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SPECIAL SECTION

Moose in wolf diets across northeastern Minnesota

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Abstract

The moose (*Alces alces*; mooz in Anishinaabemowin, Ojibwe language) population has recently declined in Minnesota, USA, and gray wolf (*Canis lupus*; ma'iingan) predation is likely a contributing factor. We analyzed diet composition of gray wolves in northeastern Minnesota during 2011–2013 to evaluate the importance of moose as prey and seasonal and regional variations in wolf diet. We identified frequency of occurrence of prey items and biomass consumed in 1,000 wolf scats collected on and adjacent to the Grand Portage Indian Reservation and Voyageurs National Park and within the 1854 Ceded Territory (greater northeastern Minnesota). White-tailed deer (*Odocoileus virginianus*; waawaashkeshiwag [plural]), moose, and beaver (*Castor canadensis*; amikwag [plural]) composed the majority of wolf diet, with moose as the primary prey in Grand Portage (35–54% of diet by biomass across seasons) and deer the primary prey in the 1854 Ceded Territory (46–62%) and Voyageurs (63–79%). Relative importance of prey species differed by study area and season. Moose calves were an important prey item in spring in the 1854 Ceded Territory (12% of diet by biomass) but not in Grand Portage or Voyageurs. Although calves were not a majority of wolf diet by biomass, many calves were preyed upon by wolves (30% of calves born each year in Grand Portage), thus affecting recruitment in a declining moose population. Deer fawns composed 12% of wolf diet in spring and 10% in summer in Grand Portage and 19% in summer in Voyageurs. Beaver composed 16% of wolf diet by biomass in

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spring and 14% in summer in Grand Portage and composed 22% of wolf diet in spring and 30% in summer in Voyageurs. At most prey densities, moose were preferred and deer avoided in Grand Portage and the 1854 Ceded Territory and beaver were preferred in Voyageurs. Our results can be used in conjunction with predation and prey studies to evaluate the effect of wolves on prey populations.

KEYWORDS

Canis lupus, diet, Grand Portage Indian Reservation, gray wolf, northeastern Minnesota, prey preference, scat analysis, Voyageurs National Park

The Grand Portage Band of Lake Superior Chippewa is a federally recognized Indian tribe in northeastern Minnesota, USA, and exercises its rights to food sovereignty through subsistence hunting and fishing. Moose (*Alces alces*; mooz [singular], moozoog [plural] in Anishinaabemowin, Ojibwe language) are a primary subsistence food used by the Anishinaabeg (people) of Grand Portage Band historically and presently. Management for and research on maintaining this moose population as a subsistence species thus sets the context for this paper examining diets of wolves (*Canis lupus*; ma'iinganag [plural]), a predator of this culturally important resource. We have used Anishinaabemowin, Ojibwe language, in plant and animal names throughout this manuscript.

Studying predator diets is a valuable way to understand trophic relationships, especially as those relationships vary over time and space, and with changes in prey availability (Latham et al. 2013). An oft-used, non-invasive, and inexpensive method to estimate predator diets is the collection and analysis of scat (Klare et al. 2011). Large sample sizes can be collected over expansive geographical scales, and identification of prey species by hair or other tissues can be readily taught (Chenaux-Ibrahim 2015, Morin et al. 2019); however, there are some biases that may be introduced by scat analyses (Gable et al. 2017*a*, Morin et al. 2019). Nonetheless, diet studies based on scat analyses can reveal potential effects on prey populations (Latham et al. 2013).

The moose population in northeastern Minnesota declined from 2006 to 2020 with the 2020 population estimate 64% less than the 2006 population estimate (DelGiudice 2020, Severud et al. 2022). From 2012 to 2020, the population estimate ranged from 2,760 to 4,350 (DelGiudice 2020). On the Grand Portage Indian Reservation, the moose population declined by 60% from 1990–2019 (Oliveira-Santos et al. 2021, Wolf et al. 2021). Health-related mortalities of adult moose (Cornicelli et al. 2012, Wünschmann et al. 2015, Carstensen et al. 2018, Oliveira-Santos et al. 2021), in combination with predation on calves (Severud et al. 2019, Wolf et al. 2021), influenced the population changes (Severud et al. 2022). Parasitic infections of moose have been identified as contributing factors to adult moose mortalities directly and indirectly by causing moose to be more vulnerable to predation (Carstensen et al. 2018).

The wolf population in northeastern Minnesota may have partly contributed to the moose population decline (Mech and Fieberg 2014, Barber-Meyer and Mech 2016). Wolves can subsidize their diet by preying on white-tailed deer (*Odocoileus virginianus*; waawaashkeskiwag [plural]) while also preying on moose calves (Barber-Meyer and Mech 2016). During calving seasons, concentrations of moose calves in geographically focused calving areas may lead to higher rates of predation in relatively small areas of the landscape (Van de Vuurst et al. 2022). The primary cause of mortality in collared moose calves in northeastern Minnesota during 2013–2016 was predation, with wolves causing 77% of predation-related mortalities (Severud et al. 2019, Wolf et al. 2021). Evaluating seasonal composition and proportion of prey species in the diet of gray wolves improves our understanding of the effect of wolf predation on moose population dynamics in Minnesota by understanding the predator perspective.

Wolves in northeastern Minnesota consume primarily white-tailed deer, moose, and beaver (*Castor canadensis*; amik; Van Ballenberghe et al. 1975, Fuller 1989, Gogan et al. 2004). When diets were evaluated on a weekly interval during summer through fall, berries, snowshoe hare (*Lepus americanus*; waabooz), black bear (*Ursus americanus*; makwa), and carcasses and bait piles from bear hunting also contributed in some areas to wolf diet (Gable et al. 2018*a*). Moose calves and white-tailed deer fawns have been important food sources for wolves in summer in northeastern Minnesota (Van Ballenberghe et al. 1975, Peterson 1977, Barber-Meyer and Mech 2016, Gable et al. 2018*a*, Severud et al. 2019). Determination of the role and extent of wolf predation on moose is essential for managers to develop effective landscape and wildlife management practices to restore moose in Minnesota.

Wolves were extirpated across much of their worldwide range because of hunting, trapping, and poisoning, and they received protection in the United States in 1973 when they were listed as a federally endangered species (Mech 1995). Following protections, wolves in the western Great Lakes Region rebounded, with the Minnesota population growing from an estimated low of 350 wolves (31,080-km^2 range) in 1963 (Cahalane 1964) to about 2,900 wolves (71,514-km^2 range) by 2008 (Erb 2008). The Minnesota wolf population was stable from 1997 to 2008 and decreased from 2008 to 2013 (Erb 2008, Erb and Sampson 2013), though there is likely some variability in wolf density at smaller spatial scales across Minnesota wolf range (Mech and Fieberg 2014; L. D. Mech, U.S. Geological Survey, unpublished data). Wolves are valued by the Anishinaabeg for the important role they play in ecosystem sustainability. Wolves prey on important cultural and subsistence species and maintaining these culturally important species into perpetuity is a high priority for Grand Portage Anishinaabeg.

Our objective was to use scat analysis to estimate seasonal composition of wolf diets in 3 areas of varying prey densities in northeastern Minnesota. We predicted that 1) deer and moose would be the primary prey species, but importance of moose and deer (as measured by preference and occurrence) would be affected by densities of these species and beaver; 2) diet composition would differ within each study area with changes in prey availability; and 3) diet composition would vary seasonally, with prey switching occurring between winter and summer, where beaver, deer fawns, and moose calves would compose a major proportion of wolf diets with fawns and calves only detectable in spring and summer.

STUDY AREA

We conducted this study during April 2011–November 2013 in the northeastern region of Minnesota, which included federal, tribal, state, county, and private land (Figure 1). Three scat collection areas within the study area were the 1854 Ceded Territory (20,234 km^2), Grand Portage Indian Reservation (227 km^2), and Voyageurs National Park (883 km^2) area (Figure 1). Collection routes were located in areas of lesser, medium, and greater moose density in the 1854 Ceded Territory (Fieberg and Lenarz 2012), lesser moose density in the Voyageurs National Park area, and greater moose density in Grand Portage.

Vegetation in the study area is typical of the southern boreal forest, with upland forests dominated by aspen (*Populus tremuloides*; azaadi, paper birch (*Betula papyrifera*; wiigwaas), balsam fir (*Abies balsamea*; zhingob), white spruce (*Picea glauca*; gaawaandag), sugar maple (*Acer saccharum*; ininaatig), white cedar (*Thuja occidentalis*; giizhik), and jack pine (*Pinus banksiana*; akikaandag; Faber-Langendoen et al. 2007). The landscape is marked with signs of glacial activity, including high ridges, deep ravines, and numerous streams, rivers, lakes, and bogs. Elevation rises from the shoreline along Lake Superior (gichigami) to 700 m above sea level. The climate is warm summer, humid continental on the Köppen climate scale (Ward 1919) and is typified by large seasonal temperature differences, with warm summers (max. 35°C) and cold (min. −45°C) winters. There is moderate precipitation (annual mean of 69 cm), and snow depth can reach 127 cm.

