound microscope between 100 – 400 x magnification to observe cuticle scale and medulla patterns, while feathers were grouped into a general avian classification. I created reference slides using known hair samples and used a combination of the slides, keys, and guides to facilitate identification of these unique patterns (Adorjan and Kolenosky 1969; Kennedy and Carbyn 1981). The first 12 identifiable cuticle scale impressions for each slide were used for diet analysis (Chenaux-Ibrahim 2015; Gable et al. 2017), while the identification of the medulla was used as a confirmation. If the medulla identification did not match any of the cuticle scale patterns identified on the slide, it was re-examined. If there were not 12 identifiable cuticle scale patterns on each slide, a new slide was made using the same methods as above.

Diet Analysis

Summer diet

Summer wolf diets can be characterized by smaller prey items that can be consumed quickly or brought back to den or rendezvous sites (Ballard et al. 1987; Peterson and Ciucci 2003; Mech and Boitani 2007; Sand et al. 2008). As a result, prey remains can be difficult to find, so I

estimated summer diets through analysis of scat samples found at wolf cluster sites and on trails. I estimated total prey biomass, given small bodied prey are often fully consumed (Hayes and Harestad 2000; Jedrzejewski et al. 2002; Sand et al. 2008). I measured both percent frequency of occurrence and percent biomass consumed for each prey species within each wolf pack, then averaged between packs for an overall wolf population diet estimate. Percent occurrence was based on the frequency of occurrence of each prey species found in scat relative to the total number of prey items found in wolf diets (Ciucci et al. 1996). Percent biomass consumed was estimated to compensate for possible overestimations of smaller prey items common in percent occurrence calculations (Floyd et al. 1978; Weaver 1993; Klare et al. 2011).

Percent biomass consumed was measured using Weaver's 1993 regression equation $y = 0.439 + 0.008x$, which calculates the mass (kg) of a particular prey item consumed per scat (y), relative to the estimated mass (kg) of the associated prey species and age class (x). The calculated mass (kg) consumed (y) was then multiplied by the frequency of occurrence of each prey species detected in scats of each pack. Percent biomass consumed was then estimated for each prey type relative to total biomass consumed for each pack. I used the live mass of prey species provided by Novakowski (1965), Aleksiuik and Frohlinger (1971), Coleman and Boag (1987), Renecker and Hudson (1993) and Gable et al. (2017) for my analysis.

Winter diet

Winter wolf diets commonly consist of larger prey species, so winter diets were measured from prey remains found at wolf predation and scavenge sites. Frequency of different prey types found at kill sites was used to estimate the percent diet composition for each wolf pack. Biomass consumed was used to estimate relative importance of each available prey species to wolves in

winter using average live mass of each prey species, sex, and estimated age class (Renecker and Hudson 1993; Knopff et al. 2010). After identifying the average live mass of prey found at each site, I calculated the amount of edible biomass consumed by wolves following the methodology of Sand et al. (2008). This method estimates the non-digestible portions of each prey species relative to their total body weight and was used because winter wolf diets were predicted to consist of larger prey species. Prey items that could not be assigned an age classification were assigned an average mass of age classes for the associated species (Morehouse and Boyce 2011), which was similar to yearling mass (Knopff et al. 2010). Biomass consumption was estimated per pack and per wolf per day.

Temporal and spatial analysis

Winter temporal patterns in predation

I used single-predictor logistic regression models to test the effect of winter conditions (i.e. snow depth, temperature and winter day) on the detection of a wolf killed bison on a given day. Significance was measured using $p < 0.05$ and explanatory power of each univariate model was measured using pseudo R^2 . All analyses were conducted using the statistical program R (version 4.0.3) (R Core Team 2017).

Winter wolf space use relative to bison

To examine whether wolves were actively selecting for bison during the late winter, I tested for a significant change in the overlap of wolf locations relative to bison distribution between early and late winter at the bison herd's home range scale and combined wolf pack territory scale. I used kernel density estimation to develop seasonal utilization distributions for the female collared bison within the herd. I divided the winter season into early and late winter based on the

first day that snow reached a depth that coincided with an increase in wolf predation on bison, informed by the temporal logistic regression model. I used a chi-square test to test the prediction that wolves spent proportionally more time within bison range during late winter than in early winter. To determine if wolves used areas of higher bison use during the late winter, I used a non-parametric Wilcox test to examine the difference in bison UD values at wolf locations in early and late winter. To verify that a statistically significant result was not the statistical artefact of a large dataset, I randomly selected 200 locations from each winter period and ran the non-parametric Wilcox test. I ran this subsampling process 1000 times to calculate the proportion of tests on subsampled data that showed statistical significance at $P < 0.05$.

Results

Wolf monitoring

The study area that contained the bison herd's home range overlapped with three wolf pack territories that extend from north of Fort McKay to the southeast edge of Lake Claire in WBNP (Figure 1). Between 2019 and 2020, seven wolves from three packs were captured, collared and monitored for movement and predation activity. The wolf packs were named after geographic features that were present within their territories, specifically the Dianne, McIvor and Southline packs. Wolf pack sizes were confirmed by remote trail cameras and aerial visuals during captures and field sessions.

The Dianne pack consisted of two adults that were monitored for 11 months, the McIvor pack consisted of six adults that were monitored for ten months, and the Southline pack consisted of nine adults that were monitored for three months of the winter season. In summer (April to

October 2019), wolf GPS collars transmitted 2,003 locations from the Dianne pack and 3,479 locations from the McIvor pack. In winter (Nov 2019 – April 2020), wolf GPS collars transmitted 1,486 locations from the Dianne pack and 1,064 locations from the McIvor pack. The Southline pack transmitted 958 locations from 22 January to 17 April 2020. I visited 58 sites and confirmed large mammal kills at 38 (66%).

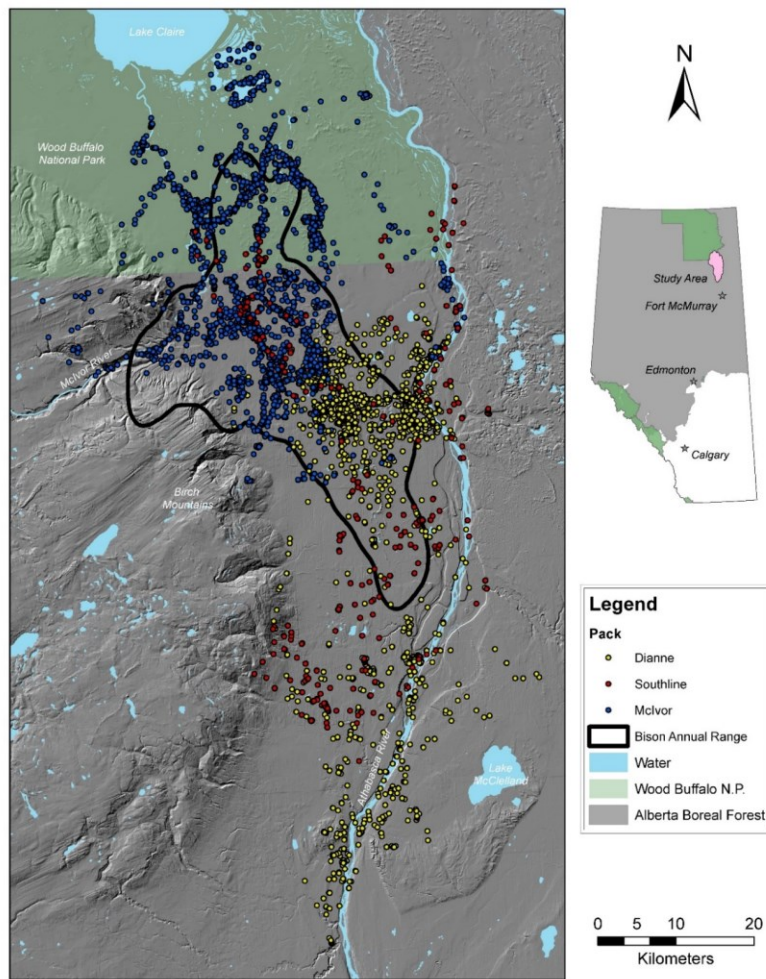


Figure 1: Dianne, McIvor, and Southline wolf pack locations (point symbols) relative to their overlap with the bison range represented as the 99% utilization distribution (black outline) near Ronald Lake, Alberta, Canada between April 2019 – April 2020. Inset map shows location of study area (pink polygon) in Alberta relative to National Parks (green) and the region of boreal forests (grey).

