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Black bear (*Ursus americanus*) and wolf (*Canis* spp.) summer diet composition and ungulate prey selectivity in Ontario, Canada

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Abstract

Understanding predator-prey dynamics is an important component of management strategy development for wildlife populations that are directly affected by predation. Ungulates often serve as a significant source of prey for many large mammal predators, and patterns of predation are known to influence population dynamics. Although black bear and wolf diets have been investigated extensively, prey preference has been less commonly examined, especially in analyses that take into account age class (i.e., juvenile and adult) of the ungulate prey. We examined black bear (*Ursus americanus*), wolf (*Canis lupus*), and hybrids (*Canis* spp.) prey preference in Ontario based on the availability of three ungulate species—elk (*Cervus elaphus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*). We analyzed the presence of prey items in black bear and wolf scats collected over 3 years by examining prey hair cuticular scale patterns. We applied correction factors to frequencies of occurrence of prey items found in predator scat and related diet composition to the availability of ungulates, determined by fecal pellet transect surveys. In addition, non-ungulate diet items were identified to obtain full diet composition profiles. We found that black bear diet consisted of more than 87% vegetation, and they were opportunistic, not selecting for any particular ungulate species in either adult or juvenile age class. Wolf diet was comprised mainly of ungulates (~73.2%), muskrat (*Ondatra zibethica*; ~8.5%), and beaver (*Castor canadensis*; ~14.6%), and although moose were at least 1.5 times more abundant than each of the other ungulate prey species in the study area, wolves preferred elk, using moose less than expected. Although we found black bear diet to be opportunistic during the summer, wolves in our study heavily utilized both juvenile and adult ungulates, however, among ungulate species, displayed preference for elk. The preference displayed by wolves provides insight that wildlife managers can use to guide further investigation and assist with the development of strategies to ensure continued elk reintroduction success, and moose and white-tailed deer population sustainability.

Keywords Black bear diet · Prey selectivity · Ungulate · Wolf diet

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Introduction

Understanding predator-prey relationships is important for identifying focal points for management of at-risk or declining prey populations. Although predation is considered one of the leading causes of mortality in many ungulate populations in North America (Schlegel 1976; Nelson and Mech 1986; Gasaway et al. 1992; Kunkel and Mech 1994; Murrow et al. 2009), information regarding key predator species is not always readily available to managers. When predator-prey relationships are poorly understood, uninformed management strategies may lead to wasted time and money, and potentially to unnecessary pressures on other species of wildlife. For example, in Yellowstone National Park, wolves (*Canis lupus*) were extirpated in the 1930s; however, in 1995 to 1996, 31 wolves were reintroduced into the park (Weaver 1978). Elk

(*Cervus elaphus*) counts declined 80% within a decade of wolf reintroduction (White and Garrot 2005). However, with further investigation, Barber-Meyer et al. (2008) found that bear accounted for the greatest proportion of elk calf deaths and with the incidental increase in bear numbers since wolf restoration, it was suggested that elk declines were not the result of wolf restoration alone.

Black bear (*Ursus americanus*) and wolves are well known as major ungulate predators across North America (Bergerud and Page 1987; Gasaway et al. 1992; Kunkel and Mech 1994; Barber-Meyer et al. 2008; Yarkovich et al. 2011; Wiwchar and Mallory 2012; Patterson et al. 2013). It is apparent that wolf and black bear diet composition changes among geographical regions and with differing prey species abundances (Lamothe and Parker 1989; Wiwchar and Mallory 2012; Newsome et al. 2016). Although wolves have been identified as having selective diets (Fuller and Keith 1980; Carbyn 1983; Potvin et al. 1987; Wiwchar and Mallory 2012), bears in general are most often recognized as opportunistic (Bastille-Rousseau et al. 2011); however, they are increasingly recognized as important predators of juvenile ungulates including elk (Schlegel 1976; Smith and Anderson 1998; Barber-Meyer et al. 2008; Murrow et al. 2009), moose (*Alces alces*) (Franzmann et al. 1980; Ballard 1992), caribou (*Rangifer tarandus*) (Mahoney et al. 1990), and deer (*Odocoileus* spp.) (Conger and Giusti 1992; Vreeland et al. 2004). Although several studies have investigated wolf prey selection, few studies have investigated ungulate prey selection by black bears. Moreover, research that investigates both adult and juvenile ungulate prey for both predator species using scat analyses is lacking. Ungulate juvenile survival is often limited by predation, with bears having the greatest impacts during the first few weeks following parturition (Ballard et al. 1981; Adams et al. 1995; Murrow et al. 2009). Juvenile survival and recruitment are the main drivers of large herbivore population dynamics due to their inherent variability in relation to adult survival (Pimlott 1967; Gaillard et al. 1998; Gaillard et al. 2000; Raithel et al. 2007). Based on the large contribution of juvenile survival to ungulate population trajectories, it is crucial that wildlife managers acquire reliable information, especially before the initiation of extreme management strategies such as predator control (Barber-Meyer et al. 2008). The consideration of predator-prey relationships among bears, wolves, and their prey species is an important component for developing conservation strategies for declining ungulate populations elsewhere (Barber-Meyer et al. 2008). As such, understanding predator-prey relationships in eastern North America should help guide management and also contribute to the general understanding of predator-prey relationships.