The moose population estimate in northeastern Minnesota (1854 Ceded Territory) ranged from 2,760–4,350 during 2012 to 2020, or 0.18–0.28 moose/km^2 (DelGiudice 2020). Deer densities in the study area ranged from

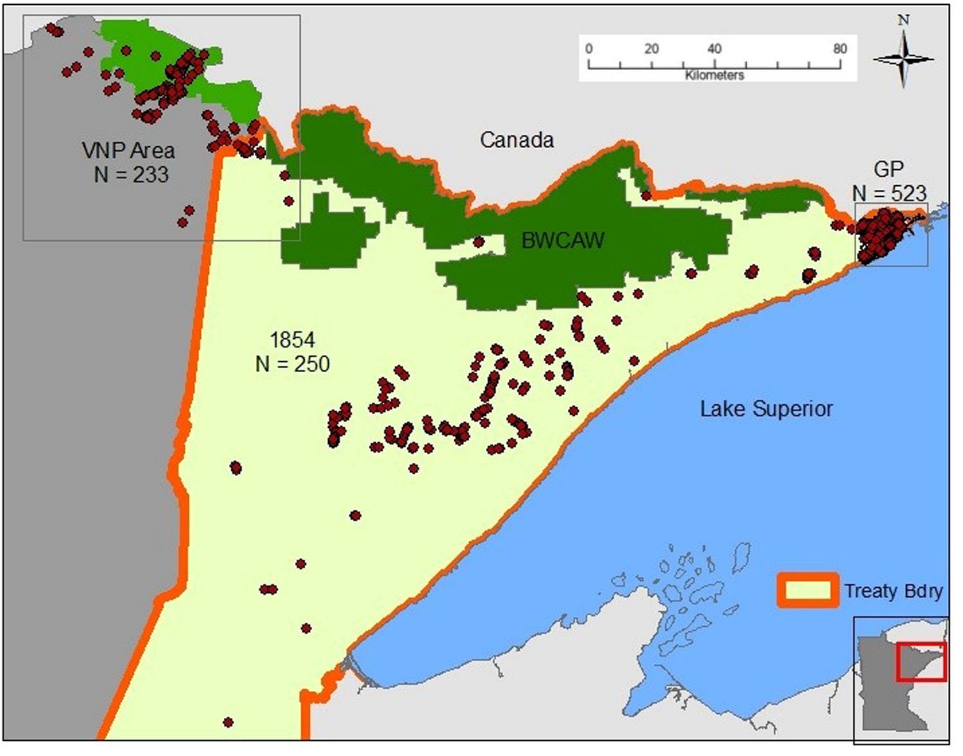

FIGURE 1 Wolf scat collection locations (n = 1,000) during 2011–2013, northeastern Minnesota, USA. There were 3 collection areas: Grand Portage (GP; 227 km^2), 1854 Ceded Territory (1854; 20,234 km^2), and Voyageurs National Park area (VNP; 883 km^2). All scats collected outside GP and VNP area were designated as within the 1854 Ceded Territory study area boundary (bdry). Scat collection did not occur in the Boundary Waters Canoe Area Wilderness (BWCAW). Dots represent wolf scat collection sites.

0.4–7/km^2 (Lenarz 2011). Mean wolf density in Minnesota in 2012 to 2013 was 3.1 wolves/100 km^2, with a mean pack size of 4.3 wolves (Erb and Sampson 2013).

Moose were present across the entire Grand Portage Reservation (0.27/km^2), but their core range was inland away from Lake Superior (Oliveira-Santos et al. 2021). White-tailed deer were present across the entire reservation, and they congregated near the shore in winter. Beavers were common, with colony density estimated at 0.30 colonies/km^2 (Smith and Peterson 1988). Black bears were common and preyed on moose calves and deer fawns in spring (Wolf et al. 2021). From wolf collaring data in 2008, there were ≥3 wolf packs, with a mean of 4 wolves per pack, and estimated wolf density was 3-4 wolves/100 km^2 (Moore et al. 2013).

In Voyageurs National Park, moose density on the Kabetogama Peninsula was about half of the density (0.13/km^2) of moose on the Grand Portage Indian Reservation. The Kabetogama Peninsula is a 305-km^2 roadless area in the center of the park. Moose were rare elsewhere in Voyageurs National Park and adjacent lands to the south (Windels 2014). White-tailed deer were common throughout the park (2011 density = 3.3/km^2; Gable et al. 2017*b*). Beavers were abundant throughout the park, with densities of active lodges exceeding 1/km^2 in many areas (Johnston and Windels 2015). Black bears were also common throughout the park (~0.33/km^2; D. Garshelis, Minnesota Department of Natural Resources, unpublished data). Abundant food resources and the absence of human-caused mortality within park boundaries have likely contributed to sustained wolf densities of 2–5/100 km^2 in and immediately adjacent to the park since at least the late-1980s (Fox et al. 2001, Gogan et al. 2004, Olson and Windels 2015).

METHODS

Scat analysis is a commonly used method to identify prey items in a carnivore diet (Weaver 1993, Trites and Joy 2005, Gable et al. 2017*a*, 2018*a*). Prey items in wolf scats are identified by analyzing macroscopic features of hair and cuticular scale patterns. Prey hairs that can be readily identified in wolf scats include moose, moose calf, white-tailed deer, deer fawn, beaver, snowshoe hare, various small mammals, black bear, wolf, and coyote (*Canis latrans*; wiisagi-ma'iingan; Adorjan and Kolenosky 1969). Calf and fawn hairs can be differentiated from adult ungulate hairs from birth until late summer (Pimlott et al. 1969, Voigt et al. 1976, Fritts and Mech 1981, Peterson et al. 1984, Gauthier and Theberge 1986). After young ungulates molt in early fall, the hairs are no longer distinguishable from hairs of adults.

Scat collection

We collected scats along roads and snowmobile trails from April 2011–November 2013. Collectors completed a standardized data sheet (Chenaux-Ibrahim 2015) that included date, Universal Transverse Mercator (UTM) location in the 1854 Ceded Territory and Voyageurs National Park area and geographical description in Grand Portage, whether scats were fresh (e.g., strong smell, moist, tracks present, or on top of new snowfall) or old (e.g., crumbly or white), and, if known, date of previous scat collection on the road or trail. We collected scats opportunistically in the Voyageurs National Park area and the 1854 Ceded Territory and systematically in Grand Portage. Grand Portage has an interconnected system of snowmobile trails (90 km/100 km^2) and roads (40 km/100 km^2) that allowed intensive sampling of wolf scats in a concentrated area. We collected scats along designated routes at least once per month and at the end of each season. Because of the dense road network and small size of Grand Portage, collectors marked scat locations on a map and georeferenced locations using ArcMap (ArcGIS 10, Esri, Redlands, CA, USA). Collectors georeferenced scats in the Voyageurs National Park area and the 1854 Ceded Territory using handheld global positioning system (GPS) units.

We collected wolf scats on roads and trails and identified them by shape and diameter (Thompson 1952). We stored frozen scats in plastic bags until analysis and used scats ≥24 mm in diameter for analysis (Thompson 1952). A minimum diameter of 30 mm has also been recommended for identifying wolf scats (Weaver and Fritts 1979). We compared 386 scats 24–29 mm to 303 scats ≥30 mm to evaluate whether there was a difference in prey occurrence by scat diameter.

We collected scats throughout the year, and scats were assigned to 3 seasons relating to moose and deer parturition and snow cover based on date of collection and estimated scat age: winter (1 Oct–10 May), spring (11 May–30 Jun), and summer (1 Jul–30 Sep). The mean moose calving date in Minnesota in 2013 was 14 May (Severud et al. 2015). Mean date of fawn parturition was approximately 26 May in northcentral Minnesota during 2001–2002 (Carstensen et al. 2009). Moose calf hair was first identified in scats collected on 11 May; therefore, we assigned scats collected on or after 11 May through 30 June to the spring season. We assigned older scats collected at the beginning of a season to the previous season.