Summer diet

I visited 48 sites from the Dianne pack and 46 sites from the McIvor pack to search for wolf scat and prey remains. The prey remains found in summer included beaver ($n = 3$), Canada goose (*Branta canadensis* Linnaeus, 1758) ($n = 1$) and remains from winter mortalities of a moose ($n = 1$) and bison ($n = 1$). I collected 49 and 25 scat samples at Dianne and McIvor pack cluster sites, respectively. I collected an additional 69 samples from Dianne pack trails, den, and rendezvous sites. Overall, I collected 143 wolf scat samples from 97 locations during the summer period.

Scat samples containing only one species represented 86.2% of samples and samples containing two prey species represented 13.8% of samples. I used neonate and calf masses for ungulate content in wolf scat because there were no medium or large bodied prey (> 20 -kg) remains found at cluster sites. Carcass consumption estimates were not incorporated as there were no medium to large-bodied prey found in summer diets and carcass consumption is considered to be very high with smaller prey (< 20 -kg) items (Hayes and Harestad 2000; Jedrzejewski et al. 2002; Sand et al. 2008).

Cuticle scale and medulla pattern identification of sub-samples revealed the collective summer wolf diet of the Dianne and McIvor packs measured in percent biomass consumed, consisted of 63% beaver, 16% muskrat, 10% cervids (white-tailed deer and moose), 6% wood bison, and trace amounts of avian prey (Figure 2). The diet of the Dianne pack consisted of 73% beaver, while the diet of the McIvor pack was more diverse with more large prey items such as 10% cervids and 8% wood bison, but still dominated by beaver at 53% (Figure 2).

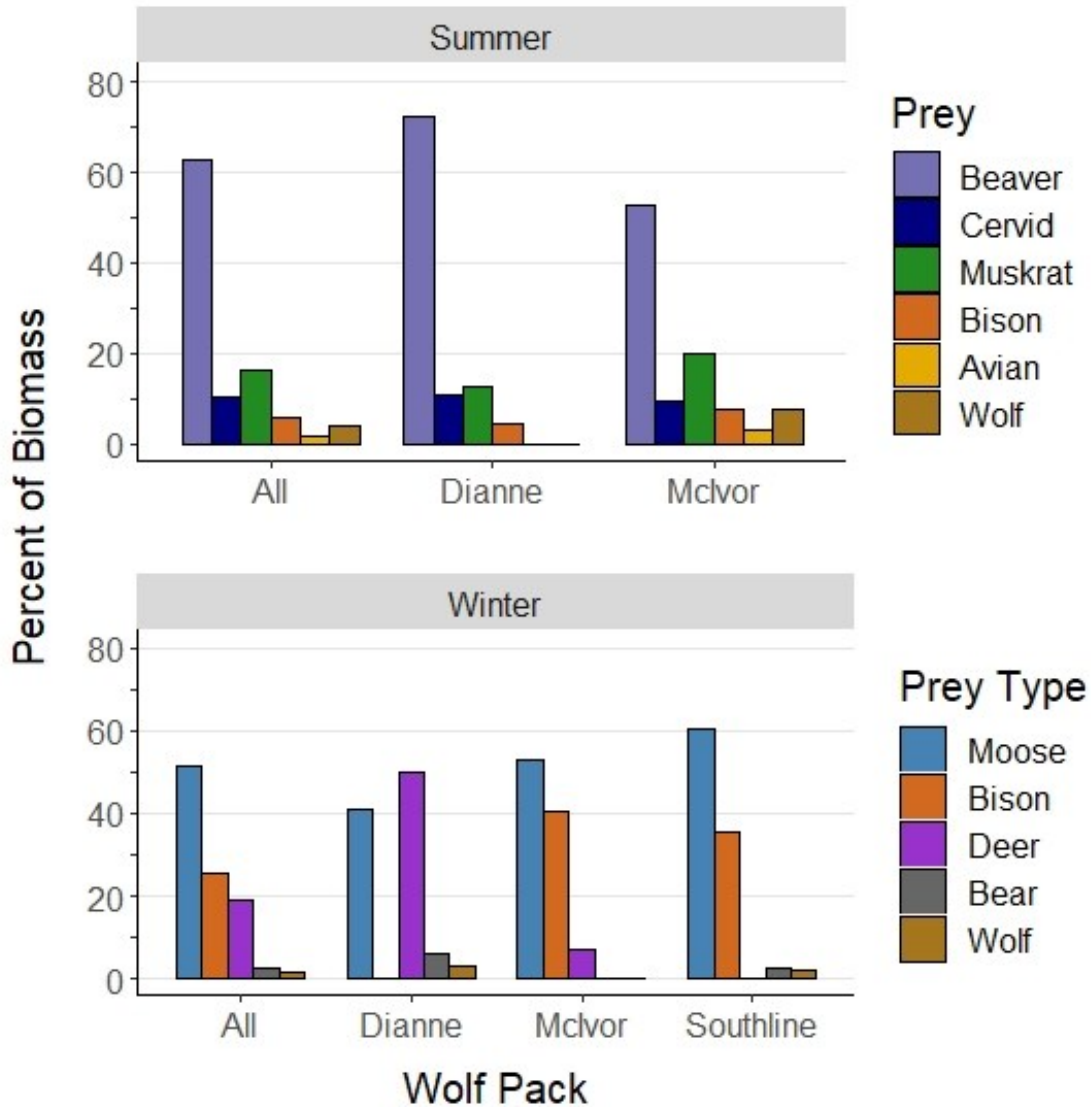


Figure 2: Top panel: Summer (April – October 2019) diet of the Dianne and McIvor wolf (*Canis lupus*) packs in the Ronald Lake area, Alberta, Canada, analyzed through contents of wolf scat. This figure displays the percentage of hair of each prey species found in all wolf scat samples for each pack, and the two combined (All). Bottom panel: Winter (November 2019 – April 2020) diet of the Dianne, McIvor and Southline wolf packs near Ronald Lake, analyzed by the frequency of prey species found at wolf cluster sites for each pack and the three combined.

Winter diet

In the winter, I visited 22 Dianne pack, 20 McIvor pack, and 16 Southline pack cluster sites, finding remains at confirmed kills sites of 14 deer, 13 moose, six bison, three wolves and two black bears (*Ursus americanus* Pallas, 1780), with an additional three scavenged moose (Appendix 4). The combined winter diet of all packs based on cluster site investigation, consisted of 36% white-tailed deer, 34% moose, 15% bison, 8% wolf, and 5% black bear (Figure 2).

The Dianne pack predominantly preyed on deer (73%), the McIvor pack was more evenly distributed among prey species (36% bison and moose, 27% deer), while the Southline pack preyed mainly on moose (58%; Figure 2). The Dianne pack killed the greatest number of prey items over winter and consumed the most biomass per wolf per day, but the least biomass per pack per day relative to the other packs. In contrast, the McIvor and Southline packs had a similar number of kills, but with higher biomass consumed per pack relative to the Dianne pack (Figure 3).

I estimated wolves killed and consumed 14.87 kg of prey biomass/pack/day and 2.69 kg of prey biomass/wolf/day. Total prey biomass available to each pack varied between the three packs, with the Dianne pack consuming an estimated 6.29 kg of prey biomass per day in winter, the McIvor pack consuming 12.09 kg, and the Southline pack consuming an estimated 26.23 kg (Figure 4). Moose provided the most biomass of the prey types to the McIvor (53%) and Southline (60%) packs, while deer provided the most biomass to the Dianne pack (50%). The Southline pack showed the most monolithic diet, with moose comprising an estimated 60% of

their available biomass. Bison represented 40% of McIvor pack killed biomass, while bison contributed 35% to the Southline pack total.