We aimed to gain insight regarding predator-prey relations within a multiple predator-prey system, in the Burwash region of Ontario, Canada. The goal of this study was to determine if black bear or wolves displayed prey preference based on the

availability of three ungulate species—elk, moose, and white-tailed deer (*Odocoileus virginianus*). By identifying prey preference, managers may be better able to determine sources of potential pressures on prey species in order to facilitate further investigation and incorporate this information into management strategies. We related the availability of the three ungulate prey species within our study area to the composition of ungulate prey in wolf and black bear diets. Additionally, non-ungulate diet items were also identified to construct more comprehensive diet composition profiles for black bear and wolves.

Methods

Study area

The study area was approximately 450 km² in area and consisted mainly of mixed conifer-hardwood forest of the Great Lakes-St. Lawrence Ecotonal Forest Region (46° 20' 30", 80° 50' 30"—46° 11' 30", 80° 50' 00") (Rowe 1972; Chambers et al. 1996). Topography included rugged rock outcrops, valleys, marshes, swamps, and bogs/fens typical of the Precambrian Shield and maximum elevations of 300 m (Jost et al. 1999). Approximately 4000 ha of abandoned agricultural fields were present throughout the study area, along with several tertiary roads used for logging or recreational purposes. Regional climate is continental (Ranta 1979) where July, the warmest month of the year, has a 15 °C mean temperature (Vankat 1979) and January, the coldest month of the year, has a −12.5 °C mean temperature (Chambers et al. 1996). The average seasonal (December to February) snow depth in the area was 28 cm from 1980 to 2010 (Environment Canada). Populations of elk, moose, and white-tailed deer exist within the study area (OMNR 2009). The two most common ungulate predators within our study area were black bear and wolves. Due to the “*Canis* soup” in the upper Great Lakes region (Wilson et al. 2009) where wolves commonly hybridize with coyotes or other wolf-coyote hybrids, it was difficult to distinguish between wolves and their hybrids. In light of this, we used the term “wolves” to describe the large canids and their hybrids that populated our study area. It was estimated that there were 0.2 to 0.3 wolves per 10 km² (Kittle et al. 2008) and 2.4 black bear per 10 km² (OMNR 2014) in the study area.

Predator scat collection

We collected black bear and wolf scats annually from May 1 to August 31, 2013, to 2015. Although it is well known that wolves predate on ungulates in all seasons, the spring/summer season was selected as the collection period because (1) of the high sightability of scats during this time, (2) because it was the core period of black bear activity, and (3) because ungulate calves are born during this period. We used an ATV to search

for scats along all of the accessible, unimproved, roads that were used for logging and/or recreation that totalled approximately 65 km, distributed throughout the study area. ATV driving speeds were maintained at 10–15 km/h to ensure consistent detectability of predator scats. Each road was sampled once every 2 weeks and, because fresh scats (<2 weeks old) were collected, the entire scat was removed to eliminate re-sampling. Scats were identified, collected, and recorded by the same observer to remove bias (e.g., misidentification from using multiple observers) (Spaulding et al. 2000). We placed each scat sample in a plastic bag, which were then frozen prior to analysis. The number of scats collected each year were limited, so we pooled all years together to increase sample size (e.g., no. of wolf scats collected ranged from 65 to 106 samples per year; no. of bear scats collected ranged from 116 to 221 samples per year).