Hair identification

We processed scats following a standard operating procedure, which combined methods from several scat analysis studies (Chenaux-Ibrahim 2015). Briefly, we transferred scats to nylon stockings and boiled them for >30 minutes under a fume hood to kill parasites (Patterson et al. 1998, Chavez and Gese 2005, Klare et al. 2011). We washed scats in the nylon stockings in a dishwasher until only bone and hair remained. We air-dried the undigested remains in a fume hood for 24 hours and then weighed the sample.

After washing and drying, we spread scats out on a plate to identify prey species from hairs. We used the point-frame method to select the hairs that would be identified in each scat (Chamrad and Box 1964, Ciucci et al. 2004). A grid the same size as the plate was pre-marked with 25 points. We placed the grid over each scat and randomly selected 1 hair from each point for identification. We classified hairs into 9 different prey categories, including moose, moose calf, white-tailed deer, deer fawn, beaver, snowshoe hare, small mammals, black bear, and canid, which could include wolf or coyote. We identified moose calf hair and deer fawn hair in scats deposited from May through August. We classified ungulate hairs in scats deposited after August as moose or deer because calves and fawns had undergone a molt to winter hair. We recorded presence or absence of birds (feathers, beaks, and feet), vegetation, insects, and trash in scats.

We examined all hairs with a dissecting microscope to compare color, shape, diameter, and length. We analyzed the medulla, the innermost part of the hair, using a compound microscope with the contrast positioned to the brightest light. The hairs of ungulates and snowshoe hares have distinctive medulla patterns, which allowed for initial classification of the hair as ungulate, snowshoe hare, or other (Adorjan and Kolenosky 1969). We identified all beaver hairs and most hairs of other species macroscopically. Identification of hairs occasionally required additional analysis by examining scale patterns, especially when differentiating between moose and deer and identifying to age class (Chenaux-Ibrahim 2015). We could not differentiate between coyote and wolf hair, so these hairs were classified as canid.

We extracted hair scale patterns by taking negative impressions of hairs with Duco Cement® (Carrlee and Horelick 2010). We spread a thin layer of Duco Cement® on a microscope slide, and placed a hair in the cement. After 3 minutes, we pulled the hair out and taped it to the slide. We identified scale patterns using known hair samples from the region and a reference manual (Adorjan and Kolenosky 1969). Before performing hair identification in scats, observers took a blind test using 100 known hair samples representing all expected prey species (Ciucci et al. 1996); all observers exceeding 95% accuracy in identification.

Occurrence and biomass of prey items

We evaluated adequacy of sample size by calculating the Brillouin index (Brillouin 1956, Glen and Dickman 2006):

$$H_i = \frac{\left[lnln(N!) - \sum ln(ni!) \right]}{N}, \tag{1}$$

where H_i represents the diversity of wolf diet, N is the number of prey items in all samples, and n_i is the number of prey items in the ith category. We calculated the cumulative diversity and resampled randomly for 10 repetitions and then plotted against number of scats collected for each location and season.

To estimate the proportion of prey items in the diets of wolves, we calculated the frequency of occurrence, which was the number of detections of a particular prey item per total prey item detections in all scats (Barber-Meyer and Mech 2016). Frequency of occurrence does not account for prey body mass, which causes the importance of small prey and young animals to be overrepresented (Floyd et al. 1978, Weaver 1993, Ciucci et al. 1996). Estimating relative biomass consumed reduces bias by accounting for prey species body mass (Van Ballenberghe et al. 1975, Fuller and Keith 1980, Peterson et al. 1984). We corrected for bias from prey mass (Floyd et al. 1978, Weaver 1993):

$$Y = 0.439 + (0.008 \times X), \tag{2}$$

where Y represents the correction factor for prey consumed per scat (kg) and X is the live mass of prey (Table 1). We then multiplied the correction factor by the number of scats containing the prey item, which was greater than

TABLE 1 Estimated live mass of prey and prey mass per wolf scat used for biomass equations during 2011–2013, northeastern Minnesota, USA. We estimated adult deer and moose mass combining both sexes (Forbes and Theberge 1996). We estimated biomass using the equation $Y = 0.439 + 0.008 \times X$ (Floyd et al. 1978, Weaver 1993), where X represents the prey live mass (kg) and Y the prey mass (kg) per collectible scat.

Prey	Prey live mass (kg)	Prey mass (kg)/scat
White-tailed deer	75	1.039
Fawn (May–Jun)	4	0.471
Fawn (Jul–Aug)	14	0.551
Moose	444	3.993
Calf (May–Jun)	20	0.599
Calf (Jul–Aug)	57	0.895
Beaver	20	0.599
Snowshoe hare	1.5	0.451
Bear	100	1.239
Canids	32	0.695

total scats collected because scats can contain >1 prey item. We calculated percent biomass by dividing the mass (kg) of a particular prey consumed by the mass (kg) of all prey consumed.

Statistical analysis

We performed a one-way analysis of variance using JMP 10 software (SAS Institute, Cary, NC, USA) at a significance level of $P = 0.05$ to test for statistical differences in diet by biomass consumed among the 3 study areas and among 3 seasons, within each area and combining all years. We pooled scats among years because of small sample sizes (Table 2).

To evaluate whether wolves prefer deer, moose, or beaver in each study area and season, we calculated Manly's preference index (Müller 2006):

$$\alpha_i = \left(\frac{r_i}{n_i}\right) \times \left[\frac{1}{\left(\sum r_j/n_j\right)}\right], \tag{3}$$

where α_i represents Manly's preference of prey type i, r_i and r_j are the proportion of prey type i or j in the diet by biomass, and n_i and n_j are the proportion of prey type i or j available in the environment by biomass. There is no preference if $\alpha_i = 1/m$ (m = number of prey types). Prey i is preferred if α_i is $>1/m$ and avoided if α_i is $<1/m$.

Because actual densities of prey populations are not precisely known, we performed a sensitivity analysis over a range of densities of deer, moose, and beaver across northeastern Minnesota. We multiplied prey density by prey mass (Table 1) to estimate mass of prey per area (kg/km^2) and divided by total kg/km^2 to identify proportions of availability (Table 3). Moose density estimates were based on moose population estimates from aerial surveys in Grand Portage, northeastern Minnesota, and Voyageurs National Park (S. A. Moore, Grand Portage Department of Biology and Environment, unpublished data; Windels 2014, DelGiudice 2015). Deer density estimates were based on the Minnesota Department of Natural Resources estimated deer densities across northeastern Minnesota (Dexter 2012, Grund 2014). We calculated 2 beaver densities (2 beavers/km^2 and 6 beavers/km^2) based on

TABLE 2 Number of wolf scats collected (n = 1,000) by location, year, and season, northeastern Minnesota, USA. We assigned scats to 3 seasons based on collection date: spring (11 May–30 Jun), summer (1 Jul–30 Sep), and winter (1 Oct–10 May).

Location	Year	Spring	Summer	Winter
1854 Ceded Territory	2012	28	12	38
	2013	71	10	84
	Total	99	22	122
Grand Portage	2011	47	55	112
	2012	44	17	128
	2013	71	26	24
	Total	162	98	264
Voyageurs National Park area	2012	43	20	26
	2013	60	8	76
	Total	103	28	102

TABLE 3 Proportion of prey availability in northeastern Minnesota, USA, during 2011–2013. We multiplied expected densities of white-tailed deer, moose, and beaver by prey mass to estimate biomass available, which we then apportioned by species at each density to estimate proportion of each prey available (%) in the environment.

Density (prey/km^2)			Biomass available (kg/km^2)				Percent available (%)		
Deer	Moose	Beaver	Deer	Moose	Beaver	Total	Deer	Moose	Beaver
2	0.05	2	150	22	40	212	71	10	19
2	0.20	2	150	89	40	279	54	32	14
2	0.35	2	150	155	40	345	43	45	12
2	0.50	2	150	222	40	412	36	54	10
30	0.05	2	2,250	22	40	2,312	97	1	2
30	0.20	2	2,250	89	40	2,379	95	4	2
30	0.35	2	2,250	155	40	2,445	92	6	2
30	0.50	2	2,250	222	40	2,512	90	9	2
2	0.05	6	150	22	120	292	51	8	41
2	0.20	6	150	89	120	359	42	25	33
2	0.35	6	150	155	120	425	35	37	28
2	0.50	6	150	222	120	492	30	45	24
30	0.05	6	2,250	22	120	2,392	94	1	5
30	0.20	6	2,250	89	120	2,459	92	4	5
30	0.35	6	2,250	155	120	2,525	89	6	5
30	0.50	6	2,250	222	120	2,592	87	9	5

0.30 colonies/km^2 in Grand Portage (Smith and Peterson 1988) and ≥1 beaver lodge/km^2 in Voyageurs National Park (Johnston and Windels 2015) with 6 beavers/lodge (Jenkins and Busher 1979).

