White-tailed Deer (*Odocoileus virginianus*) Subsidize Gray Wolves (*Canis lupus*) During a Moose (*Alces americanus*) Decline: A Case of Apparent Competition?

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Moose (*Alces americanus*) in northeastern Minnesota have declined by 55% since 2006. Although the cause is unresolved, some studies have suggested that Gray Wolves (*Canis lupus*) contributed to the decline. After the Moose decline, wolves could either decline or switch prey. To determine which occurred in our study area, we compared winter wolf counts and summer diet before and after the Moose decline. While wolf numbers in our study area nearly doubled from 23 in winter 2002 to an average of 41 during winters 2011–2013, calf:cow ratios (the number of calves per cow observed during winter surveys) in the wider Moose range more than halved from 0.93 in 2002 to an average of 0.31 during 2011–2013. Compared to summer 2002, wolves in summers 2011–2013 consumed fewer Moose and more White-tailed Deer (*Odocoileus virginianus*). While deer densities were similar during each period, average vulnerability, as reflected by winter severity, was greater during 2011–2013 than 2002, probably explaining the wolf increase. During the wolf increase Moose calves remained a summer food item. These findings suggest that in part of the Moose range, deer subsidized wolf numbers while wolves also preyed on Moose calves. This contributed to a Moose decline and is a possible case of apparent competition and inverse-density-dependent predation.

Key Words: *Alces americanus*; apparent competition; *Canis lupus;* diet; Gray Wolf; inverse-density-dependent predation; Minnesota; Moose; *Odocoileus virginianus*; scat; White-tailed Deer

Introduction

Gray Wolf (*Canis lupus*) diet in Minnesota generally consists of White-tailed Deer (*Odocoileus virginianus*), Moose (*Alces americanus)*, and Beavers (*Castor canadensis*; Frenzel 1974; Van Ballenberghe *et al*. 1975; Fritts and Mech 1981; Kunkel 1992; Paul 2002). In multiple-prey systems, wolf diet may be influenced by "changes in species abundance, prey switching, vegetation supply, and climatic conditions" (Forbes and Theberge 1996:1512). Wolves respond to declines in primary prey by switching to secondary, "buffer" prey (Pimlott *et al*. 1969; Van Ballenberghe *et al*. 1975; Messier and Crête 1985; Forbes and Theberge 1996).

Moose in northeastern Minnesota declined 55% (to varying degrees in various areas) from a point estimate of 8840 in 2006 to 4020 in 2016 (DelGiudice 2016). Wolves were implicated in this decline based on an inverse relation between their numbers in the northeastern part of Moose range and the calf:cow ratio (the number of calves per cow observed during winter surveys; Mech and Fieberg 2014). Wolves may contribute to limiting Moose populations (Peterson *et al*. 1984; Larsen *et al*. 1989) by predation on calves (Testa *et al*. 2000; Bertram and Vivion 2002) and were a major source of calf mortality in northeastern Minnesota (Severud *et al*. 2015). Following the decline in Moose, wolves could either decline or broaden their diet (increase consumption of an alternate prey) to include deer. Wolves subsidized by deer could continue to kill Moose (even at low Moose densities) potentially resulting in an inverse-density-dependent predation rate and apparent competition (Holt 1977; Holt *et al*. 1994; Wittmer *et al*. 2005; Hebblewhite and Smith 2010), furthering the Moose decline. An inverse-density-dependent predation rate occurs when the predation rate on prey increases while the density of the prey decreases because the predator is subsidized by an alternate prey species (Wittmer *et al*. 2005; Hebblewhite and Smith 2010). Apparent competition occurs when two prey species indirectly, negatively interact through the sharing of a common predator. In such cases the increasing abundance of one prey species indirectly results in the decreasing abundance of the other prey through the numerical response of the shared predator (Holt 1977; Holt *et al*. 1994; Chaneton and Bonsall 2000). Apparent competition has been hypothesized and demonstrated in various, sympatric ungulate populations including Moose, Elk (*Cervus canadensis*), and Woodland Caribou

(*Rangifer tarandus caribou*) living in areas with wolves (Seip 1991, 1992; Hurd 1999; Wittmer *et al.* 2005). Because interactions in large-mammal terrestrial systems are particularly complex and because the data required to conclude apparent competition are difficult to acquire, apparent competition is often difficult to distinguish in natural food webs from indirect amensalism (i.e., when two prey share a common predator, and prey species "A" is negatively indirectly affected by prey species "B", but prey species "B" is not indirectly affected by prey species "A"; Chaneton and Bonsall 2000).