Hair scale pattern analysis

Identification of prey hair found in predator scat is a common, non-invasive approach used to investigate mammal diet composition of bears (Graber and White 1983; Raine and Kansas 1990; Bull and Torgersen 2001), wolves (Fuller and Keith 1980; Potvin et al. 1987; Lamothe and Parker 1989; Carter 2006; Barja 2009), and many other species (García Alaniz et al. 2010a, b). We removed each scat sample from the freezer approximately 12 h prior to processing to allow thawing. Once thawed, we rinsed each scat with water over fine sieves to allow the retention of coarse organic material, primarily bone fragments and animal hair. Three randomly selected, representative clusters of hair were pulled from each scat and dried for approximately 12–24 h. To reduce observer bias, only one person macroscopically assessed the size and color of individual dried hairs, and microscopically observed hair cuticular scale patterns. To examine cuticular scale patterns, we applied a thin layer of clear nail polish on a microscope slide and then placed three to ten individual guard hairs onto the slide to create an imprint of the hair scales (Adorian and Kolenosky 1969). Hair scale slides were compared to reference slides made from guard hairs of museum mammal species known to occur in Ontario. In addition, we followed Adorian and Kolenosky's (1969) photographic and descriptive guide to further confirm prey species, as well as to differentiate between adult and juvenile ungulates. Hair length, color, and unique scale patterns exist for each species and differences in scale pattern distinguish adult and juveniles ungulates of the same species.

Prey availability

To determine the prey availability of elk, moose, and white-tailed deer, a fecal pellet survey was employed (Smith et al. 1969; Forsyth 2005). Fecal pellet counts are useful indices for determining the abundance of ungulates (Forsyth et al. 2007),

and yield reliable data under most field conditions (Neff 1968). They are commonly used in North America to estimate ungulate population sizes (Ripple et al. 2001; Patterson et al. 2002; Hebblewhite et al. 2005). We conducted 30 pellet transect surveys in fall 2013, spring 2014, fall 2014, and 100 transect surveys in spring 2015. The mean abundances were calculated and used for all subsequent analyses. It is generally agreed that long narrow fecal pellet survey plots provide superior results compared to shorter and wider plots (Neff 1968). We conducted pellet counts along 150-m-long transects that began at pre-determined random locations. At each random transect location, a pre-determined random compass bearing was selected and walked for the entire 150 m. Every 5 m the area within a 1-m radius was examined for ungulate pellets (Forsyth 2005). Each fecal pellet survey was completed within a 30-day period. To ensure we collected scat from the examined year, we only included scat in the survey that were sitting on top of the previous year's leaf litter. We used mean defecation rates for each ungulate species to determine abundances (Neff 1968). The mean defecation rates per animal per day for white-tailed deer, moose, and elk were 13.20, 13.00, and 11.76, respectively (Neff 1968). The mean defecation rate for elk was determined by calculating the mean of the two values given in Neff (1968) $((11 + 12.52)/2)$. We calculated mean abundances of each ungulate species for each survey using the methodology outlined in Smith et al. (1969) (number of ungulates species per km^2 = average number of pellet groups per km^2 / (plot size / (defecation rate \times herd occupancy))), where herd occupancy is the number of days a given ungulate species was assumed within the study area since the approximate time of leaf-off, and used them for subsequent analysis. We assumed the number of juveniles were equal to the number of adults for each species. The ungulate abundance calculations assume animals are present in the study area for the entire duration since leaf-off, and because white-tailed deer (deer) often migrate to winter ranges or yards outside of our study area and migration timing is unknown but related to snow depth, we calculated the abundance of deer in our study area using two extremes of occurrence: (1) by predicting that deer were present in the study area during the entire study period (present in winter—a longer herd occupancy), and (2) by predicting that deer were completely absent from the study area every year between January 1 and April 1 (absent in winter—a shorter herd occupancy).