We estimated numbers of prey consumed by wolves in the Grand Portage Indian Reservation because the Grand Portage Band wants to evaluate the effect of wolves on the moose population, and because we have wolf density estimates from territory analyses and pack counts of collared wolves. The Grand Portage Reservation wolf population estimate in 2008 was 9–20 wolves (Moore et al. 2013). We estimated annual number of prey consumed using a point estimate of 15 wolves in Grand Portage. A 35-kg wolf has an estimated food requirement of 3.25 kg/day, or 0.09 kg/kg of wolf/day (Peterson and Ciucci 2003). The average mass of adult wolves in Grand Portage is 28.5 kg (S. A. Moore, unpublished data); thus, the estimated food requirement in Grand Portage is 2.6 kg/wolf/day. We calculated the number of prey type *i* consumed each season by wolves using:

$$N_i = \frac{(2.6WDB_i)}{P_i}, \tag{4}$$

where N_i is the number of prey type *i* consumed per season, *W* is the estimated wolf population, *D* is the number of days per season (spring was 49 days, summer was 91 days, and winter was 225 days), B_i is the proportion of biomass consumed for prey type *i*, and P_i is the estimated live mass of prey type *i* (Kojola et al. 2004). We summed the number of prey type *i* consumed during each of the 3 seasons to estimate the number consumed per year.

RESULTS

Scat collection

We examined 1,000 scats: 524 from Grand Portage, 243 from the 1854 Ceded Territory, and 233 from the Voyageurs National Park area (Table 2). One food item was present in 83% of scats, 2 food items in 16.5% of scats, 3 food items in 0.4% of scats, and 1 scat contained 4 food items. Non-mammal food items including birds, grasshoppers, seeds, vegetation, and trash were found in 5.6% of scats. Single or few canid hairs were found in many scats with only 1% of scats containing all or mostly canid hairs. Prey composition, as represented by mean percent occurrence, was similar in scats with a diameter 24–29 mm and in scats with a diameter ≥30 mm ($P = 0.50$; Figure 2). The Brillouin model, H_i, reached an asymptote at 15–50 scats, indicating that sampling effort was adequate (Figure 3).

The mean, minimum, and maximum distances between scat collection locations were 7, 0, and 17 km in Grand Portage; 38, 0, and 189 km in the 1854 Ceded Territory; and 17, 0, and 95 km in the Voyageurs National Park area. The mean number of days between scat collections was 1.7, 2.4, and 2.5 days in Grand Portage, the 1854 Ceded Territory, and the Voyageurs National Park area, respectively. We collected all scats on designated roads and trails in Grand Portage; thus, many scats were collected on the same day within 1 km of another scat. About 2% of scats collected in the 1854 Ceded Territory were within 1 km of another scat, and about 4% of scats collected in Voyageurs National Park were within 1 km of another scat.

Biomass consumed

Moose (including calves) represented 35–54% of wolf diet biomass in Grand Portage, 32–42% of wolf diet biomass in the 1854 Ceded Territory, and 3–13% of wolf diet biomass in the Voyageurs National Park area (Figure 4; Table 4). In Grand Portage, consumption of adult moose was greater in winter (54% biomass) than in spring (30%) and summer (42%) when beavers, fawns, and calves were available ($F_{2,521} = 8$, $P < 0.001$). Proportion of diet biomass

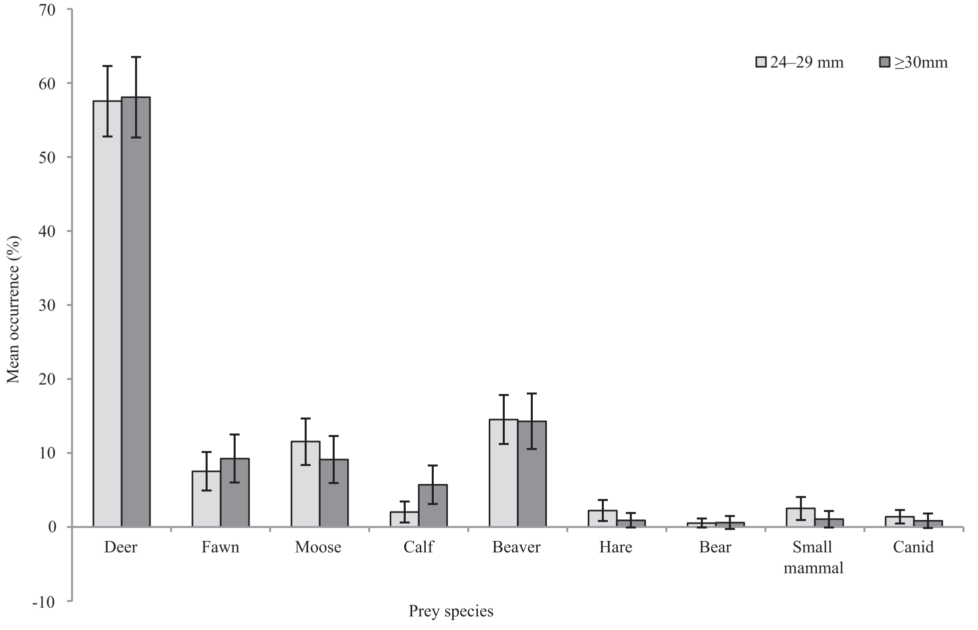

FIGURE 2 Comparison of prey occurrence in wolf scats with diameters 24–29 mm (*n* = 386) and diameters ≥30 mm (*n* = 303) during 2011–2013, northeastern Minnesota, USA. Bars represent mean occurrence (%) of each prey type in all wolf scats. Error bars represent 95% confidence intervals.

of adult moose was similar among the seasons in the Voyageurs National Park area (0–13% biomass) and in the 1854 Ceded Territory (30–38%; Figure 4; Table 4). Consumption of calves was 12 times greater by biomass in spring (12%) than in summer (0%; $F_{2,240} = 23$, $P < 0.001$) in the 1854 Ceded Territory.

White-tailed deer (including fawns) represented 38–47% of wolf diet biomass in Grand Portage, 46–62% in the 1854 Ceded Territory, and 63–79% in the Voyageurs National Park area (Figure 4; Table 4). In Grand Portage, consumption of adult deer was greater in winter (38% biomass) than in spring (35%) and summer (29%) when beavers, fawns, and calves were available ($F_{2,521} = 16$, $P < 0.001$). Adult deer were important food items in summer (55%) and winter (62%), with proportions lesser in spring (40%) ($F_{2,240} = 15$, $P < 0.001$) in the 1854 Ceded Territory. Proportion of diet biomass of adult deer was greater in winter (79%) and less in summer (44%; $F_{2,230} = 19$, $P < 0.001$) in the Voyageurs National Park area. Proportion of diet biomass of fawns was 4.75 times greater in summer (19%) than spring (4%; $F_{2,230} = 22$, $P < 0.001$) in the Voyageurs National Park area.

Differences in diet among locations

Adult moose represented 30–54% of prey by biomass in Grand Portage, which was greater than the 30–38% in the 1854 Ceded Territory and the 0–13% in the Voyageurs National Park area ($F_{2,997} = 17$, $P < 0.001$). Adult deer represented 44–79% of prey biomass on an annual basis in the Voyageurs National Park area and 40–62% in 1854 Ceded Territory, biomass proportions in these areas were greater than the 29–38% in Grand Portage ($F_{2,997} = 16$, $P < 0.001$). Fawns represented greater prey biomass in Grand Portage (10–12%) than in the 1854 Ceded Territory (2–6%) and Voyageurs National Park area (4–19%; $F_{2,997} = 6$, $P = 0.004$), and calves represented greater prey biomass in the 1854 Ceded Territory (0–12%; $F_{2,997} = 9$, $P < 0.001$) than in Grand Portage (2–5%) and Voyageurs National Park (1–3%).