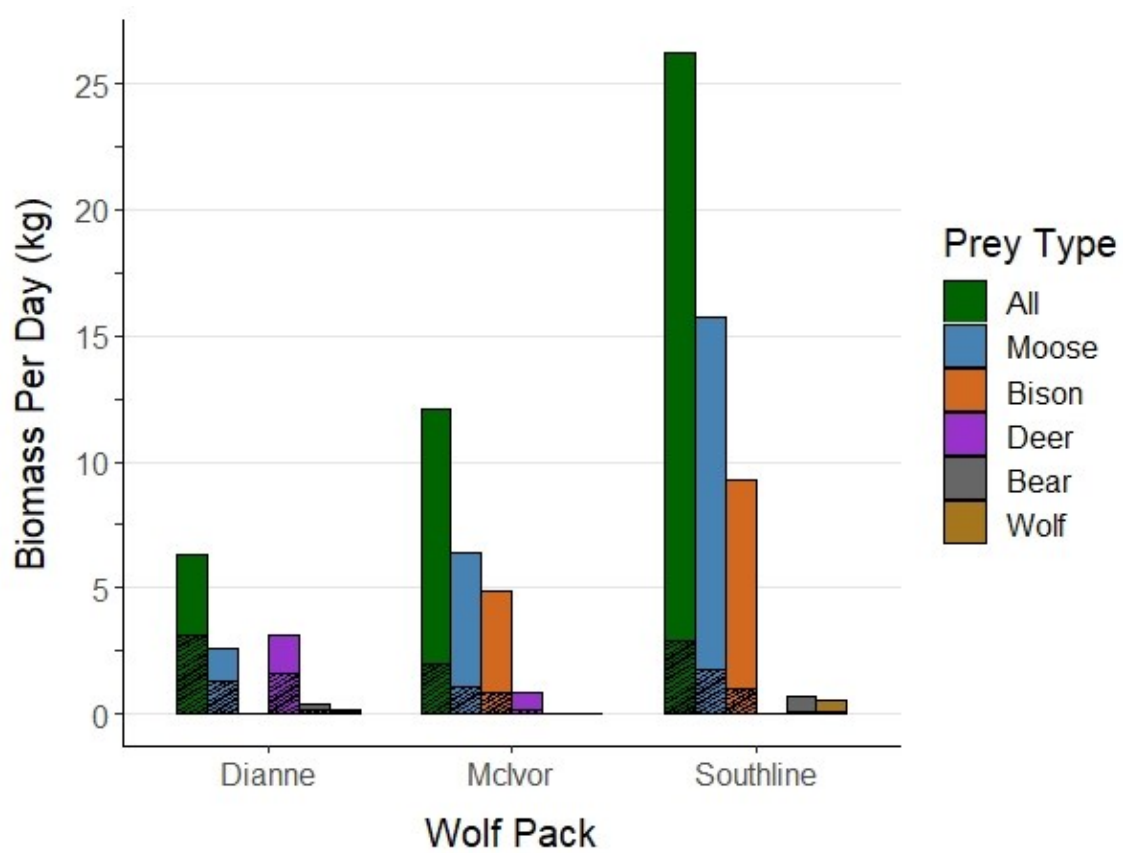


Figure 3: Winter (Nov 2019 – April 2020) diet of the Dianne, McIvor, and Southline wolf (*Canis lupus*) packs in the Ronald Lake area of Alberta, Canada, analyzed by biomass consumed per day of each prey type for pack (coloured) and individual wolf (hashed).

Remains of bison were discovered at both McIvor and Southline kill sites, which constituted 40% of the McIvor pack winter kills and 17% of the Southline pack winter kills (Figure 2). The majority of kills were of vulnerable individuals including two calves, one yearling and one older animal (> 10 years). The remaining two bison kills were of a seemingly healthy cow and one unconfirmed age-sex status. All wolf kill sites were characterized by wolf handling times of greater than 16 hours. The majority of kill sites (97%) were characterized by wolf handling times of greater than 20 hours and spent more than 24 hours at 85% of the confirmed kills. Wolf carcasses were found at three cluster sites, either partially or completely consumed, and were considered territorial kills.

Winter temporal patterns in predation

Bison kills occurred in late winter relative to cervids, with the first record of a bison kill occurring on 3 March 2020 (Figure 4) when snow depths exceeded 30-cm (Figure 5). The probability of a bison kill on any given day in the winter season was best supported by the number of days since first continuous snow accumulation (i.e., Winter day; $\beta = 0.048$; S.E. = 0.020, $p = 0.015$; pseudo $R^2 = 0.25$). Results showed that the probability of wolves killing a bison began to increase in early February and increased further until mid-April during initiation of snow melt (Figure 5). Snow depth was also a significant predictor of the timing of bison kills ($\beta = 0.150$; S.E. = 0.080, $p = 0.050$; pseudo $R^2 = 0.14$), but was less supported than winter day. However, both snow depth and winter day were correlated ($r = 0.935$; $p < 0.001$). Results showed that the probability of wolves killing a bison began to increase at a 20-cm snow depth and continued to increase beyond 40-cm (Figure 5).

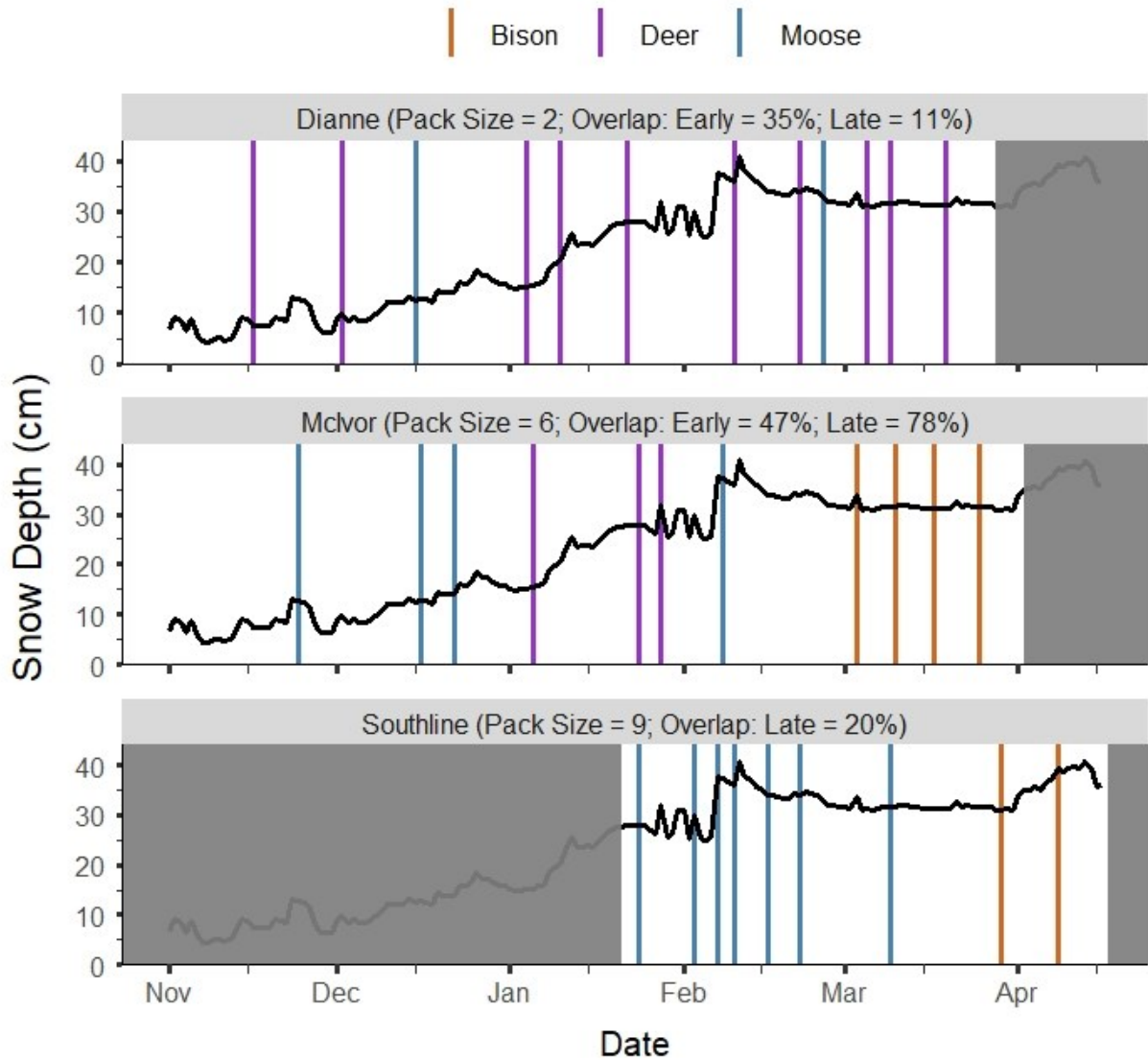


Figure 4: Timing of large prey kills (vertical lines) of the Dianne (top), McIvor (middle) and Southline (bottom) wolf (*Canis lupus*) packs in relation to snow depth (cm, black continuous line), grouped by prey type through the winter season (1 Nov 2019–17 April 2020) near Ronald Lake, Alberta, Canada. Percent overlap represents the proportion of each wolf territory that lies within the bison range in early and late winter. Grey areas represent time that wolf packs were not monitored.