Data analysis

Carnivores consume fewer hairs of prey items with larger mass because smaller prey species have higher surface to volume ratios and are covered with more hair per mass than larger mammals, which may lead to bias in scat results as smaller prey consumed could be overrepresented (Weaver 1993). Although the frequency of occurrence of prey items is the

most highly utilized metric in predator diet research, results can be misleading and are often of low ecological significance (Klare et al. 2011). Mass calculations using correction factors are the best approximation of true diets according to Klare et al. (2011). To reduce bias, we applied the Weaver (1993) correction factor to our occurrence data using the equation $y = 0.439 + 0.008x$, where y is the mass of prey per collectable scat and x is the average body mass of each prey item, which enabled us to determine the frequency of total weight of each prey species in both black bear and wolf diets. Average prey mass was calculated using the median of ranges given for each mammal species (except juveniles) following Eder (2002). To determine mass of juvenile ungulates, we used the median between the average birth mass (white-tailed deer, 3.4 kg; Verme 1969; elk, 14.8 kg; Johnson 1951; moose, 16.3 kg; Keech et al. 1999) and median adult mass (white-tailed deer, 73 kg; elk, 340 kg; moose, 385 kg; Eder 2002). We performed chi-squared tests to determine if black bear and wolves utilized ungulate adult or juvenile prey species significantly more or less than expected in comparison to each ungulate prey species. Prey preference is commonly calculated using the Jacobs' index (Hayward et al. 2006, 2012; Lyngdoh et al. 2014), which we utilized for both black bear and wolves in relation to ungulate adult and juvenile prey species using the following equation (Jacobs 1974):

$$D = \frac{(r_i - p_i)}{(r_i + p_i - 2r_i p_i)}$$

where r_i is the proportion of species i found among all scat collected for each predator species and p_i is the proportion of ungulate species i available in the study area. D is the Jacobs' index and values range from a maximum preference of +1 to a minimum preference of -1 (Boitani and Powell 2012).

Results

Abundances

Deer had the lowest mean abundance when predicted to be present within our study area throughout the year, followed by elk, then moose (Table 1). However, when deer were assumed not to be present in the study area during the winter, elk appeared to have the lowest mean abundance, followed by deer, then moose; however, standard errors did overlap in some instances.

Black bear diets

We collected and examined a total of 503 black bear scat samples. Black bear diets in our study area were comprised of approximately 87% vegetation based on the frequency of

the total weight of diet items found in scat (Table 2). Mammals comprised approximately 13% of the total black bear diet. The frequency of total weight of the mammal portion in black bear diets was comprised of 53% juvenile ungulates, 33% of adult ungulates, and 14% non-ungulates. Similar to the trend seen in ungulate abundance, moose adults and juveniles accounted for the greatest proportion of ungulate prey species in the mammal portion of black bear diet followed by elk, then white-tailed deer. In relation to ungulate availability, black bear did not exhibit significant prey preference among all species of juveniles (deer present in winter: $X^2 = 0.53$; $df = 2$; $p = 0.78$; deer absent in winter: $X^2 = 3.45$; $df = 2$; $p = 0.185$) nor adults (deer present in winter: $X^2 = 0.16$; $df = 2$; $p = 0.92$; deer absent in winter: $X^2 = 0.40$; $df = 2$; $p = 0.82$). The black bear Jacobs' indices for all ungulate species (adults and juveniles) were close to what was expected when deer were predicted to be present during the winter (Fig. 1) or absent during the winter (Fig. 2).

Wolf diets

We collected and examined a total of 247 wolf scat samples. Wolf diets in our study area were comprised entirely of mammals (Table 3). The relative total weight of mammals in wolf diets was comprised of 44% juvenile ungulates, 29% of adult ungulates, and 27% non-ungulates including muskrat (*Ondatra zibethica*) and beaver (*Castor canadensis*). In relation to ungulate availability, wolves exhibited significant prey preference (juvenile ungulates: deer present in winter: $X^2 = 6.04$; $df = 2$; $p = 0.048$; deer absent in winter: $X^2 = 7.19$; $df = 2$; $p = 0.03$; and adult ungulates: deer present in winter: $X^2 = 11.71$; $df = 2$; $p = 0.003$; deer absent in winter: $X^2 = 16.05$; $df = 2$; $p = 0.0003$). Wolf Jacobs' indices were greatest for both juvenile and adult elk and least for juvenile and adult moose (Figs. 1 and 2).