To determine whether wolf abundance declined following the Moose decline or whether wolves increased consumption of an alternate prey (i.e., prey switched) in our study area of northeastern Minnesota (the southwestern part of the Mech and Fieberg [2014] study area), we compared wolf numbers and diet in that area before and after the Moose decline.

Methods

Our study area ("scat study area"; Figure 1) was approximately the southwestern third of a 2060 km², long-term wolf study area (Mech 2009) in the east-central Superior National Forest (47.8806°N, 91.4162°W, approximate centre of our long-term study area) of northeastern Minnesota, USA (see Nelson and Mech [1981] for a detailed description).

White-tailed Deer are more abundant in the scat study area, whereas Moose, although they inhabit our scat study area, are more abundant to the northeast in the larger wolf study area (Frenzel 1974; Mech 2009; Mech and Fieberg 2014) where Moose may reach densities of greater than or equal to 0.2 moose/km² (e.g., ≥ 8 moose/34.7 km² survey plot) in some locations (DelGiudice 2016). Pre-fawning deer densities (i.e., densities of deer before fawns are born each year) during 2011–2013 were approximately 1.5–2.0 deer/km² (Grund 2014).

During 2011–2013, we collected wolf scats greater than or equal to 25 mm wide (to minimize collecting scats from smaller sympatric canids such as Coyotes [*Canis latrans*; Weaver and Fritts 1979]) along logging roads and trails while conducting other field work that occurred primarily during June–August, but sometimes during the fall and winter (Figure 1), in generally the same area as Paul (2002). We collected 38 scats in 2011, 27 in 2012, and 57 in 2013. A portion of some scats were used to bait traps, and scats were frozen in preparation for analysis. Scats were placed in individual nylon stockings, boiled, rinsed, and then spread out on a plate and allowed to air dry (Ibrahim 2015).

We analyzed scat contents macro- and microscopically for deer, Moose, Beaver, Snowshoe Hare (*Lepus americanus*), and small mammal remains. The entire scat contents were examined macroscopically and bones, teeth, claws, feathers, trash, vegetation, soil/rocks, etc. were recorded. We randomly selected 25 hairs from each scat using a grid overlain on the spread-out, dried scat (Ciucci *et al.* 2004; Ibrahim 2015) and examined
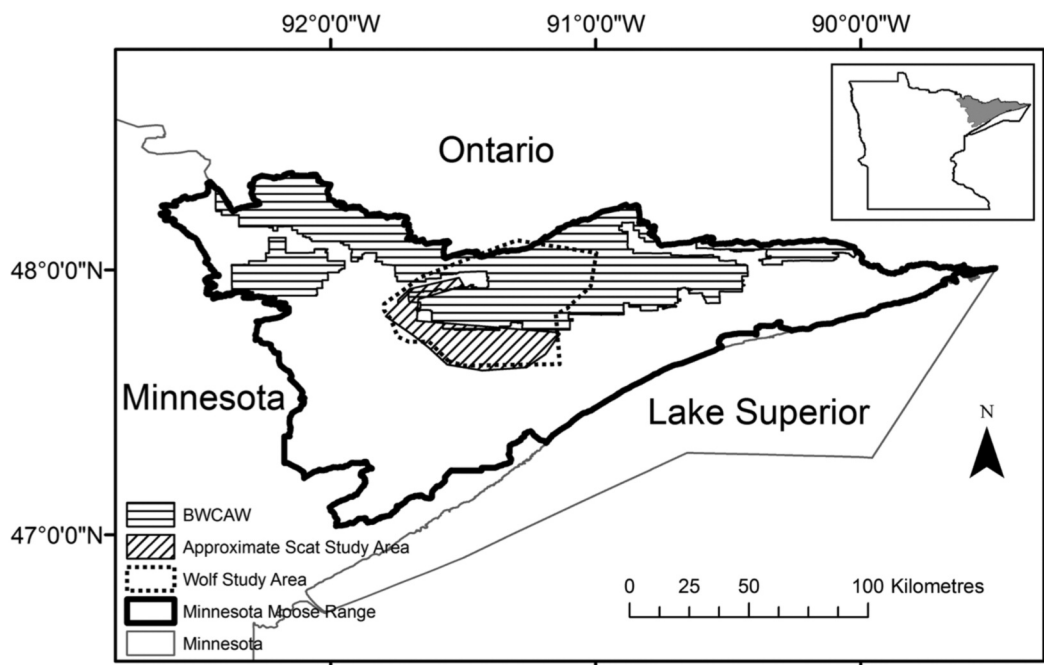