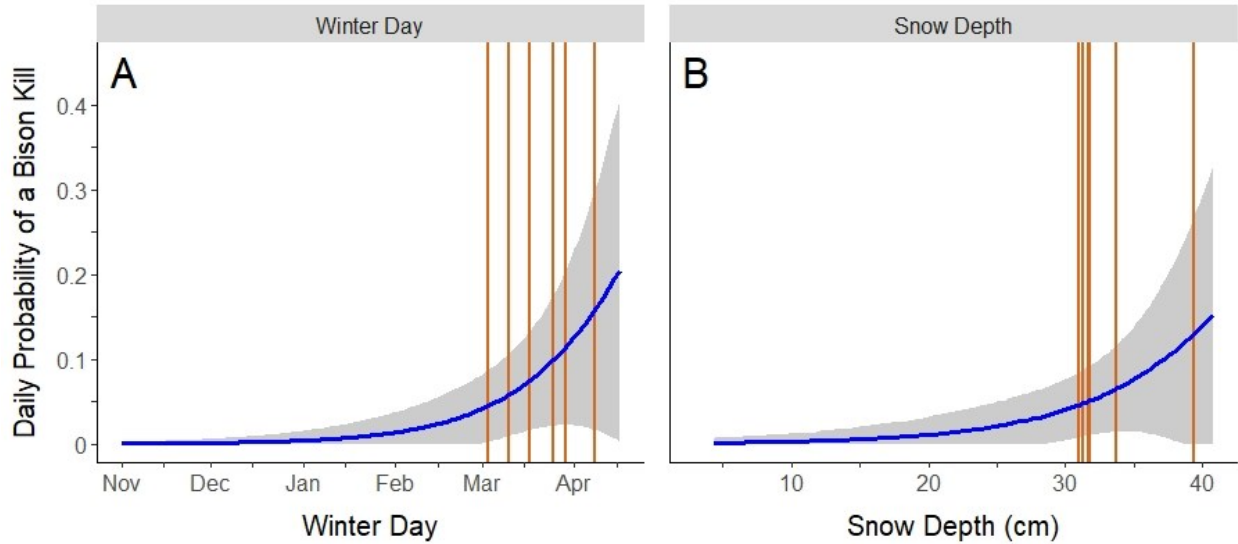


Figure 5: Predicted daily probability of a bison (*Bison bison athabascae*) kill from wolves (*Canis lupus*) over the period 1 Nov 2019–17 April 2020 near Ronald Lake, Alberta, Canada, based on logistic regression models. (A) The effect of winter day (i.e. days since first snow accumulation); and (B) snow depth. The grey area around the blue curves and the orange lines represent the 95% confidence intervals and bison kill events respectively.

Winter wolf space use relative to bison

The collared wolves in this study spent proportionally less time within the bison range during late winter (47.5% of all late winter locations) than early winter (57.9% of all early winter locations) ($\chi^2 = 166.2$, $df = 1$, $p < 0.001$) (Figure 6). However, when wolves were within the bison range, they used locations with higher bison UD values in late winter (mean = 0.142) relative to early winter (mean = 0.108, $W = 533024$, $p < 0.001$, and 982 of 1,000 subsampled tests showed statistical significance at $P < 0.05$). The difference in bison UD values at wolf locations between winter periods showed a Cohen’s effect size of 0.229.

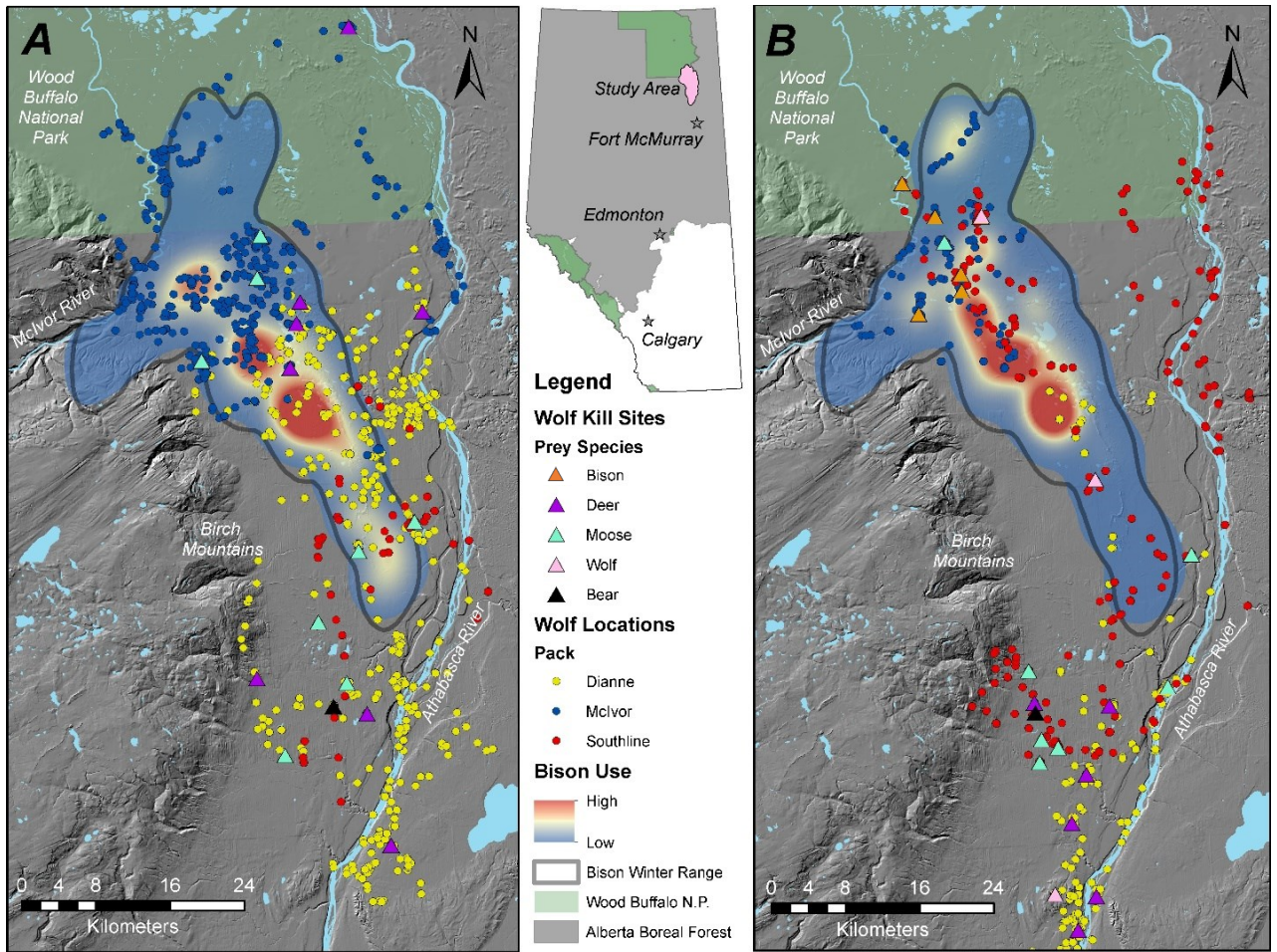


Figure 6: Dianne, McIvor, and Southline wolf pack locations (point symbols) and predation sites (triangular symbols) relative to their overlap with the bison range represented as the 99% utilization distribution near Ronald Lake, Alberta, Canada. Panel A represents 1 Nov 2019 – 6 Feb 2020 (early winter) and panel B from 7 Feb – 17 April 2020 (late winter) when probability of bison predation increases. Inset map shows location of study area in Alberta.

Discussion

Wolf diets in the Ronald Lake region of northeast Alberta, Canada followed my predictions with a shift from beaver in summer to moose in winter, supplemented by bison in late winter when they were most vulnerable. Summer wolf scat analysis showed that the Dianne pack diet consisted almost exclusively of beaver. The McIvor pack exhibited a more variable summer diet that included some bison, but also primarily consisted of beaver. Although moose dominated the collective wolf winter diets by biomass, the number of moose and deer killed was equivalent and winter wolf diets included all available large mammal prey in the study area. Further, a noticeable shift to bison prey was observed for two of the wolf packs in late winter, following my initial predictions.

The proportional composition of prey in winter diets varied among the packs. I suggest that the observed differences in diet composition are in part the result of variation in pack sizes (MacNulty et al. 2014; Horne et al. 2019). MacNulty et al. (2014) found that the optimal group size for capturing bison in Yellowstone National Park exceeded 11 wolves, while the average pack size in Wood Buffalo National Park, a system where wolves specialize in hunting bison, is 12 to 16 in winter (Carbyn et al. 1993). While neither of these studies suggest that smaller wolf packs are incapable of killing bison, they suggest that smaller wolf packs have lower success preying on bison. The packs in the Ronald Lake region were small in comparison, with the Dianne, McIvor, and Southline packs having 2, 6, and 9 wolves, respectively. This information suggests that the Dianne pack may have had more difficulty killing larger prey items than the two larger packs. The territory of the McIvor pack had the most overlap with the bison range throughout the year. This large degree of spatial overlap relative to the other wolf packs likely

provided the McIvor pack with additional experience encountering and preying on bison (Smith et al. 2000; Shave et al. 2020).

