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Grey wolf selection for moose calves and factors influencing prey species consumption in southeastern Manitoba

Taylor Naaykens[1], James D. Roth[1], Daniel Dupont[2]

[1]Department of Biological Sciences, University of Manitoba, Winnipeg, MB, Canada R3T 2N2
[2]Manitoba Conservation and Water Stewardship, Winnipeg MB, Canada, R3J 3W3

contact author: jim.roth@umanitoba.ca

Abstract

Moose populations in southern Manitoba have declined in recent years, and although the cause of the decline is yet unknown, wolf predation has been suggested as a potential contributing factor. We used fecal analysis combined with telemetry data to test the influences of social structure, relative prey abundance, and season on wolf consumption of moose and other prey species. We tested for influences of social structure, relative prey abundance, and summer time period specifically on consumption of moose calves in summer, and compared consumption of moose calves to the relative occurrence of calves in the overall moose population. Wolves hunting in a pack were more likely to consume moose than solitary wolves, while solitary wolves were more likely to consume other non-ungulate prey. Solitary wolves were more likely to eat deer in areas where deer were more abundant, but we found no difference in consumption of moose by solitary wolves between areas of greater moose abundance. Beaver were consumed more in summer, but consumption of other prey species did not differ seasonally. We found no effect of social structure, relative prey abundance, or summer time period on consumption of moose calves. Wolves killed calves preferentially, in excess of their relative abundance, only in late summer. Management of wolves aimed at decreasing wolf numbers in southeastern Manitoba may also reduce predation on adult moose by decreasing pack sizes and interrupting the social organization.

Keywords: Alces alces, Canis lupus, social structure, calves, diet, fecal analysis

1. Introduction

Apex predators can influence ecosystem dynamics by limiting populations of selected prey species (Ripple and Beschta, 2012). In terrestrial systems, the importance of the top-down effects of predation on limiting prey populations, relative to the bottom-up effects of nutrient limitation, has been heavily debated (Hairston et al., 1960; Kay, 1998; Ripple and Beschta, 2008). Throughout the boreal forest biome, however, predation by grey wolves (*Canis lupus*) can limit prey populations when the bottom-up effects of nutrient limitation are negligible (Messier and Crête, 1985; Crête and Manseau, 1996; Hayes et al., 2003; Ripple and Beschta, 2003). Wolves are opportunistic generalists, able to consume a variety of prey items, but they typically depend on only one or two prey species for the bulk of their diet (Mech, 1970). Many factors can influence what prey species are selected by wolves, including season, the number of wolves hunting cooperatively at a given time, and the relative abundance of coexisting prey species (Potvin et al., 1988; Mech and Boitani, 2003; Latham et al., 2011). Furthermore, individuals of a particular prey species may be more susceptible to predation based on their health relative to other individuals in the population (Mech, 1970; Sand et al., 2012). Predicting the pattern of prey selection in a given wolf-prey system at a given time can be difficult, owing to the unique combination of ecological factors that characterize each system (Mech and Boitani, 2003). In many parts of North America, wolf-prey systems are subject to drastic seasonal environmental changes. In particular, seasonal snow accumulation can restrict wolf access to certain prey species, while increasing the vulnerability of others. Beavers (*Castor canadensis*), a common prey item for wolves, become relatively inaccessible to wolves in winter by remaining inside their lodges and below the ice (Muller-Schwarze, 2011). However, beaver remains have been reported in winter wolf scats, as beavers are the bait of choice for trappers, and wolves have occasionally been observed attempting to dig beavers out of their lodges in winter (Dupont, pers. obs.). Ungulates (hoofed mammals such as deer, moose, elk, and caribou), on the other hand, become more vulnerable to predation in the winter, as their movement and access to food can be impeded by deep snow conditions (Mech and Boitani, 2003). In winter, the diets of wolves in North America tend to be dominated by ungulates (Mech, 1970). Where more than one species of ungulate is present, optimal foraging theory suggests that wolf diet will be determined by the most abundant species with the lowest handling time (Charnov, 1976). For instance, where white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces*) coexist, deer tend to make-up a disproportionately large part of the wolf diet (Mech, 1970; Potvin et al., 1988) because they are easier to handle and have shorter legs and smaller hooves than moose, making them much easier to catch in snow (Nelson and Mech, 1986). Additionally, deer attempt to flee in the face of wolf attacks, whereas moose tend to stand their ground and aggressively defend themselves, presenting a greater risk of injury to any attackers (Mech and Boitani, 2003). Despite the greater risk inherent in hunting moose, wolves travelling in a pack may tend to focus more on the larger species as it provides more food per capita (Zimmerman, 2015). Wolves are well known for hunting in cooperative packs that average between 3-4 individuals, with variation among regions (Ballard et al., 1987). Packs are formed by a mating pair and their progeny, with the mating pair typically leading the hunt (Borg et al., 2015). The general tendency, in terms of prey selection, is that larger packs focus on large prey, like moose, while smaller packs target small prey (Mech and Boitani, 2003). However, wolf populations exploited by human hunting may be represented by smaller pack sizes, though still target large prey (Mech and Boitani, 2003). Large pack size is not absolutely necessary for hunting large prey, as wolves in pairs, and even solitary wolves, have been recorded killing prey as large as moose and bison (Mech, 1970). Wolves tend to travel in nomadic packs during winter, but then radiate out from a central den site during the pup-rearing period from spring to early fall (Mech and Boitani, 2003; Demma and Mech, 2009). During this time, wolves will not necessarily travel as a single pack, but rather travel alone or in small groups, returning to the den to provide pups with food (Mech, 1970). Maturing individuals may periodically leave the group in exploratory pre-dispersal movements, or disperse permanently from their natal pack to mate and establish their own pack (Mech, 1970). During such excursions, the diets of solitary individuals may be comprised more of small, easily catchable prey, in order to maximize energetic profitability while minimizing risk of injury and energy expenditure inherent in attacking larger prey (Mech and Boitani, 2003).