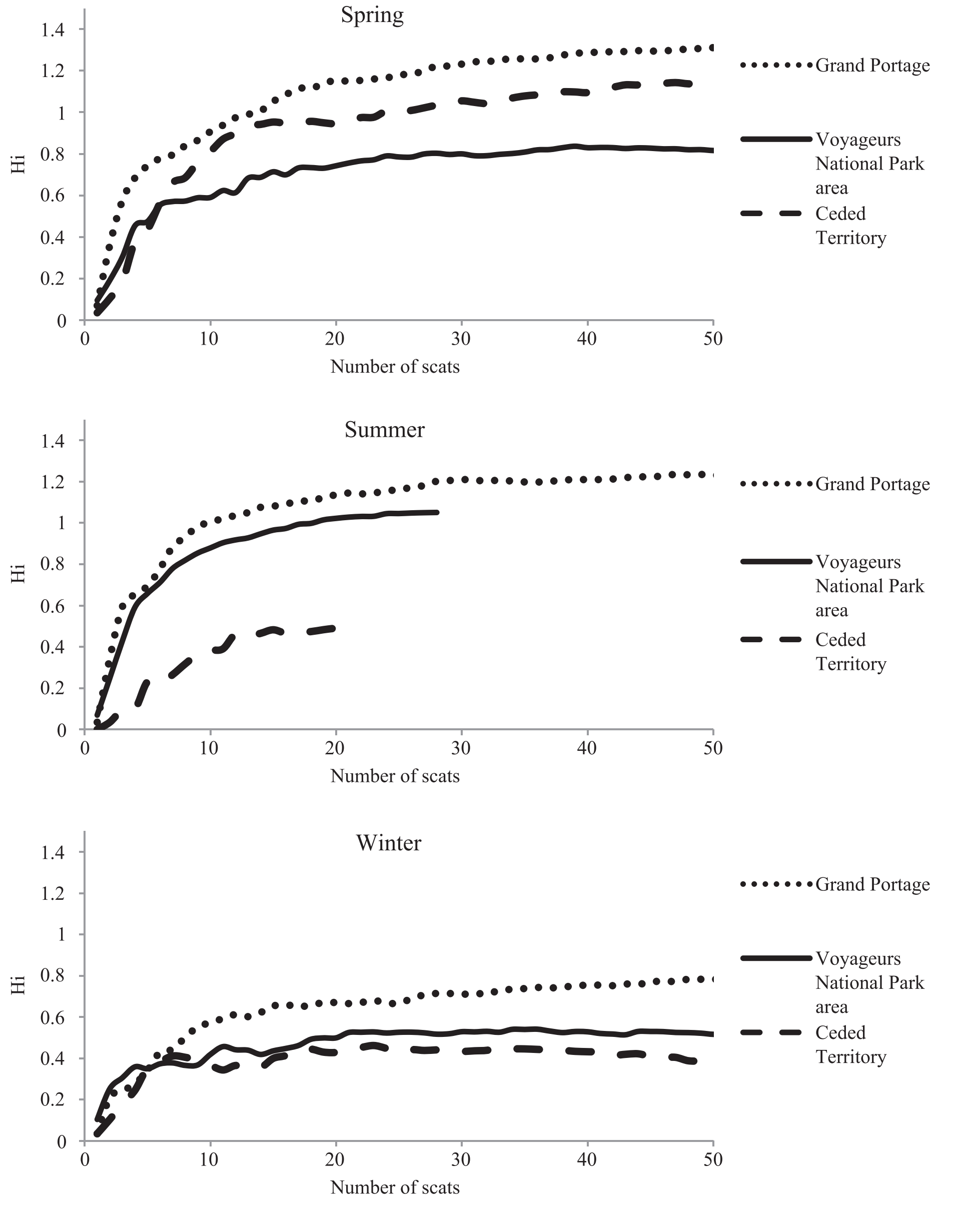

FIGURE 3 Dietary diversity found in wolf scats (n = 1,000) during 2011–2013, northeastern Minnesota, USA. We calculated diet diversity by season using Brillouin index (H_i) to measure adequacy of sample size analysis in each of the 3 study areas: Grand Portage, 1854 Ceded Territory, and Voyageurs National Park. Adequate sample size is reached when H_i reaches an asymptote.

Beaver represented 6–16% of prey biomass in Grand Portage and 7–30% in the Voyageurs National Park area, which was greater than in the 1854 Ceded Territory (0–5%; $F_{2,997}$ = 25, P < 0.001; Figure 4; Table 4). Snowshoe hare, black bear, and canids composed 1–4% of diet by biomass in Grand Portage, 4–8% in the 1854 Ceded Territory, and 1–3% in the Voyageurs National Park area (Figure 4; Table 4). Black bear was not found in scats in the Voyageurs National Park area.

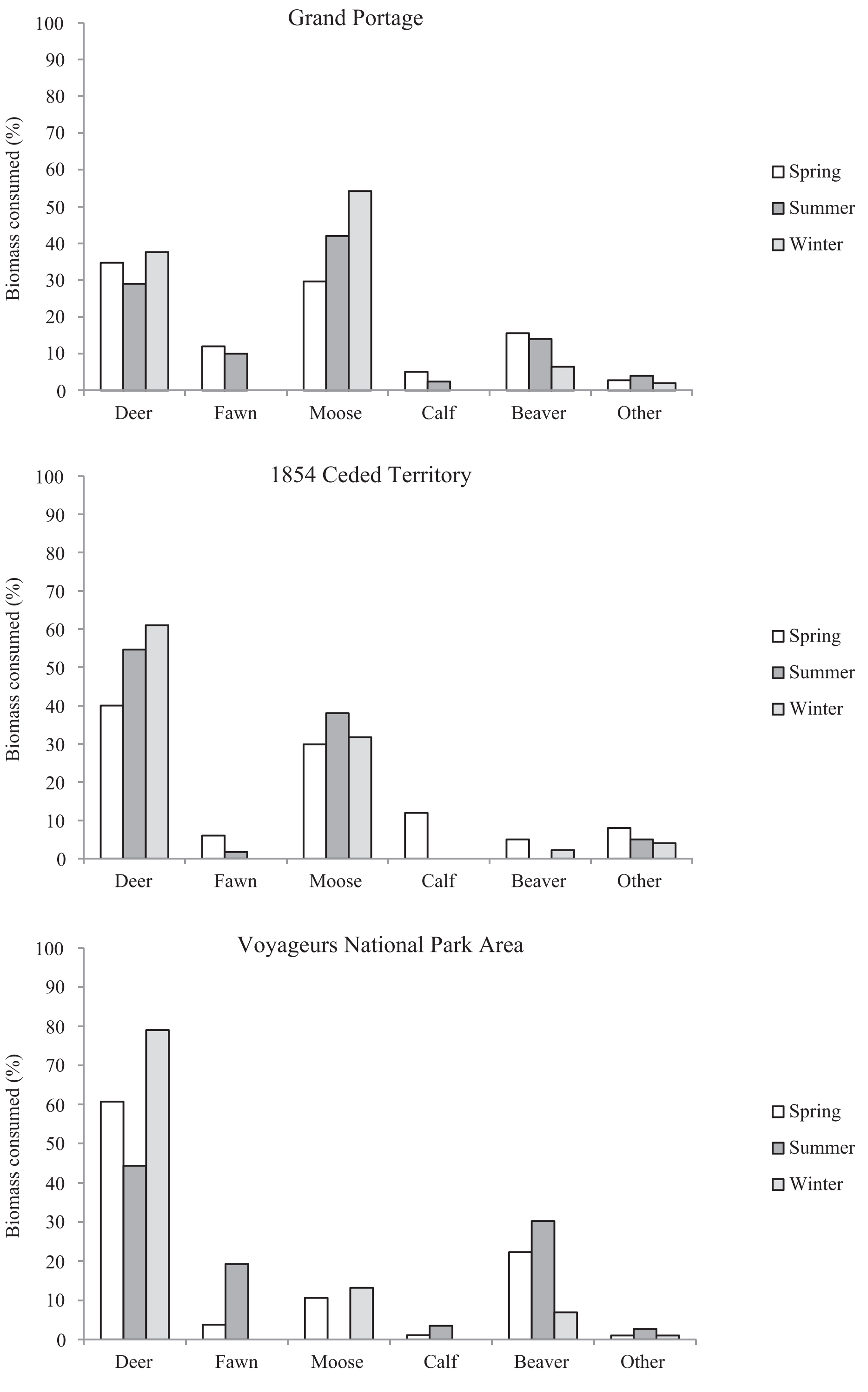

FIGURE 4 Biomass of prey items in wolf scats (n = 1,000) collected during 2011–2013, northeastern Minnesota, USA. Bars represent biomass consumed (%) per season (spring, summer, and winter) using a regression equation to correct for bias from live prey mass (Floyd et al. 1978, Weaver 1993).

TABLE 4 Wolf diet composition from scats collected in Grand Portage, the 1854 Ceded Territory, and Voyageurs National Park area during 2011–2013, northeastern Minnesota, USA. We calculated frequency of occurrence (freq.), which was the number of detections of a particular prey item per total prey item detections in all scats (Barber-Meyer and Mech 2016). We estimated biomass (biom.) consumed (kg) using the equation $Y = 0.439 + 0.008 \times X$ (Floyd et al. 1978, Weaver 1993), where X represents the live mass of prey and Y the mass of prey consumed per scat. We multiplied Y by the number of scats containing the prey item (number of scats), which was greater than total scats collected because scats can contain more than one prey item. We calculated percent biomass by dividing the biomass (kg) of a particular prey consumed by the biomass of all prey consumed.