FIGURE 1. Study area for Gray Wolf (*Canis lupus*) scat collection (Approximate Scat Study Area) during 2011–2013, the long-term wolf study area, the Boundary Waters Canoe Area Wilderness (BWCAW), and Moose (*Alces americanus*) range in northeastern Minnesota, USA. Inset shows the state of Minnesota (including Minnesota's Lake Superior territory) with the main map area of interest shaded.

them with a dissecting scope (Swift® Tri–power, San Jose, CA) at 1–4 magnification. At least one hair representative of each species (and age class in ungulates) of the 25 hairs was examined (and occasionally negative impressions of the hairs; Kennedy and Carbyn 1981) with a compound microscope (Swift® M3500D, San Jose, CA) at four or 10 magnification. We used hair colour, texture, shape, length, diameter, medulla pattern, and scale pattern to identify the prey species, and age class in ungulates (i.e., fawn or calf versus adult; Adorjan and Kolenosky 1969; Kennedy and Carbyn 1981; Carrlee and Horelick 2011; Ibrahim 2015). It was generally harder to determine ungulate age class as summer

progressed and adult coats were emerging. Thus, greater uncertainty exists in August than in our June age-determinations. Nevertheless, we are reasonably confident in our age-class designations because we used many features to identify them (i.e., characteristics listed in the previous sentence). When the weight of evidence was equal for more than one age class, we coded age class as "unknown". We did not try to differentiate juveniles after August.

We calculated frequency of occurrence of prey categories and calculated biomass consumed (kg) using prey weights (Table 1) as given by Kunkel (1992) and Weaver's (1993) modification of Floyd et al.'s (1978)

TABLE 1. Gray Wolf (*Canis lupus*) scat contents and estimated prey consumption* in the Superior National Forest, Minnesota, USA (2011–2013).

Prey	Prey weight (kg)	Prey weight (kg) / scat	# of scats containing the prey item	Frequency of occurrence	Kg consumed	% of kg consumed	# of individuals consumed	Relative % individuals consumed
JUNE (POOLED YEARS), *n* scats = 51								
Adult deer	58.00	0.9030	14.0	27.5	12.6	40.9	0.2	7.2
Fawn deer	6.30	0.4894	35.0	68.6	17.1	55.4	2.7	90.3
Calf Moose	23.40	0.6262	1.0	2.0	0.6	2.0	0.0	0.9
Beaver	11.25	0.5290	1.0	2.0	0.5	1.7	0.1	1.6
JULY–AUGUST (POOLED YEARS), *n* scats = 55								
Adult deer	58.00	0.9030	7.0	10.9	6.3	18.2	0.1	6.3
Fawn deer	13.95	0.5506	30.0	50.0	16.5	47.4	1.2	68.7
Calf Moose	53.10	0.8638	10.5	18.8	9.1	26.1	0.2	9.9
Beaver	11.25	0.5290	5.5	10.9	2.9	8.4	0.3	15.0
2011 (POOLED SEASONS), *n* scats = 38								
Adult deer	58.00	0.9030	11.0	25.0	9.9	40.6	0.2	12.2
Fawn deer	11.40	0.5302	22.0	52.3	11.7	47.6	1.0	73.1
Calf Moose	43.20	0.7846	1.0	2.3	0.8	3.2	0.0	1.3
Beaver	11.25	0.5290	4.0	11.4	2.1	8.6	0.2	13.4
2012 (POOLED SEASONS), *n* scats = 27								
Adult deer	58.00	0.9030	6.0	20.7	5.4	32.5	0.1	8.8
Fawn deer	11.40	0.5302	17.5	62.1	9.3	55.6	0.8	77.0
Calf Moose	43.20	0.7846	0.5	3.5	0.4	2.4	0.0	0.9
Beaver	11.25	0.5290	3.0	10.3	1.6	9.5	0.1	13.3
2013 (POOLED SEASONS), *n* scats = 57								
Adult deer	58.00	0.9030	17.0	28.8	15.4	40.1	0.3	14.9
Fawn deer	11.40	0.5302	25.0	44.1	13.3	34.6	1.2	65.6
Calf Moose	43.20	0.7846	10.0	18.6	7.9	20.5	0.2	10.2
Beaver	11.25	0.5290	3.5	6.8	1.9	4.8	0.2	9.3
ALL YEARS, ALL SEASONS[†], *n* scats = 122								
Adult deer	58.00	0.9030	34.0	25.8	30.7	38.5	0.5	12.4
Fawn deer	11.40	0.5302	65.0	50.8	34.5	43.2	3.0	71.1
Calf Moose	43.20	0.7846	11.5	9.9	9.0	11.3	0.2	4.9
Beaver	11.25	0.5290	10.5	9.1	5.6	7.0	0.5	11.6