Changes in relative prey abundance may cause wolves to target certain prey, regardless of pack size (Mech and Boitani, 2003). Relative prey abundance plays a role in determining wolf diet (Messier, 1991), and feeding habits may shift with changes in prey populations (Voight et al., 1976). In a multi-prey system, a particular prey species may dominate wolf diet simply because of its high relative abundance on the landscape. For example, in northeastern Alberta, moose were the most abundant ungulate on the landscape and the primary prey of wolves in the 1990s (Latham et al., 2011). A decade later, white-tailed deer abundance increased, such that, while moose were still abundant, deer became the primary prey item due to the relative decrease in search time and greater ease of handling (Latham et al., 2011).

Within a given prey species some individuals may also be more susceptible to predation than others. Wolves tend to kill injured, sick, weak, or otherwise debilitated individuals, as well as individuals from more vulnerable age classes (Pimlott et al., 1969; Peterson, 1977). The tendency for wolves to take less fit or more vulnerable individuals is largely a mechanical process, whereby weakened individuals are simply less successful at fleeing or fighting off an attack than healthy, prime-aged individuals (Peterson, 1977). Within moose populations, juveniles (< 1-year old) are often the most commonly killed age class, though contribute proportionally less to wolf diet, in terms of biomass, than adults (Mech and Nelson, 2013). Calves are born in early spring and remain vulnerable throughout their first year of life, during which time they are defended from predators by their mother (Mech and Boitani, 2003). While calves may be easy to handle on their own, it takes the efforts of a whole wolf pack to separate the cow from the calf (Mech and Boitani, 2003). It is thought that wolves can have their greatest demographic effects on moose populations by their predation on young-of-the-year (Pimlott, 1967; Mech, 1970). This effect is exacerbated when wolves co-occur with bears, who can also be an important predator on neonate moose (Zager and Beecham, 2006). While the effects of wolf predation on prey populations have been studied extensively, they remain a subject of great controversy owing to the variation of ecological factors that render the systems in each case study unique (Gese and Knowlton, 2001; Mech and Peterson, 2003).

In accessible regions of southern Manitoba, moose populations have experienced a decline over the last several years (Leavesley, 2010). Although the exact cause of the decline has not been determined, possible contributing factors include predation, harvest by human hunters, habitat degradation, and transmission of meningeal brain worm (*Parelaphostrongylus tenuis*) and giant liver fluke (*Fascioloides magna*) (Shura and Roth, 2013). Wolf predation has been suggested as a contributing factor in the decline, prompting a 5-year trapper incentive program in 2011 intended to increase the wolf harvest and temporarily reduce predation pressure on moose, though it is unclear the extent to which wolves play a role. A recent study of a multi-prey system in southeastern Manitoba used stable isotope analysis to reconstruct wolf diet and found moose to be important summer prey (Mocker, 2015). However, this study was unable to distinguish between adult and calf moose in the wolf diet and it is possible that the importance of moose in the wolf summer diet could be heavily focused on calves. For moose populations typified by low and variable calf survival, predation on calves has been shown to be a major limiting factor (Larsen et al., 1989; Testa, 2004; Bertram and Vivian, 2002).

The objective of this research was to estimate the importance of moose calves in the summer diets of wolves using analyses of scats collected by following five satellite-collared wolves equipped with satellite transmitters, in order to better understand the role wolves may play in the moose decline. If the main population limiting effect of wolves on moose is through reducing recruitment, selection for calves should be reflected in the scat contents.

Scat analysis, in conjunction with telemetry data, also allowed us to examine the effects wolf social structure, in terms of solitary versus group animals, on diet. We also examined the effects of relative prey densities, in terms of high moose versus deer abundance, as well as season. We expected that scats from solitary wolves would contain less moose and moose calves, and more deer, beaver and other alternative prey, as preying on moose would be more dangerous and energetically costly when solitary compared to hunting with a pack. In areas of high relative moose density, we expected more moose and moose calves and less deer would be consumed, and more deer would be consumed in areas of high relative deer density. In winter, we expected that more deer and moose would be consumed, as they would be inhibited by snow to varying degrees, while beaver and other alternative prey would be consumed more in summer as they are less accessible beneath the snow. Overall, this study attempted to characterize the diets of grey wolves in southeastern Manitoba and provide a deeper understanding of which factors are important to prey selection by testing the following hypotheses:

H1: Wolves selectively kill moose calves throughout summer because they are more vulnerable than adult moose.

Prediction: The proportion of scats containing calves is greater than the proportion of calves in the overall moose population.

H2: Solitary wolf diet differs from pack wolf diet because solitary wolves cannot easily take down large prey.

Prediction: Scats from solitary wolves contain less moose and moose calves, and more deer, beaver and other alternative prey.

H3: Regional differences in relative prey abundance affects wolf diet, as wolves are more likely to consume prey species that they have a higher probability of encountering.