	Spring				Summer				Winter			
	freq.	Number of scats	biom. (kg)	biom. (%)	freq.	Number of scats	biom. (kg)	biom. (%)	freq.	Number of scats	biom. (kg)	biom. (%)
Grand Portage												
Deer	32	63	65	35	31	40	42	29	58	168	175	38
Fawn	23	46	22	12	19	25	14	10				
Moose	7	14	56	30	11	15	60	42	22	63	252	54
Calf	8	16	10	5	3	4	4	2				
Beaver	25	49	29	16	25	33	20	14	17	50	30	6
Other[a]	5			3	11			4	3			1
Total			188	100			144	100			463	100
1854 Ceded Territory												
Deer	38	45	47	40	71	17	18	55	72	96	100	62
Fawn	12	14	7	6	4	1	1	2	1			
Moose	8	9	36	30	13	3	12	38	10	13	52	32
Calf	21	24	14	12								
Beaver	8	9	5	5					5	6	4	2
Other[a]	14			8	13			5	13			4
Total			118	100			32	100			161	100

(Continues)

TABLE 4 (Continued)

	Spring				Summer					Winter		
	freq.	Number of scats	biom. (kg)	biom. (%)	freq.	Number of scats	biom. (kg)	biom. (%)	freq.	Number of scats	biom. (kg)	biom. (%)
Voyageurs												
Deer	52	66	69	61	31	11	11	44	81	91	95	79
Fawn	7	9	4	4	26	9	5	19				
Moose	2	3	12	11					4	4	16	13
Calf	2	2	1	1	3	1	1	3				
Beaver	33	42	25	22	37	13	8	30	12	14	8	7
Other[a]	3			1	3			3	4	2		1
Total			112	100			26	100			120	100

[a]Other category included snowshoe hare, black bear, and canid.

Prey preference and number of prey consumed

To estimate prey preference, we fixed the proportion of each prey species biomass consumed in the wolf diet, with adult deer combined with fawns and adult moose combined with calves (Table 4). Because prey density was less certain, we used a sensitivity analysis approach with densities of 2 and 30 deer/km^2; 0.05, 0.20, 0.35, and 0.50 moose/km^2; and 2 and 6 beavers/km^2 to calculate prey preference. Across this range of densities, the proportion of available prey by biomass would range from 30–97% deer, 1–54% moose, and 2–41% beaver (Table 3).

In Grand Portage, moose would be avoided only in spring at lower beaver and deer densities and moose densities ≥0.35/km^2 and preferred at all other moose, deer, and beaver densities and seasons (Figure 5). In the 1854 Ceded Territory with an estimated lesser beaver density, moose would be preferred across the range of moose and deer densities and only avoided in winter at lower deer density and moose density ≥0.50/km^2 (Figure 6). In the Voyageurs National Park area with a higher beaver density, moose would be preferred in spring at lower deer densities and moose densities ≤0.05/km^2 and at higher deer densities and moose densities ≤0.35/km^2 (Figure 6). Moose would be preferred in summer only at moose densities ≤0.05/km^2 and higher deer densities, and in winter, at lower deer densities and moose densities ≤0.05/km^2 and at higher deer density across all moose densities.

With an estimated population of 15 wolves in Grand Portage, wolves would consume approximately 15 adult and sub-adult moose, 66 adult and sub-adult deer, and 67 beavers each year based on diet composition from scats. An estimated 7 calves and 79 fawns would be consumed in spring and summer. The average winter moose

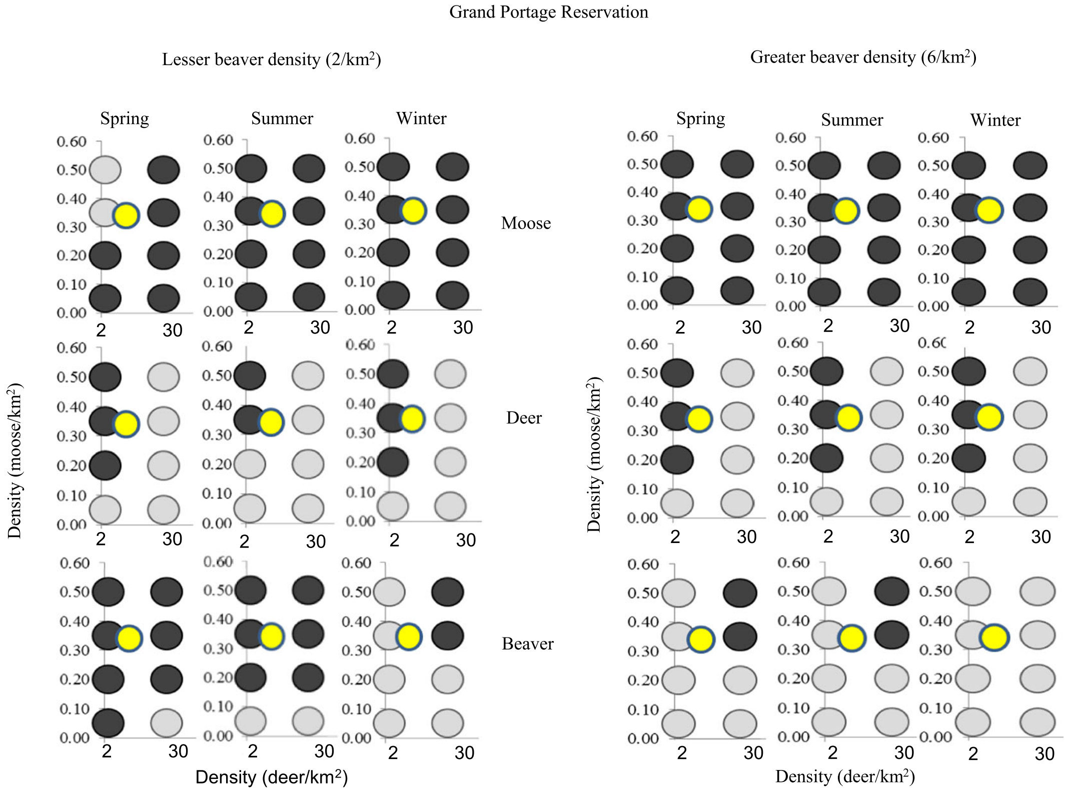

FIGURE 5 Preference and avoidance of moose, white-tailed deer, and beaver by wolves in the Grand Portage Reservation, Minnesota, USA, during 2011–2013. Black dots represent preference and gray dots represent avoidance for moose (top), deer (middle), and beaver (bottom). Yellow dot is the approximate density of moose and deer. Estimated beaver density is 2/km^2 (left) and 6/km^2 (right).