*Prey weights as used by Kunkel (1992), prey weight per scat (kg) calculated from Weaver's (1993) equation, # of scats that contained the prey item, frequency of occurrence = # of detections of particular prey item/total prey item detections in all scats (e.g., this included 10 scats that contained two prey items so the total items detected [132] was greater than the total number of scats collected [122]), kg consumed = number of scats × prey weight/scat, number of individuals consumed = kg consumed/average prey weight, and relative percent of individuals consumed = number of individuals consumed of one prey type/the sum of all individuals of all prey types consumed as reflected by the scat contents. In five scats with two primary prey, we considered these as ½ scat for each prey for biomass–consumed calculations. Although we did not consider small mammals as primary prey (four were detected during July–August 2001 and one during July–August 2012), we included them in frequency of occurrence calculations as well as a deer of unknown age class (132 total prey item detections).
[†]All seasons included 17 scats we collected during September–March (13 adult deer and four Beavers).

biomass equation. For scats that contained two primary (i.e., not small mammal) prey (5/122 scats or 4%), we assumed they contained equal amounts of biomass consumed (Ciucci *et al*. 1996) because interior soft tissue (e.g., muscle and organs) and hairless portions (e.g., Beaver tails and feet) would not be represented by the proportion of hair. To better understand the influence of wolf diet on prey populations, we also calculated the number of individuals eaten (kg consumed/average prey weight), and the relative percent of individuals consumed (number of individuals consumed of one prey item/the sum of all individuals of all prey items consumed) as reflected by scat contents by prey type. To compare our results to those from a previous study in our area (Paul 2002) that used different prey weights, we re-calculated Paul's (2002) biomasses using prey weights given in Kunkel (1992) and Weaver's (1993) biomass equation. Chi-square tests were used to assess differences in the summer counts of prey items between the studies (i.e., June–August 2002 and June–August 2011–2013; Paul 2002) in Statistix v. 10 (2015).

As part of a long-term research project (Mech 2009), wolves were captured and radio-collared (Institutional Animal Care and Use Committee 2015). We located wolves approximately weekly via aerial radio-telemetry and calculated winter pack counts for the larger study area as the maximum pack size observed during weekly locations from December–March each year (Mech 2009). We calculated winter wolf populations using only the packs residing in the scat study area (Figure 1).

Results

Winter wolf counts in our scat study area showed an increase from 23 wolves during 2001–2002 to 45 in 2010–2011, at least 42 during 2011–2012, and a minimum (poor survey conditions) of 37 in 2012–2013.

Of 38 scats collected in 2011, 27 in 2012, and 57 in 2013, none contained adult Moose or Snowshoe Hare: deer were the most common prey (adult 34/122 scats, fawn 67/122), then calf Moose (13/122) and Beaver (12/122; Table 1). Only five of 122 (4%) scats included two primary prey (two fawn deer and Beavers, two fawn deer and calf Moose, and one Beaver and calf Moose). Five others (4%) included both fawn deer and small mammal. In one scat, small mammal was the only prey.

Deer fawns were most frequently detected (51%) and represented the most biomass (43%) and individuals consumed (71%; Table 1). Adult deer were the second most detected, percent of biomass, and relative individuals consumed (Table 1). Although Beavers and calf Moose occurred about equally in our scat contents, because Beavers are smaller, more individuals were consumed than calf Moose (Table 1).

More deer and fewer calf Moose and Beavers were detected during June–August 2011–2013 than in June–August 2002 ($\chi^2 = 19.87$, df = 3, $P = 0.0002$; Tables 1 and 2). Because we did not detect any adult Moose, we could not compare that category (although Paul [2002] reported seven scats containing adult Moose during June 2002 and two during July–August 2002).

TABLE 2. Recalculation of prey contents in wolf (*Canis lupus*) scats* for June and July–August 2002 (see Table 4 in Paul [2002]) in part of the Superior National Forest, Minnesota, USA.