Prediction: Scats from areas of high moose density contain more moose and moose calves and less deer, while scats from areas of high deer density contain more deer and less moose and moose calves.

H4: Wolf diets vary seasonally, as ungulates are easier to catch in snow and more readily available than smaller alternative prey in winter.

Prediction: Scats produced in winter are more likely to contain ungulate prey, while scats produced in summer are more likely to contain beaver and other alternative prey.

2. Methods

2.1. Study Area

The study was based in Game Hunting Area (GHA) 26 in southeastern Manitoba, between Lake Winnipeg and the Ontario border, centered at 95°55′6″W, 50°55′33″N (Mocker, 2015). The landscape is dominated by Boreal Shield forest, where typical vegetation consists of jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and trembling aspen (*Populus tremuloides*) (Davis, 2012). Much of the landscape is also dominated by wetlands, characterized by Sphagnum moss and black spruce (*Picea mariana*) (Davis, 2012). Wolves co-occur with black bears (*Ursus americanus*) in the study area. Moose and white-tailed deer are both found within GHA 26, although moose are concentrated in the northern portion of the area and deer are concentrated in the south (Mocker, 2015). Beaver, and snowshoe hare (*Lepus americanus*) are also common throughout the study area. Since 2010, licensed moose hunting has not been permitted within GHA 26 and, in selected parts of the area, there has been a conservation closure restricting treaty-based harvesting since 2012.

2.2. Scat Collection and Processing

We used wolf scats collected by Manitoba Conservation and Water Stewardship throughout 2014 and 2015. Scats were collected by tracking the movements of five wolves, from three different packs, to potential resting, kill, or scavenge sites. Scats collected at these sites were assumed to have been produced by the collared wolf or members of its pack. We used Global Positioning System (GPS) data from three wolves collared in February 2014 and two wolves collared in February 2015. The locations of potential sites for scat collection were determined by identifying GPS clusters in the telemetry data. Clusters were defined as a minimum of two telemetry points occurring within 300 m and 4 days of each other (DeCesare 2012). Most sites visited, however, were formed by a minimum of 8 telemetry points, partially due to limited resources for field investigations. A limit of 8 telemetry points was used because it represented clusters that were most likely to be kill sites (DeCesare 2012). Some smaller clusters, ranging between 3-7 telemetry points, were also visited based on their location on the landscape, such as in a swamp or on a riverbank to increase prey representation in wolf diet across the landscape. Sites were not visited more than once for scat collection. Telemetry data was analyzed for cluster sites every 2-3 weeks. Cluster sites were subsequently visited within 1-30 days following analysis and designated as kill, scavenge, or resting sites based on presence and state of prey carcasses (e.g., scattered remains versus relatively intact, some with heads or antlers sawed off) and wolf beds. Nineteen scats were also collected opportunistically along trails while travelling to cluster sites. Fresh scats were easily identified, but became difficult to age beyond one month. However, it is unlikely that scats of different ages were accidentally combined, as most scats were collected at specific cluster locations which were visited within a specific timeframe and only once by a collared wolf. Prey remains in the scats were recorded on the basis of presence/absence. To avoid pseudoreplication, we considered a single sample to be all scats found at the same site (Marucco et al., 2008). We stored the scats in a -80°C freezer for a minimum of two days to kill any potential parasites (e.g., *Echinococcus granulosus* and *E. multilocularis*). To further decrease any risk of parasitic infection, gloves and a mask were worn while handling all scats. Each scat was initially rinsed in a sieve (mesh size 1.0mm) with warm water to remove non-identifiable amorphic material. The remaining hairs, bone, and other non-digestible materials were stored in labeled paper bags and left to air dry for a minimum of three days. Within each scat, hairs were separated from other non-digestible material such as bones. We thoroughly mixed the hairs in each sample to achieve sample homogeneity, and spread the remains evenly across a white cutting board. The scat was roughly sectioned into quarters and we arbitrarily selected hairs from each section of the scat, for a total of twenty hairs per scat. Swanson (1989) found that identifying more than three hairs per scat was sufficient for multiple species detection, but we selected twenty hairs to increase the likelihood that all prey species in the scat were accounted for, as well as to increase certainty that identification of prey hairs was accurate. We also did a final visual sweep of the scat to ensure that hairs from all species present in the sample had been accounted for. Only guard hairs were considered for identification as underfur is very difficult to distinguish, particularly among ungulate species. We used a reference collection of hairs from representative prey species, gathered from the trophic ecology lab at the University of Manitoba, to identify hairs found in the scat by examining color banding patterns and microscopic appearance under an Olympus BX43 compound microscope. For prey species not included in the reference collection, such as fox, rodent, and bear, images from the Alaska Fur ID Project (Carrlee, 2010) were used for comparison and identification. To distinguish between adult moose and calf hair, we made casts of cuticular scales by placing the hair on a microscope slide covered with clear nail polish and compared the resulting imprint with keys from Adorjan and Kolenosky (1969). This method of identification is commonly used in scat analyses for ungulate age identification (Adorjan and Kolenosky, 1969; Hill, 1979; Ballard et al., 1987). Calf hair imprints display a pattern of imbricate, or overlapping, scales with elongated crenate edges throughout the entire length of the hair (Adorjan and Kolenosky, 1969). Adult moose hair imprints also display an imbricate scale pattern, but with discontinuous crenate scales, rather than elongate, and the crenate edges gradually appear flattened towards the distal region of the hair (Adorjan and Kolenosky, 1969). We compared the proximal and distal regions of each imprint to see if cuticular appearance changed from one end to the other, indicating an adult moose hair. The gross appearance of calf versus adult hairs was also used to help make age determinations.