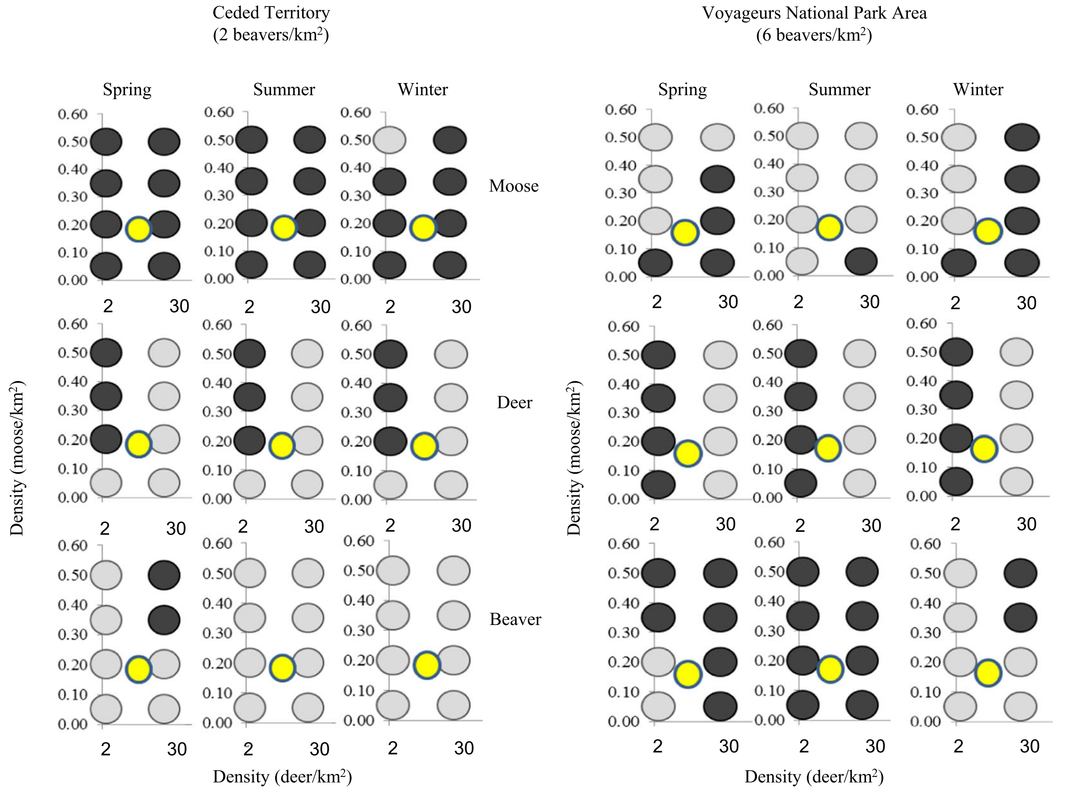

FIGURE 6 Preference and avoidance of moose, white-tailed deer, and beaver by wolves in the 1854 Ceded Territory (left) and Voyageurs National Park area (right), Minnesota, USA, during 2011–2013. Black dots represent preference and gray dots represent avoidance for moose (top), deer (middle), and beaver (bottom). Yellow dot is the approximate density of moose and deer.

population in Grand Portage from 2011–2013 was 48 adult and sub-adult moose, with 59% female and a pregnancy rate of 83% (S. A. Moore, unpublished data). Assuming 24 calves are born (48 × 0.59 × 0.83), wolves would have consumed almost 30% of calves born each year. With an estimated 15 adult and sub-adult moose consumed, wolves would have consumed approximately 30% of the adult and sub-adult moose population (n = 48).

DISCUSSION

Moose calf predation by wolves is extensive in some areas of northeastern Minnesota, particularly in the northern part of the study area. Consumption of moose calves was greater in spring than in summer in the 1854 Ceded Territory, where previous research reported intense wolf predation on calves during the first 50 days of age (Severud et al. 2019). While moose calves did not represent a major proportion of wolf diet by biomass, because of their relatively small size, a great number (≥30% of estimated calves born each year) are preyed upon by wolves. Other studies of calf survival in the region indicated 30-40% of moose calves are preyed upon by wolves (Severud et al. 2019, Wolf et al. 2021, Van de Vuurst et al. 2022), yet wolf diet studies adjacent to primary moose range in Minnesota reported low to non-existent levels of moose consumption in summer, likely because of lower densities of moose calves on the landscape (Gable et al. 2017*a*, 2018*a*). The proportion of diet biomass of moose calves was less than half as much in Grand Portage and the Voyageurs National Park area compared to the 1854 Ceded

Territory. In areas with high wolf densities, wolves affect the moose population through predation on calves in spring and summer. Van de Vuurst et al. (2022) illustrated that moose calving locations are aggregated across the landscape and indicated that high rates of wolf predation can occur in focused areas of high calf density. Wolves can limit moose populations through predation on calves (Testa et al. 2000, Bertram and Vivion 2002). On the Grand Portage Indian Reservation, with a population of 15-20 wolves, about 7 calves (30%) and 78 fawns would be consumed during spring and summer (S. A. Moore, unpublished data). When wolf populations are higher relative to similar or lower moose densities, they would potentially be preying on >50% of calves born each year (S. A. Moore, unpublished data).

Moose are a significant component of wolf diet across northeastern Minnesota. Availability of other prey species varies across northeastern Minnesota, and wolf diet composition changes across the landscape with prey availability. In Grand Portage, moose were the primary prey, followed by deer and then beaver. In the 1854 Ceded Territory, deer were the primary prey and moose were the secondary prey, while beaver were not an important food item. In the Voyageurs National Park area, deer were the primary prey, followed by beaver and then moose. In past studies of wolf diets based on scat analysis in Minnesota and Canada, the primary prey during winter and summer was deer and moose, with moose the primary prey item in Ontario, Canada, and deer the primary prey item in Minnesota (Figure 7; Floyd et al. 1978, Fritts and Mech 1981, Fuller 1989, Weaver 1993, Forbes and Theberge 1996, Gogan et al. 2004). Snowshoe hare and other species composed a minor portion of wolf diets. Globally, wolf diets are dominated by large and medium-sized ungulates (Newsome et al. 2016), but beavers can be seasonally important prey where beaver densities are high (Gable et al. 2018*b*).

Moose and deer were the primary prey year-round, but importance of prey type varied by season and location, consistent with reviews of wolf diets globally (Newsome et al. 2016, Gable et al. 2018*b*). Proportion of diet biomass of adult moose did not vary among seasons in the 1854 Ceded Territory or the Voyageurs National Park area. In Grand Portage where moose was the primary prey and where scats were collected intensively, proportion of diet biomass of adult moose and deer was greater in winter than spring and summer, supplanting the summer diet composed of beaver. Proportion of diet biomass of adult deer was greatest in summer and winter in the 1854 Ceded Territory and in winter in the Voyageurs National Park area. In a study based on stable isotope and scat analyses in Saskatchewan, Canada, wolves consumed primarily plains bison (*Bison bison*; mashkode-bizhiki) and then white-tailed deer and mule deer (*O. hemionus*), elk (*Cervus elaphus*; omashkooz), and moose in summer, and white-tailed deer composed the greatest percentage of wolf diet in winter, likely because of the debilitating effects of deep snow on deer condition and mobility (DelGiudice 1998, Shave et al. 2020). Beaver were important as a prey item in spring and summer in Grand Portage and the Voyageurs National Park area. Voyageurs National Park has relatively higher beaver densities compared to Grand Portage and the 1854 Ceded Territory (Johnston and Windels 2015), and the contribution of beavers to wolf diets during the ice-free period (Apr–Oct) has been documented (Gable et al. 2016, 2018*a*, *b*; Gable and Windels 2018).

Moose, including calves, were generally preferred prey in Grand Portage and the 1854 Ceded Territory in the northeastern part of the study area where moose density is higher but were consumed less than available in the Voyageurs National Park area where moose densities are lower. In a wolf diet study based on scat analysis in 2013 to 2015 in Ontario, juvenile and adult elk were preferred even though moose were 1.5 times more abundant than elk and white-tailed deer (Popp et al. 2018). In northeastern Minnesota while the moose population declined by over half during 2002 to 2013, the wolf population nearly doubled because of the availability of white-tailed deer as alternative prey (Barber-Meyer and Mech 2016). The increasing wolf population was supported by white-tailed deer in the winter, and wolves continued to prey on moose calves in the summer (Barber-Meyer and Mech 2016).

Collecting enough scats each season is necessary to accurately estimate carnivore diet composition. Factors such as size of study area and ability and time to collect scat will affect sampling effort and must be considered. For example, in this study, our design allowed a systematic approach to scat collection on the Grand Portage Indian Reservation, but we relied on opportunistic collections from our study partners in the 1854 Ceded Territory and Voyageurs National Park, which may have imparted bias due to the sampling times and locations from which