Prey	Prey weight (kg)	Prey weight (kg) / scat	# of scats containing the prey item	Kg consumed	% of kg consumed	# of individuals consumed	Relative % individuals consumed
JUNE (2002)[†]							
Adult deer	58.00	0.90300	9	8.1	16.3	0.1	4.8
Fawn deer	6.30	0.48940	25	12.2	24.6	1.9	66.3
Adult Moose	227.00	2.25500	7	15.8	31.7	0.1	2.4
Calf Moose	23.40	0.62620	15	9.4	18.9	0.4	13.7
Beaver	11.25	0.52900	8	4.2	8.5	0.4	12.8
Snowshoe Hare	1.08	0.44764	0	0.0	0.0	0.0	0.0
JULY–AUGUST (2002)[†]							
Adult deer	58.00	0.90300	3	2.7	7.8	0.1	3.4
Fawn deer	13.95	0.55060	18	9.9	28.5	0.7	52.0
Adult Moose	232.00	2.29500	2	4.6	13.2	0.0	1.5
Calf Moose	53.10	0.86380	16	13.8	39.8	0.3	19.1
Beaver	11.25	0.52900	7	3.7	10.7	0.3	24.1
Snowshoe Hare	1.08	0.44764	0	0.0	0.0	0.0	0.0

*Prey weights as used by Kunkel (1992), prey weight per scat (kg) calculated from Weaver's (1993) equation, # of scats containing the prey item, kg consumed = number of scats × prey weight/scat, number of individuals consumed = kg consumed/average weight of prey, and relative percent of individuals consumed = number of individuals consumed of one prey type/the sum of all individuals of all prey types consumed as reflected by the scat contents.

[†]During June, two deer were not identifiable to age class and during July–August, two deer and one Moose were not identifiable to age class, so these detections were not included in this comparison analysis.

Discussion

The wolf population nearly doubled in our scat study area from winter 2002 to 2011, while Moose calf:cow ratios in northeastern Minnesota more than halved from 0.93 in winter 2002 to 0.24 in 2011, 0.36 in 2012, and 0.33 in 2013 (DelGiudice 2016). Although wolf summer diet in 2011–2013 consisted of fewer Moose and more deer than summer 2002 prior to the Moose decline (Paul 2002), Moose calves remained a summer food item during 2011–2013. We suspect that wolves did not decline initially following the Moose decline because they were subsidized, at least temporarily, by deer.

Deer densities were low in 2002 and 2011–2013 (i.e., ≤ 2 deer/km^2; Grund 2014), but differences in winter severity indices (WSI; number of days with minimum temperature less than or equal to −17.8ºC plus number of days with greater than or equal to 38 cm snow on the ground: < 100 = mild, 100–180 = moderate, > 180 = severe; Kohn 1975) among those periods suggest differences in deer vulnerability to wolf predation (Mech *et al*. 1971; DelGiudice *et al*. 2006). The winter before Paul's (2002) study was mild (WSI approximately 51–79; MN DNR 2015). Winters 2010–2011, 2011–2012, and 2012–2013 included just one mild winter (WSI = 120–180+, 51–79, and 120–159, respectively; MN DNR 2015). Furthermore, the one "moderate" winter (2012–2013) during our scat study was atypical because the 38 cm snow depth threshold for daily point accumulation in WSI calculations was not exceeded until mid-February (Tom Rusch, personal communication). Despite the less than "severe" WSI, a local wildlife manager reported that "winter (2012–2013) exceeded both 1995–1996 and 2013–2014 in deer mortality" (Tom Rusch, personal communication; 1995–1996 and 2013–2014 both exceeded WSI of 200 and were considered "severe"). Thus, although deer densities have remained relatively low between 2002 and 2011–2013, deer were, on average, likely more vulnerable to wolf predation during our scat study compared to 2002.

Wolves typically prey on more vulnerable prey (Mech *et al*. 1971). When a prey species is more vulnerable (e.g., deep snow would typically hinder deer more than Moose; Mech *et al*. 1971), wolves that were more numerous due to an alternate prey subsidy could then take advantage of a new vulnerability in either species. As well, the average vulnerability of a prey population changes during the biological year and subsidized wolf numbers would have a greater negative impact on Moose calf and deer fawn recruitment than if there were fewer wolves overall.