Calf hairs are deep brown or black in color, and 4-5 cm long, whereas adult hairs are 5-8 cm long (mane hairs are 15-16 cm long) and are typically white at the proximal end and gradually change to grey, with a brown band 1 cm below the black apex (Adorjan and Kolenosky, 1969). Taken together, cuticular scale pattern, length, and color where used to make the final age class determination. This method of determination is only useful until the end of August, by which time most calves should have grown into their winter coat, which is indistinguishable from that of an adult (Messier and Crete, 1985; Theberge and Theberge, 2004). For this reason, the analysis of calf selection only included samples from clusters formed from May 1 to August 30, so as not to mistake calves for adults. A total of 96 samples were processed from 2014 and 2015, 65 of which were from May-August. Eighteen of these samples were made up of 2-4 scats collected at the same site and so were combined into a single sample to avoid pseudoreplication. Across years, 80 samples were collected from summer clusters and 21 samples were collected from winter clusters. Summer and winter were determined by presence or absence of snow on the ground, as reported in the Pinawa weather station archives (Environment Canada 2014, 2015). Snow was absent from April 23-November 11, 2014, and April 13-November 23, 2015.

2.3. Telemetry Data

Satellite collars provided data regarding wolf movements by transmitting signals relaying their GPS locations. In February 2014, four wolves were collared using Lotek 2D Iridium collars programmed to take GPS fixes every two hours. Two wolves were collared from the Gem-Flintstone wolf pack range, located in the south-east portion of the study area, and two wolves were collared from the Quesnel-Bissett wolf pack range, located towards the northern border of the study area. In February 2015, collars were deployed on three wolves, of which two were Lotek 2D Iridium collars and one was a Lotek Lifecycle collar which was programmed to take fixes twice daily. Two collars, one Iridium and one Lifecycle, were deployed on wolves from the Manigotagan wolf pack range across the northern portion of the study area, and one Iridium collar was deployed in the Frenchman wolf pack range. The wolves were captured and collared using physical restraint methods without the use of chemical immobilization. A helicopter was used to locate and approach the animals, and a net gun was used for immobilization. Net gunning was conducted when snow depth was a minimum of 20cm to minimize the risk of injury to the wolves, as well as chase distance and time. Hazing time did not exceed 10 minutes and chase time did not exceed 5 minutes. Chases were called off if the animal indicated signs of extreme stress or exertion. Immobilized wolves were physically restrained using a capture fork, muzzled, blindfolded, and hobbled. Collars were placed on wolves if the collars constituted a maximum of 3% of the body weight, as is standard for animal collaring projects. The collars were meant to last two years, after which time the collars would be released remotely off of the animals by means of a drop-off mechanism. However, all but one collar stopped transmitting within the first year of deployment. Two collars were retrieved in winter 2015 because the collared wolves had been trapped by local trappers, and one was retrieved in February 2016 because the wolf was re-collared. While five of the collars lasted several months, two collars, one from the Quesnel-Bissett pack and one from the Frenchman pack, stopped transmitting early in the year, and were not included in the present study. Using ArcGIS software and telemetry data provided by Manitoba Conservation, we delineated home ranges of the satellite-collared wolves using minimum convex polygon analysis (MCP) (Burch et al., 2005). This method creates polygons enclosing all GPS data points transmitted by a given collar, which represent wolf home range (Mohr, 1947). The polygons were created in ArcGIS, using the Hawth's Tools extension (Beyer, 2004). Home ranges provided the criteria for which to include scats collected opportunistically from unknown wolves. As all scats were collected by tracking satellite-collared wolves, the GPS coordinates of scats collected opportunistically should fall within the home range of a collared wolf. If a scat was found in a delineated home range, its contents were included with scats from the corresponding collared wolf, and a deposition date estimated for that scat based on the date of the nearest telemetry point for that wolf. If a scat was collected from an area where home ranges overlapped, the scat was assigned the wolf ID and deposition date of the nearest telemetry point. Only one opportunistically collected sample was excluded from the total sample size because it was not located within a home range. Each scat was classified as being from the north (moose range) or south (deer range) based on aerial survey data of moose and deer abundances in 2010 and 2013 (Leavesley, 2010). Telemetry data and site investigations were used to determine when a collared wolf was travelling alone versus with a pack. Initially, collars were deployed on two wolves in each of four packs for a total of eight collars. Although three of the transmitters failed, data from those that continued to emit signals from the same pack could be used to determine if the pack had split up. Investigations of cluster sites also produced estimates of pack size. Whether a wolf was travelling alone or with a pack was determined by how many sets of wolf tracks were at the site, how many trails could be seen in the vegetation, and other signs of wolf activity including the number of scats and beds present at the site. In addition, trail cameras placed at several sites throughout the study area were sometimes used for confirmation that a collared wolf was travelling alone. Three cameras were deployed at kill sites in October 2014 to determine the number of wolves travelling in the Quesnel-Bissett pack, and two were deployed in August 2014 at resting sites to determine the number of wolves traveling with the Gem-Flintstone pack. Two more cameras were deployed in May 2015 at den sites in the Manigotagan pack's territory.