Discussion

Vegetation comprised approximately 87% of the relative total weight of black bear diet in our study, with the remaining 13% comprised of mammals, most of which were ungulates. Similarly, in Quebec, Canada, an area without elk, black bear diet consisted of 90% vegetation with moose being the second most important diet item during the spring and summer (Mosnier et al. 2008). In Yosemite National Park, USA, black bear diet was comprised of 75% vegetation, with mule deer (*Odocoileus hemionus*) being the only common vertebrate food item (Graber and White 1983). In Oregon, USA, animal remains accounted for only 10% of black bear diet and diet composition varied among seasons, with ungulates being most important during the spring and fall (Bull and Torgersen 2001). Black bear in our study area utilized a

Table 1 Abundances (no./km²) for three ungulate species in the Burwash region of Ontario, Canada (SE = standard error). Deer estimates were based on the presence of deer in the study area

throughout the four time periods assessed (present in winter) and also based on their seasonal absence from the study area between January 1 and April 1 (absent in winter)

	White-tailed deer		Elk	Moose
	Present in winter	Absent in winter		
Fall 2013	1.12	1.58	1.08	1.95
Spring 2014	1.91	3.51	1.23	3.75
Fall 2014	0.08	0.12	1.03	1.19
Spring 2015	0.04	0.07	1.36	1.11
Mean (SE)	0.79 (0.45)	1.32 (0.81)	1.17 (0.07)	2.00 (0.61)

variety of mammal species; however, did not show preference for elk, deer, or moose. Although it is widely acknowledged that black bears are opportunistic, black bear predation has been reported to be the primary cause of juvenile ungulate population decline in some regions (Lewis et al. 2016). We did not find evidence of ungulate adult or juvenile species preference in black bear diet during the summer months, supporting the theory that black bear consume ungulate prey opportunistically. Although we were unable to statistically compare ungulate versus juvenile preference, the ungulate component of black bear diet in our study did consist of more juveniles than adults (~61% of ungulates). Because wolves rarely use all of elk or moose carcasses (Paquet 1992) and ungulates die due to non-predator related events such as road-kill, scavenging opportunities may have been created for black bear, especially later in the summer when juveniles are more mobile. As such, it is important to recognize that the ungulate items we detected in black bear scats may have been from predation or scavenging behavior. Regardless, all three ungulate species collectively made up a rather small component of bear summer diets.

Unlike black bear, summer diets of wolves in our study area were comprised largely of ungulates (73% of all items detected (relative total weight)). This finding is consistent with other studies that have examined wolf diets (Mech et al. 2001;

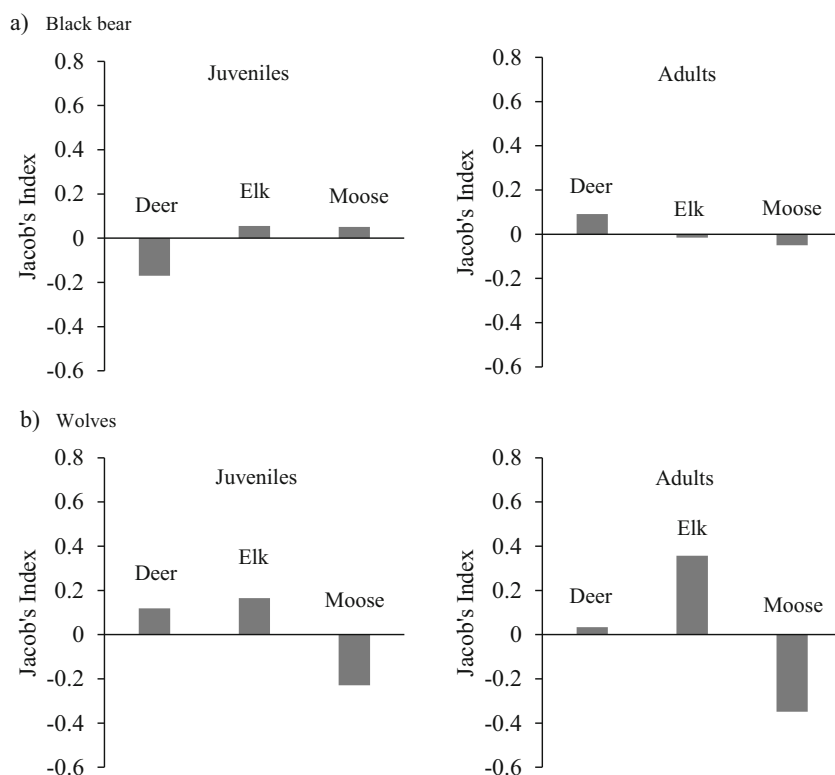
Arjo et al. 2002; Barja 2009). In our study, juvenile and adult elk were consistently consumed more than expected and juvenile and adult moose were utilized less than expected. Based on diet proportions, the majority (63%) of the ungulate items detected in our wolf scat samples were from juveniles, which is not surprising given our scat collection coincided with all three ungulate species calving/fawning seasons. Wolves elsewhere are known to disproportionately kill younger, older, and likely more debilitated ungulates than prime adults (Fuller and Keith 1980; Huggard 1993b; Christianson and Creel 2014). Higher rates of predation on juvenile ungulates compared to adults has been documented in other studies as juveniles have increased vulnerability in comparison to adults; especially during the winter when predator evasion may be impeded in snow (Ballard et al. 1987, Jedrzejewski et al. 1992).