Our findings suggest that, in at least part of the Moose range, wolves prey-switched and consumed more deer. At the same time, wolves continued to prey on Moose calves, contributing to the Moose decline and resulting in a possible case of apparent competition and inverse-density-dependent predation (Wittmer *et al*. 2005; Hebblewhite and Smith 2010). We cannot definitively conclude that apparent competition and inverse-density-dependent predation of Moose calves occurred. We do not have precise information on changing prey densities in our scat study area and we did not evaluate predation rates. We measured wolf diet as reflected by scat contents. But we think apparent competition and inverse-density-dependent predation likely because 1) wolf populations nearly doubled in our study area between the two scat studies presumably increasing predation pressure, 2) calf:cow ratios in the wider Moose range more than halved between the two studies, and 3) Moose calves remained a summer food item for wolves in the later scat study. Because both Moose and deer can be negatively, indirectly affected through a shared wolf predator, we do not think this is a case of indirect amensalism (i.e., where only one of the two prey species is negatively, indirectly affected through sharing a common predator; Chaneton and Bonsall 2000).

Although our results cannot be generalized to the entire northeastern Minnesota Moose range, wolves and deer inhabit most of that range. Our findings might help explain the role of wolves and deer in the range-wide Moose decline and offer the apparent competition/inverse-density-dependent predation hypothesis to be tested further.

Another factor (not mutually exclusive) in the Moose decline is that deer in our study area could have resulted in increased incidence of brain worm (*Parelaphostrongylus tenuis*) in Moose. This would further alter Moose vulnerability as well as lead to direct Moose mortality from the parasite (Karns 1967; Lankester 2010). Because our study focused mainly on summer wolf diet (when adult Moose are rarely killed by wolves), we cannot evaluate whether *P. tenuis* was a factor influencing increased wolf predation on Moose. Additional research regarding the importance of health-related factors in the Moose decline and in predisposing Moose to wolf predation is needed and is ongoing by the Minnesota Department of Natural Resources (M. Carstensen, personal communication).

Subsequent to our wolf diet study, wolf populations in our study area declined (L.D.M. and S.M.B-M., unpublished data). Thus, we suspect that the local deer population declined following increased wolf predation. Ultimately, it appears that the wolf population eventually tracked the declining Moose population (L.D.M. and S.M.B-M., unpublished data), with a lag due to increased deer vulnerability.

We collected scats opportunistically along trails and logging roads. Our results may have differed if we had collected scats near kills (Potvin *et al*. 1988) or homesites (where adults provision pups). Another regional study that examined 1000 wolf scats and included a more complex suite of prey (i.e., also adult Moose, Black Bear [*Ursus americanus*], Snowshoe Hare, and various small mammals) determined that wolf dietary diversity could be determined with as few as 15–50 scats (Ibrahim 2015). Because we considered a more

reduced suite of primary prey our sample likely reflects average summer wolf diet breadth in our scat study area. Although we did not detect Snowshoe Hare and adult Moose in wolf scats during our study, we expect that wolves did consume them but at such low rates that summer wolf predation would not negatively affect their populations in our study area.

Scat studies cannot differentiate scavenging and predation, and their effect on prey populations might differ among large ungulate prey species (Forbes and Theberge 1992, 1996). Although biomass calculations are less biased than frequency of occurrence (Ciucci *et al*. 1996), they do not account for prey condition (poorer prey would weigh less), caching, nor incomplete carcass consumption (e.g., bones), and food lost to scavengers (Peterson and Ciucci 2003).

Additional data on seasonal prey densities and seasonal wolf diet would improve future research. Collecting more scats in the Boundary Waters Canoe Area Wilderness (i.e., northeast of our sampling area; Figure 1), would improve our understanding of wolf diet in an area with fewer (almost no) deer (Nelson and Mech 2006) and more Beavers (S.M.B-M. and L.D.M., unpublished data).

Examining location clusters from GPS-collared wolves (Demma *et al*. 2007) should be used to more precisely determine the influence of wolf predation on Moose and the importance of Moose to the wolf diet. To best determine the influence of wolf predation on Moose, radio-tagged adult and calf Moose should be studied for cause-specific mortality (Severud *et al*. 2015). We recommend continued multi-faceted research (e.g., use of thermal refugia, habitat use with respect to deer, etc.) of both radio-tagged adult and calf Moose to best determine the causes for the recent decline in Moose.

Acknowledgements

Literature Cited
Adorjan, A. S., and **G. B. Kolenosky.** 1969. A manual for the identification of hairs of selected Ontario mammals. Research Branch, Ontario Department of Lands and Forests, Toronto, Ontario, Canada.

Bertram, M. R., and **M. T. Vivion.** 2002. Moose mortality in eastern interior Alaska. Journal of Wildlife Management 66: 747–756.