2.4. Data Analysis

We used Fisher's exact tests to investigate H2, H3, and H4. Prey types included moose, deer, beaver, and other (including rodents, fish, bear, fox, snowshoe hare, and bird). Subsequent analyses specifically examined consumption of moose calves, and tested for an influence of social structure, relative prey abundance, and time period within the summer. To determine if we needed to control for pack ID, we used only samples from individuals travelling in a group, as one pack produced no samples from solitary individuals while another produced mostly solitary samples with a few samples from group individuals. Packs did not differ in consumption of moose (Fisher's exact test, p=0.075), moose calves (p=0.721), deer (p=0.093), beaver (p=0.173), or other prey (p=0.461), so subsequent analyses pooled samples from different packs. Samples found in the southern part of the study area, where moose were rare and deer predominate, were all from solitary wolves. Additionally, season and social structure may be correlated, given that wolves tend to travel in nomadic groups in the winter and may become solitary in summer (Mech and Boitani, 2003; Demma and Mech, 2009). Therefore, we limited our analysis of the effect of social structure on wolf diet to samples from the northern part of the study area collected in summer. We could not test for effects of social structure in winter, as only one solitary wolf sample was collected in winter and did not facilitate a balanced comparison. Likewise, our analysis of the effects of relative prey density (northern versus southern samples) was limited to samples from solitary wolves in the summer, and our analysis of the effects of season was limited to samples from group individuals in the north. When testing for an effect of time period within summer on consumption of moose calves, we used all samples found within three assigned time periods: parturition, one-month post-parturition, and late summer.

To determine if wolves selected for calves when consuming moose, as proposed in H1, we included only samples from May-August, when calf and adult moose could be distinguished, and used the binomial exact test. This goodness-of-fit test compared observed counts of moose in each age category against expected counts based on the assumed proportion of calves versus adults in the overall moose population. For this analysis, we assumed samples were independent, as previous analyses found no differences in diet among packs.

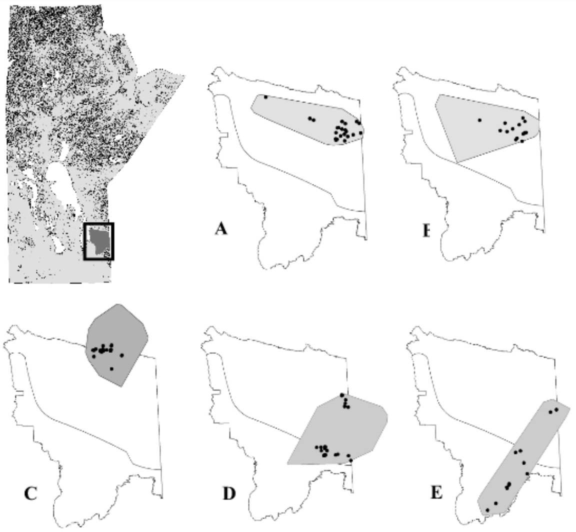

Figure 1: *Game Hunting Area 26, located in southeastern Manitoba. Home ranges of satellite-collared wolves within GHA 26, from the Manigotagan pack (A and B), Quesnel-Bissett pack (C), and Gem-Flintstone pack (D and E) are indicated by grey polygons. Dots represent fecal sample locations. Manigotgan home ranges represent telemetry data from 2015. Quesnel-Bissett and Gem-Flintstone home ranges represent telemetry data from 2014. Line bisecting the study area represents the division between predominantly moose versus deer abundance.*

To account for declining calf abundance over the course of the summer, we adjusted the proportion of calves assumed in the overall population for three summer time periods: 1) May 1 to June 15 represented the period of parturition, when most calves would be born, 2) June 16 to July 16 represented one-month post-parturition, and 3) July 17 to August 30 represented late summer. Several studies have reported moose parturition occurring from around mid-May to mid-June (Ballard et al., 1991; Bowyer et al., 1998; Lenarz et al., 2005) but early May was also included in the period of parturition due to observations of moose calf remains at kill sites earlier in May (Dupont, unpublished data). The period of one-month post-parturition was selected because it was the period for which an estimate of calf mortality was available in the literature (Musante et al., 2010), and the late summer period accounted for the remainder of time in which calf hair could be distinguished from adult hair. Adult moose in Manitoba experience an annual mortality rate of 21% (Manitoba Conservation, unpublished data), but we assumed that most adult mortality occurred in fall and late winter, corresponding with the periods of peak male and female vulnerability (Mech and Boitani, 2003). Data obtained from Manitoba Conservation describing the estimated population size, age structure, cow pregnancy rates, and calf survival in GHA 26 was used to generate calf abundance estimates for Periods 1 and 3. Moose calf mortality at one-month post-parturition is unknown for GHA 26, so we used a reasonable estimate of calf survival for Period 2 from a study in Minnesota (Musante et al., 2010), which is one of few studies on calf survival in which wolves and black bears co-occur and grizzly bears are absent. In Alaska and the Northwest Territories, grizzly bears are a major predator of moose calves and may cause a steeper decline in calves than what might be observed in Manitoba (Gasaway et al., 1992; Stenhouse et al., 1995).

For all analyses we used a significance level of $\alpha = 0.05$, as Fisher's exact test is already highly conservative and the Bonferroni correction is considered overly conservative and of too low statistical power to be practical for use on multiple statistical tests (Moran, 2003; Nakagawa, 2004).