Collectively, winter wolf diets were dominated by moose and white-tailed deer through most of the winter with bison appearing in late winter. Prey switching is a common occurrence in predator-prey systems driven by various factors (Murdoch 1969; Patterson et al. 1998; Garrott et al. 2007; Abrahms et al. 2016). For wolf-bison systems, predation events have been shown to occur more often in the late winter, attributed largely to snow conditions (Carbyn et al. 1993; Smith et al. 2000; Jaffe 2001). Snow accumulation through the winter limits bison movements and food access, both of which increase energy expenditures (Telfer and Kelsall 1984; Carbyn et al. 1993; Smith et al. 2000). Increased energy use at this time of year is compounded by lower nutritional availability of their preferred food items (Hecker et al. 2021) and may lead to decreased physical condition and increased vulnerability to predation (Sinclair and Norton-Griffiths 1979; Metz et al. 2012; Wilmers et al. 2020).

Wolf predation success on bison has been shown to increase in winter periods of deep snow (Carbyn et al. 1993; Smith et al. 2000; Jaffe 2001), but it remains unclear if this increased vulnerability is predominately driven by snow depth causing physical impedance for bison, or if deterioration in body condition increases their vulnerability (Smith et al. 2000; Metz et al. 2012; Nelson and Mech 1986; Kautz et al. 2020). Bison kills occurred when snow depths exceeded 30-cm, but this depth should not be viewed as a threshold or critical depth at which bison become more vulnerable. There was a marked delay between the plateau of increasing snow depth and the onset of bison predation events (Figure 5), indicating that bison vulnerability was likely

influenced by more than simply snow depth alone. Snow depth and the number of days since first snow accumulation were both positively related to the occurrence of bison kill events, with the latter being the most supported factor. The effect of winter duration (days since first snow accumulation) likely encompasses effects of snow depth, nutritional deficits, and other factors that may be influencing bison vulnerability (Delgiudice et al. 1988). Ungulate body condition is commonly thought to affect vulnerability at this time of year (Hudson and Christopherson 1985; Parker et al. 2009; Metz et al. 2012; Kautz et al. 2020), and there is merit in developing more reliable methods of estimating bison physiological condition to further explore this aspect of bison vulnerability to predation (Taillon et al. 2011).

Evidence of bison predation by wolves was found only in late winter cluster sites for the McIvor and Southline packs. While I extracted bison hair samples from summer wolf scat, there was no evidence of a bison kill event in the summer season, however there was evidence of scavenging. Given this evidence, I suggest that the bison hair content in the McIvor pack scat samples were likely a result of scavenging on a bison that had died before the summer period, shortly before wolf collars were deployed. The possibility remains that predation events on bison calves may not have been detected in the field despite implementing a shorter two-hour GPS collar location acquisition to improve detection rates of rapidly consumed prey and an extensive search methodology with a two-person crew. However, predation events may have been missed by my cluster analysis due to the randomized selection process of sampled clusters, or misclassified during field visits due to minimal or no remains left at sites. Given these uncertainties, I cannot conclude with certainty from the site visits and scat content whether wolves killed bison during the summer, but it seems unlikely, particularly for mature bison.

The McIvor pack began preying on bison in early March, while the Southline pack initiated this switch at the end of March. Shifts in prey selection by wolves have been observed in the winter season in other systems (Carbyn et al. 1993; Becker et al. 2008; Sand et al. 2016), but my findings saw that once these packs began to prey on bison, they exclusively killed bison until the end of the monitoring period (17 April 2020). This shift in prey selection does indicate a degree of prey switching behaviour by the wolves in this system. Wolves are thought of as generalist predators (Murdoch 1969) and while more information is required to fully understand the nature of wolf prey selection in this system, these results suggest wolves can target bison during times of increased vulnerability. Observing this apparent prey switching behaviour in more than one pack strengthens the conclusion that our results suggest the possible change to a targeted selection pattern in response to heightened prey vulnerability rather than a simple behavioural change by one pack.

The relative strength of this apparent prey switching behaviour may be evidenced by similar changes in their use of areas frequented by bison in early and late winter (Sih 2005, Williams and Flaxman 2012, Kittle et al. 2017). If wolves spent significantly more time in the bison range and in areas of high bison use in late winter relative to early winter, this would provide further evidence of changes in their prey selection pattern. These packs showed dramatic differences in both intra and inter-seasonal space use. The McIvor Pack territory remained consistent throughout the year, whereas the Dianne Pack seemingly abandoned their summer territory and moved south in winter where they primarily preyed on deer. The Southline Pack maintained a territory in the southern extent of the bison herd's home range for most of the winter, then moved north into the McIvor Pack territory in late winter. Collectively, when wolves were within the

bison range, they spent significantly more time in areas of high bison use in late winter relative to early winter. The increased wolf occurrence in areas frequented by bison in late winter suggests that wolves were targeting bison at the time they are most vulnerable to predation. However, wolves did not spend significantly more time within the bison range in late winter than in early winter, suggesting that wolf prey switching may not have been strong enough to drive changes at broader spatial scales. These results indicate that collectively, wolves targeted bison during times of increased vulnerability at fine spatial scales within the bison range, but not at broad spatial scales within the collective wolf pack territories.

My findings of seasonal influences on shifts in wolf diet and prey selection have shown new associated spatial corollaries of prey switching in the winter season and are important in helping to understand the ecology of the small and threatened population of the Ronald Lake wood bison. The observed prey-switching behavior provides baseline information and identifies that while the bison herd may be affected by wolf predation, my results indicate that the herd experienced a predation rate of approximately 2.3%. Given the relatively low predation level (Joly and Messier 2005) and the frequently stabilizing nature of prey switching on prey population dynamics (Murdoch 1969), the effect of predation on this herd is likely minimal, and indirect effects of predation risk requires further study (Christianson and Creel 2008). There remains the possibility that an additional unidentified wolf pack may partially overlap with the bison herd's home range, potentially influencing the estimated predation rate. Additionally, the observed behaviours in this study represent one year of data, so the conclusions drawn here would further benefit from additional years of study. Further study would provide opportunity to evaluate the consistency of these patterns.

The southern portion of the bison herd's habitat has been of interest for industrial exploration and development for oil reserves. The associated habitat alterations from resource extraction has the potential to threaten the herd through habitat loss, affect the risk of disease exposure from nearby bison herds infected with Brucellosis and Tuberculosis (Joly and Messier 2005), and alter the predator-prey dynamics between wolves and bison. This work establishes a baseline of wolf-bison predator-prey dynamics and highlights the importance of continued monitoring of this relationship in the future.

References

- Abrahms, B., Jordan, N.R., Golabek, K.A., McNutt, J.W., Wilson, A.M., and Brashares, J.S. 2016. Lessons from integrating behaviour and resource selection: activity-specific responses of African wild dogs to roads. *Anim. Conserv.* **19**(3): 247–255. doi:10.1111/acv.12235.
- Adorjan, A.S., and Kolenosky, G.B. 1969. A manual for the identification of hairs of selected Ontario mammals.
- Alberta Agriculture and Forestry. 2020. Alberta Climate Information Service (ACIS). Available from <https://acis.alberta.ca>.
- Alberta Government. 2017. Status of the American bison (*Bison bison*) in Alberta: 2017. Edmonton.
- Aleksiuk, M., and Frohlinger, A. 1971. Seasonal metabolic organization in the muskrat (*Ondatra zibethica*). I. Changes in growth, thyroid activity, brown adipose tissue, and organ weights in nature. *Can. J. Zool.* **49**(8): 1143–1154. doi:10.1139/z71-174.
- Anderson, C.R., and Lindzey, F.G. 2003. Estimating cougar predation rates from GPS location clusters. *J. Wildl. Manage.* **67**(2): 307. doi:10.2307/3802772.
- Andersson, M., and Erlinge, S. 1977. Influence of predation on rodent populations. *Oikos* **29**(3): 591–597.
- Ball, M.C., Fulton, T.L., and Wilson, G.A. 2016. Genetic analyses of wild bison in Alberta, Canada: implications for recovery and disease management. *J. Mammal.* **97**(6): 1525–1534. doi:10.1093/jmammal/gyw110.
- Ballard, W.B., Whitman, J.S., and Gardner, C.L. 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildl. Monogr.* **98**: 3–54.
- Becker, M.S., Garrott, R.A., White, P.J., Gower, C.N., Bergman, E.J., and Jaffe, R. 2008. Chapter 16