North American wolf diets are dominated by large ungulates and medium-sized mammals (Newsome et al. 2016). Prey use by wolves is thought to be dependent on prey availability (Paquet and Carbyn 2003; Newsome et al. 2016). Wolves most often consume prey species that are the most abundant and may change their diet in response to changes in prey availability (Barja 2009; Wiwchar and Mallory 2012). Although moose are larger than elk and were the most abundant ungulate in our study area, elk were the ungulate prey

Table 2 The number of black bear scat samples ($N = 503$) in which various diet items were detected, the frequency of occurrence for each item, and frequency of relative total weight of each item

Diet item	Number	Freq. of occurrence	Freq. of relative total weight
Small mammal	5	0.99	0.42
Muskrat	5	0.99	0.43
Beaver	8	1.59	0.96
Juvenile deer	7	1.39	1.00
Adult deer	5	0.99	0.99
Juvenile elk	6	1.19	2.14
Adult elk	2	0.40	1.22
Juvenile moose	9	1.79	3.55
Adult moose	3	0.60	2.03
Vegetation	453	90.06	87.25

Fig. 1 Jacobs' index of black bear (a) and wolves (b) for juvenile and adult white-tailed deer, elk, and moose, when white-tailed deer were assumed present in the study during the winter



item of choice for wolves. Deer were used as or less than expected by wolves and may not have been selected for due to their relatively low abundance and seasonality.

Similar to our results, elk were consumed by wolves 15 times more often than moose despite elk only being 2.4 times more abundant than moose in Riding Mountain National Park,

Fig. 2 Jacobs' index of black bear (a) and wolves (b) for juvenile and adult white-tailed deer, elk, and moose, when white-tailed deer were assumed absent in the study area during the winter