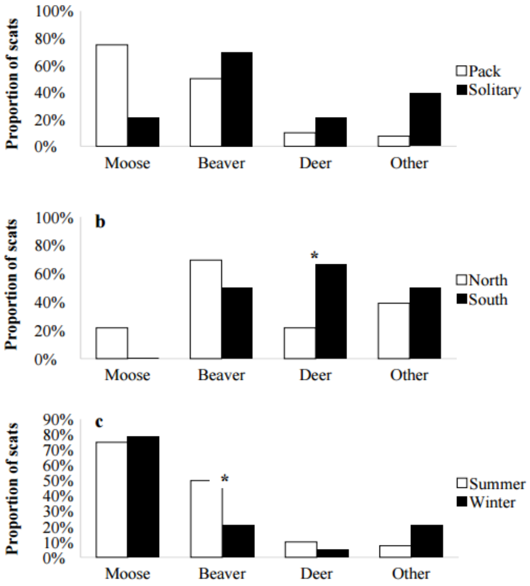

Figure 2: *Proportions of wolf scats containing each prey type from a) solitary versus pack wolves (n=63 samples from the northern region in summer), b) the north (high moose abundance) versus the south (high deer abundance) (n=35 samples from solitary wolves in summer), and c) winter versus summer (n=59 samples from pack wolves in the northern region). Asterisks indicate significance.*

3. Results

The home ranges of the Quesnel-Bissett and Manigotagan wolves were located in the northern portion of the study area, while the home ranges of the Gem-Flintstone wolves were near or below the north/south border (Figure 1). All samples collected in 2015 came from Manigotagan wolves traveling together in the northern portion of the study area, while all 2014 samples came from the Gem-Flintstone and Quesnel-Bissett packs. Given these confounding differences, we were unable to examine annual variation in wolf diet.

A total of 145 prey items were found in 96 fecal samples. Sixty-two samples were collected throughout 2014 and thirty-four samples were collected in 2015. We used samples from all site types when investigating effects on wolf diet because prey remains at all site types still reflect wolf diet in terms of what the animal is consuming. When comparing the

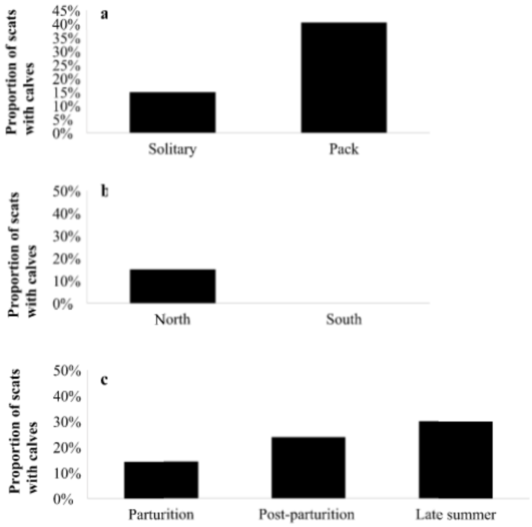

Figure 3: *Proportion of scats containing moose calves from a) solitary versus pack wolves (n=52 samples from the northern area in summer), b) north versus south (n=30 samples from solitary wolves in summer) and c) across three periods of summer (n=62).*

diets of solitary versus pack wolves, using only samples in the northern region during summer, pack wolves were more likely to consume moose than solitary wolves (Fisher's exact test, p<0.0001), while solitary wolves were more likely to consume other prey (p=0.006) (Figure 2a). Social structure did not affect consumption of deer (p=0.267) and beaver (p=0.187) (Figure 2a). During summer, deer were consumed more by solitary wolves in the southern region (p=0.024) than in the northern region, while solitary wolf consumption of moose, beaver, and other prey did not differ between locations (p=0.141, 0.293, and 0.721, respectively) (Figure 2b). Pack wolves in the north consumed beavers more in summer than winter (p=0.048), but no seasonal differences were present in the consumption of moose (p=1.000), deer (p=1.000), or other prey (p=0.197) (Figure 2c).

From May to August of 2014 and 2015, when calves and adult moose could be distinguished, 62 samples, containing 101 prey items, were collected. When considering only samples collected in the northern portion of the study area, wolf social structure did not significantly affect consumption of moose calves (p=0.117) (Figure 3a). Additionally, we found solitary wolves did not differ in consumption of moose calves between areas of high moose versus high deer concentration (Fisher's exact test, p=0.279) (Figure 3b). Considering all 62 samples, consumption of moose calves did not vary significantly with summer time period (p=0.566) (Figure 3c).

To compare wolf consumption of moose calves to their abundance in the overall moose population, we used only scats collected at resting sites and kill sites, as scavenged carcasses of moose that were not killed by wolves may not reflect selection by wolves when hunting. At parturition, one-month post-parturition, and late summer, two of seven, five of nine, and nine of fifteen wolf scats contained calves, respectively. Assumed proportions of the moose population that were calves, in each time period, were 37%, 29%, and 13%, respectively (Figure 4). Wolves did not preferentially select calves at parturition (binomial exact test, p=0.783) or at one-month post-parturition (p=0.077), but calves were consumed proportionately more than their abundance in late summer (p<0.0001; Figure 4).