- Wolf prey selection in an elk-bison system. Choice or circumstance? *In* The Ecology of Large Mammals in Central Yellowstone, 1st edition. Elsevier Inc. pp. 305–337. doi:10.1016/S1936-7961(08)00216-9.
- Bergman, E.J., Garrott, R.A., Creel, S., Borkowski, J.J., Jaffe, R., and Watson, F.G.R. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. *Ecol Appl.* **16** (1): 273-284. <https://doi.org/10.1890/04-1532>.
- Bruggeman, J.E., White, P.J., and Watson, F.G.R. 2008. Chapter 28 Effects of snow and landscape attributes on bison winter travel patterns and habitat use. *Terr. Ecol.* **3**: 623–647.
- Calenge, C. 2006. The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol. Modell.*, 197, 516-519
- Carbyn, L.N., Oosenbrug, S.M., and Anions, D.W. 1993. Wolves, bison and the dynamics related to the Peace-Athabasca Delta in Canada's Wood Buffalo National Park. *In* 4th edition. Canadian Circumpolar Institute.
- Carbyn, L.N., and Trottier, T. 1987. Responses of bison on their calving grounds to predation by wolves in Wood Buffalo National Park. *Can. J. Zool.* **65**(8): 2072–2078. doi:10.1139/z87-317.
- Carbyn, L.N., and Trottier, T. 1988. Descriptions of wolf attacks on bison calves in Wood Buffalo National Park. *Arctic* **41**(4): 297–302. doi:10.14430/arctic1736.
- Chamrad, A.D., and Box, T.W. 1964. A point frame for sampling rumen contents. *J. Wildl. Manage.* **28**(3): 473-477. Doi: 10.2307/3798199.
- Chenaux-Ibrahim, Y. 2015. Seasonal diet composition of Gray Wolves (*Canis lupus*) in Northeastern Minnesota determined by scat analysis. University of Minnesota.
- Christopherson, R.J., R.J. Hudson, and Christopherson, M.K. 1979. Seasonal energy expenditures and thermoregulatory responses of bison and cattle. *Can J. Ani. Sci* **59**(3): 611–17.

- Christianson, D., and Creel, S. 2008. Risk effects in elk: sex-specific responses in grazing and browsing due to predation risk from wolves. *Behav. Ecol.* **19**(6): 1258–1266. doi:10.1093/beheco/arn079.
- Ciucci, P., Boitani, L., Pelliccioni, E.R., Rocco, M., and Guy, I. 1996. A comparison of scat-analysis methods to assess the diet of the wolf *Canis lupus*. *Wildlife Biol.* **2**(1): 37–48. doi:10.2981/wlb.1996.006.
- Ciucci, P., Tosoni, E., and Boitani, L. 2004. Assessment of the point-frame method to quantify wolf (*Canis lupus*) diet by scat analysis. *Wildlife Biol.* **10**(1): 149–153. doi:10.2981/wlb.2004.020.
- Coleman, T.S., and Boag, D.A. 1987. Canada goose foods: their significance to weight gain. *Wildfowl* **38**(19x 7): 82–88.
- Deacy, W.W., Erlenbach, J.A., Leacock, W.B., Stanford, J.A., Robbins, C.T., and Armstrong, J.B. 2018. Phenological tracking associated with increased salmon consumption by brown bears. *Sci. Rep.* **8**(1): 11008.
- Delgiudice, G.D., Moen, R.A., Singer, F.J., and Riggs, M.R. 1988. Winter nutritional restriction and simulated body condition of Yellowstone elk and bison before and after the fires of 1988. *Wildl. Monogr.* **147**: 1-60.
- Dell'Arte, G.L., Laaksonen, T., Norrdahl, K., and Korpima, E. 2007. Variation in the diet composition of a generalist predator, the red fox, in relation to season and density of main prey. *ACTA Oecologica* **31**: 276–281. doi:10.1016/j.actao.2006.12.007.
- Droghini, A., and Boutin, S. 2018. Snow conditions influence grey wolf (*Canis lupus*) travel paths: the effect of human-created linear features. *Can. J. Zool.* **96**(1): 39–47. doi:10.1139/cjz-2017-0041.
- Dwinnell, S.P.H., Sawyer, H., Randall, J.E., Beck, J.L., Forbey, J.S., Fralick, G.L., and Monteith, K.L. 2019. Where to forage when afraid: does perceived risk impair use of the foodscape? *Ecol. Appl.* **29**(7). doi:10.1002/eap.1972.

- Elbroch, M. 2003. Mammal tracks and sign: a guide to North American species. Stackpole Books, Mechanicsburg, Massachusetts, USA.
- Elton, C., and Nicholson, M. 1942. The ten-year cycle in numbers of the Lynx in Canada. *J. Anim. Ecol.* **11**(2): 215. doi:10.2307/1358.
- Floyd, T.J., Mech, D.L., and Jordan, P.A. 1978. Relating wolf scat content to prey consumed Author (s): Theodore J . Floyd , L . David Mech and Peter A. Jordan Published by: Wiley on behalf of the Wildlife Society Stable URL : <http://www.jstor.org/stable/3800814> Accessed : 12-04-2016 17 : 52 UTC. *J. Wildl. Manage.* **42**(3): 528–532.
- Fryxell, J.M., Mosser, A., Sinclair, A.R.E., and Packer, C. 2007. Group formation stabilizes predator-prey dynamics. *Nature* **449**(7165): 1041–1043. doi:10.1038/nature06177.
- Fuller, T.K., and Keith, L.B. 1980. Wolf population dynamics and prey relationships in Northeastern Alberta. *J. Wildl. Manage.* **44**(3): 583. doi:10.2307/3808006.
- Gable, T.D., and Windels, S.K. 2018. Kill rates and predation rates of wolves on beavers. *J. Wildl. Manage.* **82**(2): 466–472. doi:10.1002/jwmg.21387.
- Gable, T.D., Windels, S.K., and Bruggink, J.G. 2017. The problems with pooling poop: confronting sampling method biases in wolf (*Canis lupus*) diet studies. *Can. J. Zool.* **95**(11): 843–851. doi:10.1139/cjz-2016-0308.
- Gable, T.D., Windels, S.K., Bruggink, J.G., and Homkes, A.T. 2016. Where and how wolves (*Canis lupus*) kill beavers (*Castor canadensis*). *PLoS One* **11**(12): 14–17. doi:10.1371/journal.pone.0165537.
- Garrott, R.A., Bruggeman, J.E., Becker, M.S., Kalinowski, S.T., and White, P.J. 2007. Evaluating prey switching in wolf-ungulate systems. *Ecol. Appl.* **17**(6): 1588–1597. doi:10.1890/06-1439.1.

- Hairston, N., Smith, F., and Slobodkin, L. 1960. Community structure, population control, and competition. *Am. Nat.* **94**(879): 421-425.
- Harvey L, Fortin D. 2013. Spatial heterogeneity in the strength of plant-herbivore interactions under predation risk: the tale of bison foraging in Wolf Country. *PLoS ONE* **8**(9): e73324.
<https://doi.org/10.1371/journal.pone.0073324>
- Hayes, R.D., and Harestad, A.S. 2000. Demography of a recovering wolf population in the Yukon. *Can. J. Zool.* **78**(1): 36–48. doi:10.1139/cjz-78-1-36.
- Hecker, L.J., Edwards, M.A., Nielsen, S.E. 2021. Assessing the nutritional consequences of switching foraging behavior in wood bison. *Ecol. Evol.* **11**(22): 16165-16176. doi: 10.1002/ece3.8298
- Hofer, H., East, M.L. 1993. The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. II. Intrusion pressure and commuters' space use. *Anim. Behav.* **46**(3): pp. 559-574.
- Holling, C.S. 1959. Some characteristics of simple types of predation and parasitism. *Can. Entomol.* **91**(7): 385-398.
- Horne, J.S., Hurley, M.A., White, C.G., and Rachael, J. 2019. Effects of wolf pack size and winter conditions on elk mortality. *J. Wildl. Manage.* **83**(5): 1103–1116. doi:10.1002/jwmg.21689.
- Hudson, R.J., and Christopherson, R.J. 1985. Maintenance metabolism. *In* *Bioenergetics of Wild Herbivores*. pp. 121–142. doi:10.1201/9781351070218.
- Huggard, D.J. 1993. Effect of snow depth on predation and scavenging by gray wolves. *J. Wildl. Manage.* **57**(2): 382. doi:10.2307/3809437.
- Hunter, M.D., and Price, P.W. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**(3): 724–732.