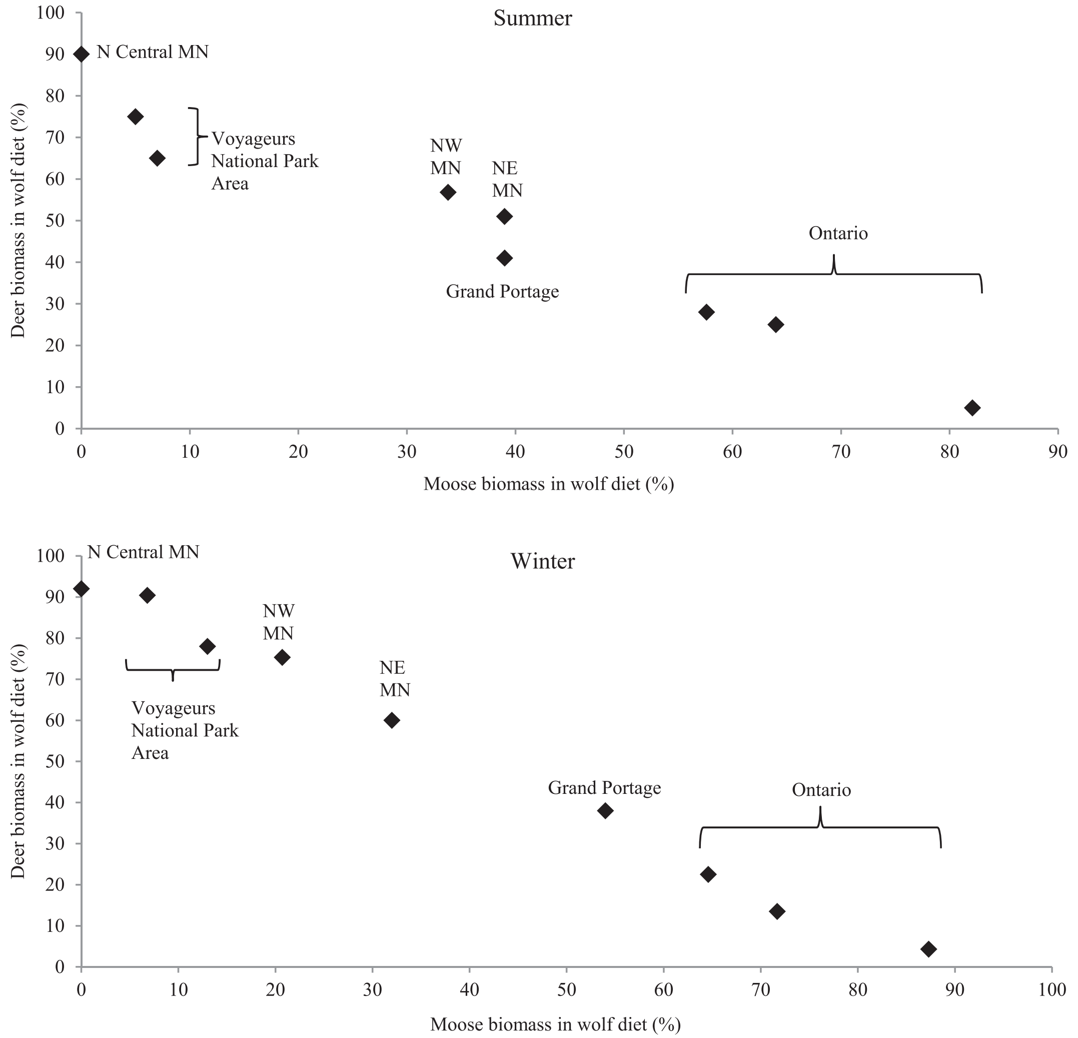

FIGURE 7 Comparison of deer and moose occurrence in summer and winter wolf diets based on scat analyses in Ontario, Canada and Minnesota, USA. Diet is represented by biomass (%), which uses a regression equation to correct for bias from live prey mass (Floyd et al. 1978, Fritts and Mech 1981, Fuller 1989, Weaver 1993, Forbes and Theberge 1996, Gogan et al. 2004, Chenaux-Ibrahim 2015).

samples were collected. Collecting 60 scats per season has been recommended as a general guideline (Trites and Joy 2005). With few prey items in wolf diets, power analysis indicates that lesser sample sizes could be used to quantify the proportion of wolf diet attributable to different prey types (B. Patterson, Ontario Ministry of Natural Resources, personal communication). Historically, in northeastern Minnesota the primary diet of wolves consists mostly of deer and moose (Van Ballenberghe et al. 1975, Fritts and Mech 1981) with beaver also an important prey (Van Ballenberghe et al. 1975, Gable and Windels 2018). By evaluating diet across seasons instead of weekly or monthly, we may have missed periodic importance of alternate food items, such as use of berries in the summer (Gable et al. 2018*a*). Our goal was to collect a minimum of 60 scats each season from each study area. The goal was met except during summer when 22 and 28 scats were collected in the 1854 Ceded Territory and the Voyageurs National Park area, respectively. The opportunistic sampling and unmet sampling goals for those areas likely influenced our results.

When assessing diets based on frequency of occurrence, moderate differences in diet (10% variation in seasonal diets, for instance) may be caused by sampling error and may not represent real differences in diet (Morin et al. 2019). Additionally, when estimating biomass consumed to evaluate diet, we did not know whether prey were killed or scavenged, the amount of prey lost to scavengers, whether the entire carcass was consumed, or prey condition. Wolves typically first consume soft components of the carcass (Carbyn 1983), and may not eat the entire carcass (Pimlott et al. 1969, Peterson 1977, Carbyn 1983, Potvin et al. 1988, Bobek et al. 1992, DelGiudice 1998), especially with larger prey (Floyd et al. 1978). To address these factors, the proportion of the carcass that was not eaten or was lost to scavengers would need to be subtracted from live mass estimates when estimating biomass consumed by wolves (Peterson and Ciucci 2003). Adult moose health in Minnesota is adversely affected by numerous conditions such as infestation by winter ticks (*Dermacentor albipictus*) and infection by brainworm (*Parelaphostrongylus tenuis*; Cornicelli et al. 2012, Wünschmann et al. 2015, Carstensen et al. 2018, Oliveira-Santos et al. 2021); wolves may be preying upon moose that are already sick or consuming moose that have died from other causes. Prey in poor condition would likely weigh less and have more hair per digestible material, causing wolves to produce more scats (Weaver 1993); thus, the prey would be overrepresented in diet.

A multi-species management approach could be effective to restore moose in Minnesota. Wolves have been found to be responsible for woodland caribou (*Rangifer tarandus caribou*) population declines in Alberta, Canada, because of seasonal prey switching and apparent competition (Latham et al. 2013). White-tailed deer was the primary prey of wolves in winter during 2002 to 2008, allowing for spatial separation between wolves and caribou in winter; however, in summer the primary prey was beaver and there was greater spatial overlap of wolves and caribou, which led to a greater proportion of wolf-caused mortalities in caribou (Latham et al. 2013). In British Columbia, Canada, a declining caribou population recovered when an invasive and abundant moose population was managed through increased hunter harvest, which caused wolf numbers to subsequently decline and caribou adult survival to increase (Serrouya et al. 2017). Those researchers suggested additional population management tools, including wolf management, to further achieve caribou population recovery (Serrouya et al. 2017), which may be options to consider in Minnesota, where wolf predation rates on moose calves appear to limit recruitment (Wolf et al. 2021, Van de Vuurst et al 2022).

Wolf pack size and where and when scats are deposited can affect randomized scat collection. Wolf diet estimates can be affected by temporal variation, inter-pack collection, and age class (Gable et al. 2017*a*). In a wolf scat study in the Greater Yellowstone Ecosystem during 2003-2010, wolf diet composition varied among packs in the same area and across years, with the most variable prey item being the number of neonate cervids (Lodberg-Holm et al. 2021). Food availability per wolf and the amount of prey lost to scavengers decreases with larger pack size (Schmidt and Mech 1997, Peterson and Ciucci 2003). But lone wolves and pairs of wolves are able to kill moose (Thurber and Peterson 1993, Vucetich et al. 2002, Mech et al. 2015). Additional factors, such as the length of time after consumption before depositing scats, which is typically 8–56 hours (Floyd et al. 1978), and how the scats collections were distributed over time and space relative to specific kills may have affected the collection efforts necessary to evaluate mean wolf diet.

CONSERVATION IMPLICATIONS

In northeastern Minnesota, limiting growth or reducing the white-tailed deer and wolf populations will likely aid in the recovery of the moose population. Deer densities can be high, especially along the Lake Superior shore in winter; thus, deer can compose most of the available prey in the environment. But even with greater availability of deer, moose still compose a significant proportion of wolf diet in winter. After calving begins in early May, moose calves are easier prey than adult white-tailed deer for wolves to obtain because adult deer can easily avoid predation on snowless ground.

Our study emphasizes the need to understand carnivore diets, especially in areas where prey switching may be occurring and when an important prey species is vulnerable and the population is declining. Moose in northeastern

Minnesota are a culturally important subsistence species that is affected by wolf predation. We demonstrate that the influence of wolf predation on moose, especially on calves, may be modulated by the relative abundance of alternate prey.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

The research presented in this article was developed and supported by the Grand Portage Band of Lake Superior Chippewa, a federally recognized Indian tribe in Northeastern Minnesota who exercise their rights to hunt, fish, and gather across their traditional land. As a sovereign nation, the Grand Portage Band is not subject to policies of an Institutional Animal Care and Use Committee. The Grand Portage Band has consistently collaborated with wildlife veterinarians under contract or Memoranda of Agreement to ensure that animal welfare standards used by the American Medical Veterinary Association (2010) are met.

DATA AVAILABILITY STATEMENT

The Grand Portage Band of Lake Superior Chippewa adheres to tenets of Indigenous data sovereignty and does not share data publicly without a data sharing and ownership agreement in place.

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