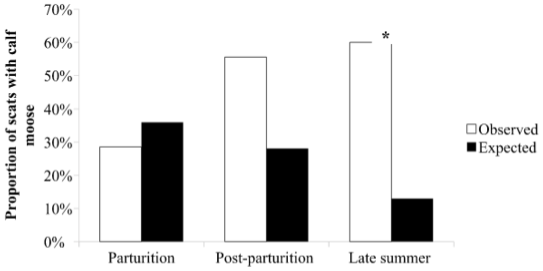

Figure 4: *Observed versus expected proportions of moose calves relative to overall moose found in wolf scats at different summer time periods: during moose parturition (n=7), post-parturition (n=9), and late summer (n=15). Asterisk indicates significance.*

4. Discussion

In GHA 26, wolf diet was influenced by social structure, relative prey species abundance, and season. In the northern part of the study area, as predicted, wolves in a pack were more likely to consume moose, while other prey were more likely to be consumed by solitary individuals. For solitary wolves, deer were more likely to be consumed in the south where they were more abundant, but no difference was demonstrated in consumption for all other prey types with relative abundance of moose vs deer. Beavers were consumed more in summer, but there was no difference in consumption of moose, deer, and other prey with season. Consumption of calf moose was not affected by social structure, nor by period of summer, though selection for calves, relative to calf abundance, was apparent near the end of summer. A recent study of wolf diet in GHA 26 (which did not distinguish between pack versus solitary wolf diets) found that moose and beaver were important prey species for wolves in the summer, while both deer and moose alternated as important prey in winter, with deer being most prominent in terms of proportion of the overall diet (Mocker, 2015). Deer are less adapted to snow conditions than longer-legged moose, and are thus more catchable by predators. Mocker (2015) suggested that winter prey handling efficiency may override importance of prey density in wolf diet. We found that pack wolves in the northern part of the study area were more likely to consume beaver in summer than in winter, but found no effect of season on consumption of moose or deer. Because all of the samples for this analysis were taken from the northern part of the study area, where deer are scarce relative to the south, lack of prominence of deer in the winter diet may be due to low deer abundance on the landscape regardless of season, conflicting with the notion that handling efficiency overrides importance of prey abundance. However, several studies have shown that, where more than one ungulate prey species coexist, wolves tend to concentrate on the smaller, easier to handle species (Peterson, 1955; Pimlott et al., 1969). In Quebec, white-tailed deer were the primary winter prey of wolves despite moose abundance, even when deer had almost disappeared locally (Potvin et al., 1988). In GHA 26, harsh winters in 2013 and 2014 caused local deer populations to decline significantly, though they are expected to have responded positively to milder winters in 2015 and 2016 (Manitoba Conservation, unpublished data). It may be that deer in the study area were even more scarce than in past years, making it less feasible for wolves to concentrate on deer in the winter, even if they may have in the past. Consumption of moose irrespective of season is compatible with Mocker (2015), as moose were found to be an important prey item in summer and in alternate winters. The finding that beavers were more likely to be consumed in summer is in agreement with the general conclusion that beaver availability increases when snow melts in summer and they emerge from their lodges. The consumption of other prey was not affected by season. Wolves are opportunistic predators that will consume whatever they can catch. The species found in the other prey category (fish, fox, rodent, snowshoe hare, bear, and bird) were uncommon in the diet and could have been encountered by chance in either season.

During summer in the northern part of the study area, moose were more likely to be consumed by pack wolves than solitary individuals, which is consistent with our prediction. Solitary wolves have been recorded killing moose on their own, but it is more energetically feasible for two or more individuals to hunt moose cooperatively (Mech and Boitani, 2003). When wolves are harvested by trappers, pack social structure can be disrupted, resulting in more solitary wolves or smaller packs on the landscape (Brainerd et al., 2008). In GHA 26, the trapper incentive program that was designed to reduce wolf numbers may have also caused such social fragmentation within the wolf population, thereby reducing the likelihood of predation on adult moose.

Solitary individuals were more likely to consume other prey than pack individuals, while social structure did not affect consumption of deer or beaver. Small prey like snowshoe hare and birds pose little risk for a solitary wolf to attack. Other prey, such as rodents or fish, can be scavenged from dump sites, and are relatively easy for solitary individuals to acquire. Pack wolves, on the other hand, may devote more time to hunting moose than other prey because moose provide more food per capita (Mech 1970). Consumption of deer and beaver regardless of social structure may be due to their size and ease of handling. Deer are large enough to be profitable prey to a wolf pack, yet small enough that a solitary wolf could still handle it on its own. Beaver are abundant throughout the study area, and are vulnerable to predation when they come onto land to forage. Wolf packs have been shown to select den sites that facilitate access to beavers in the summer as a means of easily meeting the nutritional needs of growing wolf pups (Benson et al., 2015).

The examination of the effects of relative prey abundance was limited to dietary comparisons of solitary wolves between northern and southern regions during the summer. As such, the finding that moose were no more likely to be preyed upon in the north than in the south, regardless of encounter rate, may be due to the low relative likelihood of a solitary individual capturing a moose to begin with. Deer were more likely to be consumed by solitary wolves in the south, which is more of a reflection of relative prey abundance given that solitary individuals are still capable of taking down deer.

Surprisingly, pack wolves were not found to be more successful than solitary individuals at killing moose calves. Separating a moose calf from its mother typically requires a coordinated effort, making it far less feasible for a solitary wolf to accomplish. Black bears are successful predators of moose calves, killing neonate moose near parturition when calves are not yet mobile (Zager and Beecham, 2006; Garneau et al., 2008). Solitary wolves encountering calves near parturition may be capable of killing them before the mother can intervene. Alternatively, calves may be killed by solitary wolves if the mother is debilitated in a way that reduces her ability to adequately protect the calf.