- Jaffe, R. 2001. Winter wolf predation in an elk-bison system in Yellowstone National Park, Wyoming. Montana State University.
- Jedrzejewski, W., Schmidt, K., Theuerkauf, J., Jedrzejewska, B., Selva, N., Zub, K., and Szymura, L. 2002. Kill rates and predation by wolves on ungulate populations in Bialowieza Primeval Forest (Poland). *Ecology* **83**(5): 1341. doi:10.2307/3071948.
- Joly, D.O., and Messier, F. 2005. The effect of bovine tuberculosis and brucellosis on reproduction and survival of wood bison in Wood Buffalo National Park. *J. Anim. Ecol.* 543-551.
- Kahlert, J. 2003. The constraint on habitat use in wing-moulting Greylag Geese (*Anser anser*) caused by anti-predator displacements. *Ibis*. 145: E45-E52. doi: 10.1046/j.1474-919X.2003.00146.x
- Karanth, K.U., and Sunquist, M.E. 1995. Prey selection by tiger, leopard and dhole in Tropical Forests. *J. Anim. Ecol.* **64**(4): 439. doi:10.2307/5647.
- Kauffman M.J., Varley N., Smith D.W., Stahler D.R., MacNulty D.R., Boyce M.S. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecol Lett.* **10**(8):690–700.
- Kautz, T.M., Belant, J.L., Beyer, D.E., Strickland, B.K., and Duquette, J.F. 2020. Influence of body mass and environmental conditions on winter mortality risk of a northern ungulate: evidence for a late-winter survival bottleneck. *Ecol. Evol.* **10**(3): 1666–1677. doi:10.1002/ece3.6026.
- Kennedy, A.J., and Carbyn, L.N. 1981. Identification of wolf prey using hair and feather remains with special reference to western Canadian National Parks. Edmonton.
- King, C.M., and Powell, R.A. 1990. The natural history of weasels and stoats: ecology, behaviour, and management. Oxford University Press.
- Kittle, A. M., Anderson, M., Avgar, T., Baker, J. A., Brown, G. S., Hagens, J., Iwachewski, E., Moffatt, S., Mosser, A., Patterson, B. R., Reid, D. E. B., Rodgers, A. R., Shuter, J., Street, G. M., Thompson, I. D., Vander Vennen, L. M., & Fryxell, J. M. 2017. Landscape-level wolf space use is correlated

with prey abundance, ease of mobility, and the distribution of prey habitat. *Ecosphere*, **8**(4).

<https://doi.org/10.1002/ecs2.1783>

Klare, U., Kamler, J.F., and MacDonald, D.W. 2011. A comparison and critique of different scat-analysis methods for determining carnivore diet. *Mamm. Rev.* **41**(4): 294–312. doi:10.1111/j.1365-2907.2011.00183.x.

Knopff, K.H., Knopff, A.A., Kortello, A., and Boyce, M.S. 2010. Cougar kill rate and prey composition in a multiprey system. *J. Wildl. Manage.* **74**(7): 1435–1447. doi:10.2193/2009-314.

Knopff, K.H., Knopff, A.A., Warren, M.B., and Boyce, M.S. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. *J. Wildl. Manage.* **73**(4): 586–597. doi:10.2193/2008-294.

Latham, D.M.A., Latham, C.M., Knopff, K.H., Hebblewhite, M., Boutin, S. 2013. Wolves, white-tailed deer, and beaver: implications of seasonal prey switching for woodland caribou declines. *Ecography* **36**: 1276-1290. doi: 10.1111/j.1600-0587.2013.00035.x

Lindstrom, E.R.I.K. 1983. Condition and growth of red foxes (*Vulpes vulpes*) in relation to food supply. *J. Zool.* (199): 117–122.

MacNulty, D.R., Tallian, A., Stahler, D.R., and Smith, D.W. 2014. Influence of group size on the success of wolves hunting bison. *PLoS One* **9**(11): 1–8. doi:10.1371/journal.pone.0112884.

Mattioli, L., Capitani, C., Gazzola, A., Scandura, M., and Apollonio, M. 2011. Prey selection and dietary response by wolves in a high-density multi-species ungulate community. *Eur. J. Wildl. Res.* **57**(4): 909–922. doi:10.1007/s10344-011-0503-4.

Mech, L.D., Smith, D.W., Murphy, K.M., and MacNulty, D.R. 2001. Winter severity and wolf predation on a formerly wolf-free elk herd. *J. Wildl. Manage.* **65**(4): 998–1003.

Mech, L.D. and Boitani, L. 2007. *Wolves: Behaviour, Ecology, and Conservation*. University of Chicago

Press, Chicago, IL.

Messier, F. 1995. On the functional and numerical responses of wolves to changing prey density. *In* Ecology and conservation of wolves in a changing world. *Edited by* L.N. Caryn, S.H. Fritts, and D.R. Seip. Canadian Circumpolar Institute, Edmonton, Canada. pp. 187-198

Metz, M.C., Smith, D.W., Vucetich, J.A., Stahler, D.R., and Peterson, R.O. 2012. Seasonal patterns of predation for gray wolves in the multi-prey system of Yellowstone National Park. *J. Anim. Ecol.* **81**(3): 553–563. doi:10.1111/j.1365-2656.2011.01945.x.

Mills, G.L. 1996. Carnivore behavior, ecology, and evolution. *Edited By* J. Gittleman. Cornell University Press.

Mills, S.L., Zimova, M., Oyler, J., Running, S., Abatzoglou, J.T., and Lukacs, P.M. 2013. Camouflage mismatch in seasonal coat color due to decreased snow duration. *PNAS.* 110(18) 7360-7365. doi: 10.1073/pnas.1222724110

Morehouse, A and Boyce, M. 2011. From venison to beef: seasonal changes in wolf diet composition in a livestock grazing landscape. *Front. Ecol. Environ.* **9**(8).

Murdoch, W.W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* **39**(4): 335–354.

Neilson, E.W., and Boutin, S. 2017. Human disturbance alters the predation rate of moose in the Athabasca oil sands. *Ecosphere* **8**(8). doi:10.1002/ecs2.1913.

Nelson, M.E., and Mech, L.D. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. *J. Wildl. Manage.* **50**(3): 471–474.

Novakowski, N.S. 1965. Population dynamics of a beaver population in northern latitudes. University of Saskatchewan.

- O'Donovan, S.A., Budge, S.M., Hobson, K.A., Kelly, A.P., and Derocher, A.E. 2018. Intrapopulation variability in wolf diet revealed using a combined stable isotope and fatty acid approach. *Ecosphere* **9**(9). doi:10.1002/ecs2.2420.
- Otranto, D., and Deplazes, P. 2019. Zoonotic nematodes of wild carnivores. *Int. J. Parasitol. Parasites Wildl.* **9**(December 2018): 370–383. doi:10.1016/j.ijppaw.2018.12.011.
- Parker, K.L., Robbins, C.T. and Hanley, T.A.. 1984. Energy expenditures for locomotion by mule deer and elk. *J. Wild. Man.* 474-488.
- Parker, K.L., Barboza, P.S., and Gillingham, M.P. 2009. Nutrition integrates environmental responses of ungulates. *Funct. Ecol.* **23**(1): 57–69. doi:10.1111/j.1365-2435.2009.01528.x.
- Patterson, B.R., Benjamin, L.K., and Messier, F. 1998. Prey switching and feeding habits of eastern coyotes in relation to snowshoe hare and white-tailed deer densities. *Can. J. Zool.* **76**(10): 1885–1897. doi:10.1139/z98-135.
- Peterson, R.O., and Allen, D.L. 1974. Snow conditions as a parameter in moose-wolf relationships. *Nat. Can.* **101**: 481–492.
- Peterson, R.O., and Ciucci, P. 2003. The wolf as a carnivore. *In Wolves: behaviour, ecology, and conservation. Edited by L.D. Mech and L. Boitani.* University of Chicago Press, Chicago, USA. pp. 104–130.
- Power M. E. 1992. Top-down and bottom-up forces in food webs: do plants have primacy. *Ecology* **73**(3): 733–746.
- R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.r-project.org>.
- Renecker, L.A., and Hudson, R.J. 1993. Morphology, bioenergetics, and resource use: patterns and processes. *In Hoofed Mammals of Alberta.* Lone Pine Publishing, Edmonton. pp. 141–163.

- Robbins, C. 1983. Wildlife feeding and nutrition. Academic Press, Inc, New York.
- le Roux, E., Marneweck, D.G., Clinning, G., Druce, D.J., Kerley, G.I.H., and Cromsigt, J.P.G.M. 2019. Top-down limits on prey populations may be more severe in larger prey species, despite having fewer predators. *Ecography (Cop.)*. **42**(6): 1115–1123. doi:10.1111/ecog.03791.
- Sand, H., Eklund, A., Zimmermann, B., Wikenros, C., and Wabakken, P. 2016. Prey selection of scandinavian wolves: single large or several small? *PLoS One* **11**(12): 1–17. doi:10.1371/journal.pone.0168062.
- Sand, H., Wabakken, P., Zimmermann, B., Johansson, Ö., Pedersen, H.C., and Liberg, O. 2008. Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? *Oecologia* **156**(1): 53–64. doi:10.1007/s00442-008-0969-2.
- Sato, Y., Mano, T., and Takatsuki, A. 2000. Applicability of the point-frame method for quantitative evaluation of bear diet. *Wildl. Soc. Bull.* **28**(2): 311-316.
- Shave, J.R., Cherry, S.G., Derocher, A.E., and Fortin, D. 2020. Seasonal and inter-annual variation in diet for gray wolves *Canis lupus* in Prince Albert National Park, Saskatchewan. *Wildlife Biol.* **2020**(3). doi:10.2981/wlb.00695.
- Sheppard, A.H., Hecker, L.J., Edwards, M.A., and Nielsen, S.E. 2021. Determining the influence of snow and temperature on the movement rates of wood bison (*Bison bison athabasca*). *Can. J. Zool.* **99**(6): 489–496. doi: 10.1139/cjz-2020-0280.
- Shury, T.K., Nishi, J.S., Elkin, B.T., and Wobeser, G.A. 2015. Tuberculosis and brucellosis in wood bison (*Bison bison athabasca*) in Northern Canada: a renewed need to develop options for future management. *J. Wildl. Dis.* **51**(3): 543–554. doi:10.7589/2014-06-167.
- Sih, A. 2005. Predator-prey space use as an emergent outcome of a behavioral response race. *Ecology of predator-prey interactions*. Oxford University Press Inc, New York, New York. pp. 240 - 255