Carrlee, E., and **L. Horelick.** 2011. The Alaska Fur ID Project: a virtual resource for material identification. HIC Objects Specialty Group Postprints 18: 149–171. Accessed 7 March 2016. https://alaskafurid.wordpress.com/.

Chaneton, E. J., and **M. B. Bonsall.** 2000. Enemy-mediated apparent competition: Empirical patterns and the evidence. Oikos 88: 380–394.

Ciucci, P., L. Boitani, E. R. Pelliccioni, M. Roco, and **I. Guy.** 1996. A comparison of scat-analysis methods to assess the diet of the wolf (*Canis lupus*). Wildlife Biology 2: 37–48.

Ciucci, P., E. Tosoni, and **L. Boitani.** 2004. Assessment of the point-frame method to quantify wolf (*Canis lupus*) diet by scat analysis. Wildlife Biology 10: 149–153.

DelGiudice, G. D. 2016. Aerial Moose Survey. Minnesota Department of Natural Resources, St. Paul, Minnesota, USA.

DelGiudice, G. D., J. Fieberg, M. R. Riggs, M. C. Powell, and **W. Pan.** 2006. A long-term age-specific survival analysis of female white-tailed deer. Journal of Wildlife Management 70: 1556–1568.

Demma, D. J., S. M. Barber-Meyer, and **L. D. Mech.** 2007. Use of GPS telemetry to study wolf predation on deer fawns. Journal of Wildlife Management 71: 2767–2775.

Floyd, T. J., L. D. Mech, and **P. A. Jordan.** 1978. Relating wolf scat content to prey consumed. Journal of Wildlife Management 42: 528–532.

Forbes, G. J., and **J. B. Theberge.** 1992. Importance of scavenging on moose by wolves in Algonquin Park, Ontario. Alces 28: 235–241.

Forbes, G. J., and **J. B. Theberge.** 1996. Response by wolves to prey variation in central Ontario. Canadian Journal of Zoology 74: 1511–1520.

Frenzel, L. D. 1974. Occurrence of moose in food of wolves as revealed by scat analysis: a review of North American studies. Naturaliste Canadien 101: 467–479.

Fritts, S. H., and **L. D. Mech.** 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in northwestern Minnesota. Wildlife Monographs 80: 1–79.

Grund, M. 2014. Monitoring population trends of white-tailed deer in Minnesota. Farmland Wildlife Populations and Research Group, Minnesota Department of Natural Resources, St. Paul, Minnesota, USA.

Hebblewhite, M., and **D. W. Smith.** 2010. Wolf community ecology: ecosystem effects of recovering wolves in Banff and Yellowstone National Parks. Pages 69–120 *in* The World of Wolves. *Edited by* M. Musiani, L. Boitani, and P. C. Paquet. University of Calgary Press, Calgary, Alberta, Canada.

Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. Theoretical Population Biology 12: 197–229.

Holt, R. D., J. Grover, and **D. Tilman.** 1994. Simple rules for interspecific dominance in systems with exploitative and apparent competition. American Naturalist 144: 741–771.

Hurd, T. E. 1999. Factors limiting moose numbers and their interactions with elk and wolves in the Central Rocky Mountains, Canada. Ph.D. thesis, University of British Columbia, Vancouver, British Columbia, Canada.

Ibrahim, Y. C. 2015. Seasonal diet composition of gray wolves (*Canis lupus*) in northeastern Minnesota determined by scat analysis. M.Sc. thesis, University of Minnesota, Duluth, Minnesota, USA.

Institutional Animal Care and Use Committee. 2015. Northern Prairie Wildlife Research Center, US Geological Survey, Jamestown, North Dakota, USA.

Karns, P. D. 1967. *Pneumostrongylus tenuis* in deer in Minnesota and implications for moose. Journal of Wildlife Management 31: 299–303.

Kennedy, A., and **L. Carbyn.** 1981. Identification of wolf prey using hair and feather remains with special reference to Western Canadian National Parks. Canadian Wildlife Service Report, Edmonton, Alberta, Canada.

Kohn, B. 1975. Winter severity measurements. Wisconsin Department of Natural Resources. Final Report, Job 210, Wisconsin, USA.

Kunkel, K. E. 1992. Factors affecting wolf and black bear predation of white-tailed deer fawns in Northeastern Minnesota. M.Sc. thesis, University of Minnesota, Minneapolis, Minnesota, USA.

Lankester, M. W. 2010. Understanding the impact of meningeal worm, *Parelaphostrongylus tenuis*, on moose populations. Alces 46: 53–70.