Wolves appear to select for moose calves, relative to adult moose, in late summer but not at parturition. Keech et al. (2011) demonstrated via predator treatment experiments that the effects of wolf predation on moose calves were more pronounced in late summer and early fall, while predation by black bears was most pronounced in early spring. Most ungulate calf mortality occurs within the first few weeks of life, corresponding to the time during which neonates are most vulnerable (Franzmann et al., 1980). Across North America, investigations focusing on neonatal ungulates demonstrated that predators can account for 56-100% of moose neonate deaths, particularly by black bears and brown bears (Zager and Beecham, 2006). Bears are opportunistic omnivores and, when other foods are less available prior to spring green-up, may rely more on predation to meet their energetic needs. In low-density moose populations, predation by wolves and bears can be additive, though may become compensatory as moose densities increase (McCullough, 1979; Gassaway et al., 1992). When predation is compensatory, it merely replaces other existing sources of mortality (e.g., parasitic infection) and does not affect overall survival in a prey population. In our study area, predation on moose calves may be more heavily affected by bears near the beginning of summer, with wolves contributing more to calf mortality prior to autumn simply by virtue of reduced calf abundance. Alternatively, wolves may not selectively kill moose calves near the beginning of summer because their movements may be constrained by the denning season. When wolf pups are born in spring, pack members frequently return to the denning area to provide the pups with food (Mech and Boitani, 2003). Wolves tend to select denning areas of higher relative elevation and in close proximity to water (Mech, 1970). Meanwhile, some studies have suggested that moose select calving areas away from predators to reduce predation risk to neonates (Addison et al., 1993; Bowyer et al., 1999; Poole et al., 2007). The combination of wolf movement being strongly tied to den sites and displacement of moose calves away from wolves may reduce the feasibility of selectively killing calves. As summer progresses and both wolves and moose calves become more mobile, wolves may encounter calves more frequently, allowing selection in late summer. It is possible that selection for moose calves may persist into winter, especially if calves are more impeded by snow than adults.

Furthermore, while telemetry clusters are effective for locating wolf scats, they are most useful in detecting kill sites for large prey items (Boitani and Powell, 2012). Scat analysis has been noted for better reflecting the consumption of small-bodied animals than site investigations alone (Boitani and Powell, 2012) but the detection of the cluster sites themselves may be biased towards kill sites of large-bodied prey that take more time consume. It is also possible that the moose kill data may have been biased towards detection of adult moose over calves by virtue of their small size. Calves are much smaller than adult moose and require far less handling time, especially at parturition when they are at their smallest. Calves consumed by wolves earlier in the summer may have a lower likelihood of being detected because handling times may have been too short to generate a telemetry cluster. The use of two different collar types may have also led to a bias towards larger bodied prey items detected in the diets of wolves. For example, wolves wearing the Lotek Lifecycle collars require more time to generate a large telemetry cluster, as GPS fixes are only taken twice daily as opposed to every two hours.

While recruitment of juvenile moose can limit population growth, survival of reproductive adults may be an even more influential limiting factor. Hayes et al. (2003) found, in an experimental wolf reduction treatment, that adult survival was more influential than recruitment in promoting the recovery of a declining moose population in the Yukon. Conversely, Ballard et al. (1991) found that, in south-central Alaska, the decline in the moose population was principally due to predation on calves in summer. These conflicting outcomes demonstrate how moose populations can respond differentially to predation. The significance of predation depends on the combined effects of other factors simultaneously acting on a population, as well as relative abundances of alternative prey and age structure of the population itself (Ballard and Larsen, 1987; Sand et al., 2012).

When adverse weather, poor habitat quality, or other mortality factors act to limit moose densities, the effects of predation may be exacerbated (Mech and Peterson, 2003; Zager and Beecham, 2006). Vucetich and Peterson (2004) compared the relative influences of top-down versus bottom-up effects on moose population dynamics on Isle Royale, Michigan, and found that more variation in population growth was attributable to bottom-up influences. When prey has a poor nutritional base to exploit, more individuals may be in poorer body condition and less able to survive disease, predation, or parasitic infection. In the GHA 26, parasitism is a problem facing moose. Meningeal brain worm and giant liver flukes are prevalent in the GHA 26 moose population, as moose come into more frequent contact with white-tailed deer (Schmitz and Nudds, 1994). These parasites are benign in deer but fatal to moose. Additionally, mild winters and fire suppression can increase abundance of ectoparasites, such as the winter tick (Murray et al., 2006; Scasta, 2015). Winter tick infestations have become more prevalent in many parts of North America, and can reduce moose health by inducing constant scratching and removal of fur (Murray et al., 2006). While natural forest fires can potentially reduce numbers of wingless ectoparasites (Scasta, 2015), fire suppression will often minimize this effect. It is important to acknowledge that predator-prey relationships are shaped by the interaction of many ecological influences.

Our wolf diet analysis shows that pack wolves are more likely to consume moose, although we found no effect of social structure specifically on moose calves. In addition to reducing predation pressure on moose by removing predators, the trapper incentive program may have also altered overall wolf diet by disrupting packs, resulting in more solitary wolves on the landscape. If consumption of moose calves, specifically, is not affected by wolf social structure, however, then the trapper incentive program may not affect predation on moose calves as strongly. Understanding how different mortality factors impact moose calves, and the importance calf versus adult moose survival to moose population dynamics, would help refine management strategies for promoting the recovery of low moose populations in GHA 26.

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