- Simms, D.A. 1979. North American weasels: resource utilization and distribution. *Can. J. Zool.* **57**(3): 504–520. doi:10.1139/z79-061.
- Sinclair, A.R.E., and Norton-Griffiths, M. (*Editors*). 1979. *Serengeti: dynamics of an ecosystem*.
- Sinclair, A.R.E., Pech, R.P., Dickman, C.R., Hik, D., Mahon, P., and Newsome, A.E. 1998. Predicting effects of predation on conservation of endangered prey. *Conserv. Biol.* **12**(3): 564–575. doi:10.1111/j.1523-1739.1998.97030.x.
- Smith, D.W., Bangs, E.E., Oakleaf, J.K., Mack, C., Fontaine, J., Boyd, D., Jimenez, M., Pletscher, D.H., Niemeyer, C.C., Meier, T.J., Stahler, D.R., Holyan, J., Asher, V.J., and Murray, D.L. 2010. Survival of colonizing wolves in the northern Rocky Mountains of the United States, 1982–2004. *J. Wildl. Manage.* **74**(4): 620–634. doi:10.2193/2008-584.
- Smith, D.W., Mech, L.D., Meagher, M., Clark, W.E., Jaffe, R., Philips, M.K., and Mack, J.A. 2000. Wolf-bison interactions in Yellowstone National Park. *J. Mammal.* **81**(4): 1128–1135.
- Stelfox, J.B. 1993. Distributions. *In* *Hoofed Mammals of Alberta*. Lone Pine Publishing, Edmonton. pp. 45–61.
- Stirling, I., Lunn, N.J., and Iacozza, J. 1999. Long-term trends in the population ecology of polar bears in western Hudson Bay in relation to climatic change. *Arctic* **52**(3): 294–306. doi:10.14430/arctic935.
- Sutherland, W.J. 1998. The importance of behavioral studies in conservation biology. *Anim. Behav.* **56**(4): 801–809. doi:10.1006/anbe.1998.0896.
- Szepanski, M.M., Ben-David, M., and Van Ballenberghe, V. 1999. Assessment of anadromous salmon resources in the diet of the Alexander Archipelago wolf using stable isotope analysis. *Oecologia* **120**(3): 327–335. doi:10.1007/s004420050866.
- Taillon, J., Brodeur, V., Festa-Bianchet, M., and Côté, S.D. 2011. Variation in body condition of migratory caribou at calving and weaning: which measures should we use? *Ecoscience* **18**(3): 295–

303. doi:10.2980/18-3-3447.

Tallian, A., Smith, D.W., Stahler, D.R., Metz, M.C., Wallen, R.L., Geremia, C., Ruprecht, J., Wyman, C.T., and MacNulty, D.R. 2017. Predator foraging response to a resurgent dangerous prey. *Funct. Ecol.* **31**(7): 1418–1429. doi:10.1111/1365-2435.12866.

Telfer, E.S., and Kelsall, J.P. 1979. Studies of morphological parameters affecting ungulate locomotion in snow. *Can. J. Zool.* **57**(11): 2153–2159. doi:10.1139/z79-283.

Telfer, E.S., and Kelsall, J.P. 1984. Adaptation of some large North American mammals for survival in Snow. *Ecology* **65**(6): 1828–1834.

Tse, C., Bullard, J., Rusk, R., Douma, D., and Plourde, P. 2019. Surveillance of Echinococcus tapeworm in coyotes and domestic dogs in Winnipeg, Manitoba. *Canada Commun. Dis. Rep.* **45**(7/8): 171–176. doi:10.14745/ccdr.v45i78a01.

Voigt, D.R., Kolenosky, G.B., and Pimlott, D.H. 1976. Changes in summer foods of wolves in Central Ontario. *J. Wildl. Manage.* **40**(4): 663–668.

Weaver, J.L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. *J. Wildl. Manage.* **57**(3): 534–538.

Weaver, J.L., and Fritts, S.H. 1979. Comparison of coyote and wolf scat diameters. *J. Wildl. Manage.* **43**(3): 786–788.

Webb, N.F., Hebblewhite, M., and Merrill, E.H. 2008. Statistical methods for identifying wolf kill sites using global positioning system locations. *J. Wildl. Manage.* **72**(3): 798–807.

White, T.C.R. 1978. The importance of a relative shortage of food in animal ecology. *Oecologia* **33**: 71–86.

Whittaker, D.G., and Lindzey, F.G., 1999. Effect of coyote predation on early fawn survival in sympatric

deer species. *Wildl. Soc. Bull.* **27**(2): 256-262.

Wilmers, C.C., Metz, M.C., Stahler, D.R., Kohl, M.T., Geremia, C., and Smith, D.W. 2020. How climate impacts the composition of wolf-killed elk in northern Yellowstone National Park. *J. Anim. Ecol.* **89**(6): 1511–1519. doi:10.1111/1365-2656.13200.

Williams, A. C., & Flaxman, S. M. 2012. Can predators assess the quality of their prey's resource? *Anim. Beh.*, **83**(4), 883–890. <https://doi.org/10.1016/J.ANBEHAV.2012.01.008>

Wimp, G.M., Ries, L., Lewis, D., and Murphy, S.M. 2019. Habitat edge responses of generalist predators are predicted by prey and structural resources. *Ecol.* **100**(6), e02662

Wittmer, H.U., Sinclair, A.R.E., and McLellan, B.N. 2005. The role of predation in the decline and extirpation of woodland caribou. *Oecologia* **144**(2): 257–267. doi:10.1007/s00442-005-0055-y.

Appendix

Class	Hours	Dianne	McIvor
A	> 24	21 (14)	14 (11)
B	20-24	0 (0)	2 (1)
C	16-20	8 (5)	3 (1)
D	12-16	16 (11)	24 (8)
E	8-12	47 (16)	53 (8)
F	4-8	91 (25)	114 (13)
G	2-4	65 (9)	70 (9)

Appendix 1: Summer wolf cluster sites generated by cluster analysis and separated into classifications (A – G) based on handling times of at least 2 hours from the Dianne and McIvor packs located near Ronald Lake, Alberta, Canada. The total number of summer season cluster sites was 477 with 131 visited, as shown by numbers in brackets. Due to the pre-defined maximum duration of each cluster at no more than 96 hours in length, instances of long residency times or revisits by wolves were characterized by multiple clusters.

Class	Hours	Dianne	McIvor	Southline
A	> 24	14 (13)	12 (11)	9 (9)
B	20-24	9 (3)	5 (1)	3 (2)
C	16-20	5 (2)	15 (4)	6 (1)
D	12-16	16 (3)	34 (7)	12 (4)
E	8-12	24 (0)	19 (2)	17 (0)
F	4-8	61 (1)	40 (2)	21 (1)

Appendix 2: Winter wolf cluster sites generated by cluster analysis and separated into classifications (A – F) based on handling times of at least 4 hours from the Dianne, McIvor and Southline packs located near Ronald Lake, Alberta, Canada. The total number of winter season cluster sites was 365 with 66 visited, as shown by numbers in brackets. Due to the pre-defined maximum duration of each cluster at no more than 96 hours in length, instances of long residency times or revisits by wolves were characterized by multiple clusters.

A



B



Appendix 3: Snow measuring stations placed in different landcover types within the Ronald Lake Bison Herd (*Bison bison athabascae*) home range in northern Alberta, Canada. Photo A is in summer and photo B is in winter. The numbers represent centimeters and average snow depths from four stations were used as a daily snow depth measurement.



Appendix 4: Juvenile moose (*Alces alces*) remains found at a wolf (*Canis lupus*) cluster site classified as a scavenging site due to intact bones and rumen near Ronald Lake, Alberta, Canada.



Appendix 5: Separating prey remains from wolf (*Canis lupus*) scat material collected near Ronald Lake, Alberta, Canada, using a series of sieves.



Appendix 6: Prey remains extracted from wolf (*Canis lupus*) scat samples collected near Ronald Lake, Alberta, Canada.