Larsen, D. G., D. A. Gauthier, and **R. L. Markel.** 1989. Causes and rate of moose mortality in the southwest Yukon. Journal of Wildlife Management 53: 548–557.

Mech, L. D. 2009. Long-term research on wolves in the Superior National Forest. Pages 15–34 *in* Recovery of Gray Wolf in the Great Lakes Region of the United States: an Endangered Species Success Story. *Edited by* A. P. Wydeven, T. R. VanDeelen, and E. J. Heske. Springer, New York, New York, USA.

Mech, L. D., and **J. Fieberg.** 2014. Re-evaluating the northeastern Minnesota moose decline and the role of wolves. Journal of Wildlife Management 78: 1143–1150.

Mech, L. D., L. D. Frenzel, Jr., and **P. D. Karns.** 1971. The effect of snow conditions on the ability of wolves to capture deer. Pages 51–59 *in* Ecological Studies of the Timber Wolf in Northeastern Minnesota. *Edited by* L. D. Mech and L. D. Frenzel, Jr. USDA Forest Service Research Paper NC–52. North Central Forest Experimental Station, St. Paul, Minnesota, USA.

Messier, F., and **M. Crête.** 1985. Moose–wolf dynamics and the natural regulation of moose populations. Oecologia 65: 503–512.

MN DNR [Minnesota Department of Natural Resources]. 2015. Winter Severity Index (WSI) for White-tailed Deer. Accessed 17 February 2016. http://www.dnr.state.mn.us/hunting/Deer/maps_stats_archive.html.

Nelson, M. E., and **L. D. Mech.** 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildlife Monographs 77: 3–53.

Nelson, M. E., and **L. D. Mech.** 2006. A 3-decade dearth of deer (*Odocoileus virginianus*) in a wolf (*Canis lupus*)-dominated ecosystem. American Midland Naturalist 155: 373–382.

Paul, K. 2002. Determining summer food habits of 7 wolf packs in northeastern Minnesota via scat analysis. B.Sc. thesis, University of Minnesota, St. Paul, Minnesota, USA.

Peterson, R. O., and **P. Ciucci.** 2003. The wolf as a carnivore. Pages 104–130 *in* Wolves: Behavior, Ecology, and Conservation. *Edited by* L. D. Mech and L. Boitani. University of Chicago Press, Chicago, Illinois, USA.

Peterson, R. O., R. E. Page, and **K. M. Dodge.** 1984. Wolves, moose and the allometry of population cycles. Science 224: 1350–1352.

Pimlott, D. H., J. A. Shannon, and **G. B. Kolenosky.** 1969. The ecology of the timber wolf in Algonquin Provincial Park. Ontario Department Lands and Forests Research Report on Wildlife 87: 1–92.

Potvin, F., H. Jolicoeur, and **J. Huot.** 1988. Wolf diet and prey selectivity during two periods for deer in Quebec: decline versus expansion. Canadian Journal of Zoology 66: 1274–1279.

Seip, D. R. 1991. Predation and caribou populations. Rangifer Special Issue 7: 46–52.

Seip, D. R. 1992. Factors limiting woodland caribou populations and their interrelationships with wolves and moose in southeastern British Columbia. Canadian Journal of Zoology 70: 1494–1503.

Severud, W. J., G. DelGiudice, T. R. Obermoller, T. A. Enright, R. G. Wright, and **J. D. Forester.** 2015. Using GPS collars to determine parturition and cause-specific mortality of moose calves. Wildlife Society Bulletin 39: 616–625.

Statistix 10. 2015. Statistix 10. Copyright 1985–2013. Analytical Software. Version 10.0. Build: 3/6/2015.

Testa, J. W., E. F. Becker, and **G. R. Lee.** 2000. Temporal patterns in the survival of twin and single moose (*Alces alces*) calves in southcentral Alaska. Journal of Mammalogy 81: 162–168.

Van Ballenberghe, V., A. W. Erickson, and **D. Byman.** 1975. Ecology of the timber wolf in northeastern Minnesota. Wildlife Monographs 43: 3–43.

Weaver, J. L. 1993. Refining the equation for interpreting prey occurrence in gray wolf scats. Journal of Wildlife Management 57: 534–538.

Weaver, J. L., and **S. H. Fritts.** 1979. Comparison of coyote and wolf scat diameters. Journal of Wildlife Management 43: 786–788.

Wittmer, H. U., A. R. E. Sinclair, and **B. N. Mclellan.** 2005. The role of predation in the decline and extirpation of woodland caribou. Oecologia 144: 257–267.