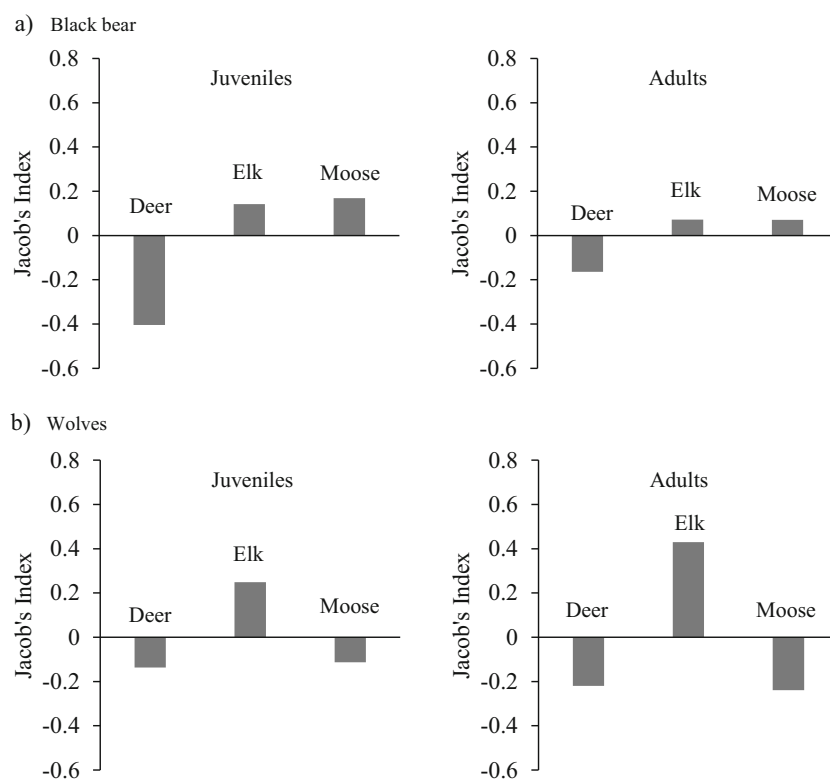


Table 3 The number of wolf scat samples ($N = 247$) in which various diet items were detected, the frequency of occurrence for each item, and frequency of relative total weight of each item

Prey species	Number	Freq. of occurrence	Freq. of relative total weight
Small mammals	22	8.91	3.73
Muskrat	49	19.84	8.47
Beaver	61	24.70	14.64
Juvenile deer	37	14.98	10.61
Adult deer	15	6.07	5.91
Juvenile elk	23	9.31	16.43
Adult elk	11	4.45	13.38
Juvenile moose	22	8.91	17.35
Adult moose	7	2.83	9.49

Canada (Carbyn 1983). Paquet (1992) further confirmed that wolves in the Riding Mountain National Park preyed primarily on elk and white-tailed deer, rather than moose. In Yellowstone National Park, elk, the most abundant ungulate in the park, comprised 91% of wolf diet; however, mule deer (*Odocoileus hemionus*), bison (*Bison bison*), moose (*Alces alces*), bighorn sheep (*Ovis canadensis*), and pronghorns (*Antilocapra americana*), were also available (Mech et al. 2001). Interestingly, both elk (Johnson 1951; Geist 2002) and white-tailed deer (Carl and Robbins 1988) calves use “the hider” anti-predator strategy during the first weeks, which leaves them relatively unprotected should a predator discover them. Conversely, moose do not use “the hider” strategy; rather mothers stay close to their young as neonates utilize “the follower” anti-predator strategy (Bogomolova et al. 1992). The difference in anti-predator strategies between moose and elk may in part explain the observed selection for elk by wolves (an easier, non-protected target). Encounters with protective large ungulates such as a moose can be very risky for wolves and have been documented to lead to wolf deaths (Mech and Nelson 1990; Weaver et al. 1992). In addition, in systems with a variety of large and small bodied ungulate species, wolves tend to prey primarily upon smaller species (Carbyn 1983; Paquet 1992; Kunkel et al. 1999; Smith et al. 2000).

Both juvenile and adult elk were the most preferred ungulate by wolves in our study area. Elk live in both small and large herds which change seasonally, wolves encounter and kill more elk than expected from larger groups (Hebblewhite and Pletscher 2002). Grouping behavior is a common anti-predator strategy of many species (Bertram 1978; Pulliam and Caraco 1984) which may benefit the prey through the dilution effect (Hamilton 1971; Bertram 1978). With increased group size, predator detection probability may also increase (Triesman 1975), which may result in increased encounter and predation rates. In addition, larger groups may be more spatially predictable (Huggard 1993a) as well as more likely to contain weak individuals (Bertram 1978). Because elk are such a gregarious species, they may be more predictable in space, providing easier targets for wolves in our study area.

This grouping anti-predator behaviour may be responsible for wolves preferring juvenile and adult elk over moose or deer (less gregarious than elk in summer months) in our study.

As many factors influence predator-prey dynamics, careful consideration should be taken before applying predator-prey results to the development of management strategies. Factors that vary among regions may influence predator-prey population dynamics (Ballard et al. 1987; Mech and Peterson 2003). Our study was limited to periods between May and August, but predator diets have been demonstrated to vary among seasons for both wolves (Pimlott 1967; Potvin et al. 1987; Barja 2009) and black bear (Raine and Kansas 1990; Bull and Torgersen 2001). Our results indicate that for the calving and summer period, black bear did not display preference among ungulate species, whereas wolves heavily utilized ungulates during the summer, with both juvenile and adult elk preferred over moose and white-tailed deer.

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