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Problems with studying wolf predation on small prey in summer via global positioning system collars

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ORIGINAL PAPER

Problems with studying wolf predation on small prey in summer via global positioning system collars

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Abstract We attempted to study predation on various-sized prey by a male and female wolf (*Canis lupus*) with global positioning system (GPS) collars programmed to acquire locations every 10 min in the Superior National Forest of Minnesota. During May to August 2007, we investigated 147 clusters of locations (31% of the total) and found evidence of predation on a white-tailed deer (*Odocoileus virginianus*) fawn and yearling, a beaver (*Castor canadensis*), ruffed grouse (*Bonasa umbellus*), and fisher (*Martes pennanti*) and scavenging on a road-killed deer and other carrion. However, we missed finding many prey items and discuss the problems associated with trying to conduct such a study.

Keywords *Canis lupus* · Global positioning system (GPS) collars · Predation · Telemetry · White-tailed deer · Wolf

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Introduction

Wolves (*Canis lupus*) are large carnivores that usually prey on large ungulates. However, many wolves throughout the world prey primarily on juvenile ungulates or small prey in summer due to their availability and vulnerability. Wolves in the Superior National Forest, Minnesota, prey primarily on white-tailed deer (*Odocoileus virginianus*) fawns during summer (Kunkel and Mech 1994; Nelson and Mech 1986; Van Ballenberghe et al. 1975). Roe deer (*Capreolus capreolus*) fawns and wild boar (*Sus scrofa*) piglets constitute the main prey in some areas of the Iberian Peninsula and Italy during summer (Barja 2009; Capitani et al. 2004). Ungulates less than 40 kg such as blackbucks (*Antilope cervicapra*) represent the main prey of wolves in India (Jethva and Jhala 2004). Therefore, the study of wolf predation on small prey during summer represents a key need for understanding the wolf's ecology.

Radiotelemetry has been widely used for locating wolves in winter and studying predator–prey dynamics (Peterson and Ciucci 2003). The difficulty of locating wolves in summer (especially in forested areas) and finding prey remains or evidence of predation on small prey are possible explanations for the scarcity of summer predation studies. Recently, use of global positioning system (GPS) collars and geographic information systems (GIS) to monitor free-ranging species brought a major advance in the study of predatory behavior by wolves. Using GPS collars, Demma et al. (2007) demonstrated the possibility of investigating summer wolf predation on white-tailed deer fawns, and Sand et al. (2008) studied summer wolf predation on moose (*Alces alces*) calves. However, most wolf predation studies using GPS collars have been conducted in winter and have been most effective for large prey (Franke et al. 2006; Sand et al. 2005; Webb et al. 2008).

High rates of data acquisition seem to be one of the keys to study predation on small prey. The amount of time that wolves spend at kills (handling time) tends to be longer for large prey. Wolves usually spend >48 h handling a moose carcass (Ballard et al. 1987; Hayes et al. 1991; Messier and Crete 1985; Peterson et al. 1984). Thus, by obtaining wolf locations hourly or longer, it is still possible to find most large-prey kill sites (Franke et al. 2006; Sand et al. 2005; Webb et al. 2008). However, finding small prey with 1-h intervals is more problematic (Sand et al. 2005). Webb et al. (2008) found that a 30-min sampling interval was too long for detecting small prey, and Zimmermann et al. (2007) recommended using GPS position intervals of ≤ 30 min.

Demma et al. (2007) tried 10- to 60-min intervals and found that they held promise for studying wolf predation on deer fawns. In the present study, we used GPS collars on wolves programmed to acquire locations at 10-min intervals to (1) investigate if 10-min sampling intervals are useful for detecting small prey, (2) analyze the characteristics of clusters of locations that could be used for studying wolf predation, and (3) test the usefulness of short-location intervals for this type of study.

Study area

We conducted our study during the spring and summer of 2007 in a 130-km^2 area in the Superior National Forest of northeastern Minnesota (48°N, 92°W). The area is basically flat, being part of an old peneplain eroded by weather, water, and glaciers. Topography varies from large stretches of swamps to rocky ridges, with elevation ranging from 325 to 700 m above sea level. Temperatures range from –45°C in the winter to 37°C in the summer. Average seasonal temperatures are 6°C in the spring, 18°C in the summer, 7°C in the fall, and -11°C in the winter. Snow depths (usually from about mid-November through mid-April) generally range from 50 to 75 cm on the level. Conifers predominate in the forest overstory, with the following species present: jack pine (*Pinus banksiana*), white pine (*Pinus strobus*), red pine (*Pinus resinosa*), black spruce (*Picea mariana*), white spruce (*Picea glauca*), balsam fir (*Abies balsamea*), northern white cedar (*Thuja occidentalis*), and tamarack (*Larix laricina*). However, as a result of extensive cutting and fires, much of the conifer is interspersed with large stands of paper birch (*Betula papyrifera*) and aspen (*Populus tremuloides*). In summer, the vegetation is very dense at ground level.

Wolves occurred throughout the study area at densities of 30 to 36/1,000 km^2 during the study (Mech 2009). White-tailed deer occurred at densities of 12 to 15/10 km^2 (M.H. Dexter, Minnesota Department of Natural Resources, unpublished report) and constituted the major prey of wolves in the area, primarily fawns during summer (Kunkel and Mech 1994; Nelson and Mech 1986; Van Ballenberghe et al. 1975).

Methods

During May 2007, we live-trapped (Mech 1974) two wolves (a female and a male) that belonged to the Perch Lake pack, aged them (Gipson et al. 2000), and fitted them with Tellus GPS/VHF collars (Televilt, Lindesberg, Sweden) for 3 months (89 days), May 25 until August 22, following the same process as detailed by Demma et al. (2007). Both wolves were 1- to 2-year-old nonbreeding individuals. No evidence of pups was found in the Perch Lake pack during the period of study. We programmed GPS collars for positioning at 10-min intervals, assuming an error of 5 to 30 m of the exact location 50% and 95% of the time, respectively, as it has been estimated from landscapes similar to ours (Dussault et al. 2001; Moen et al. 1997). We remotely downloaded location data transmitted by GPS collars (attempts every 2 days) using a VHF-receiver data logger (RX-900; Televilt International) and a handheld antenna and plotted the locations on digital topographic maps of the study area (TOPO!, National Geographic Society, Hanover, PA). (Mention of brand names does not constitute endorsement by the US government.) Downloaded data included activity levels in the x and y axes (changes in collar position during the time the collar uses to obtain the GPS fix). We assumed that the highest x and y activity levels were related to greater activity and that activity levels = 0 corresponded with the wolves resting. We defined clusters as groups of consecutive locations <100 m away from the next without directionality (minimum duration = 1 h). For small clusters (distance between the most distant locations both in the latitudinal and longitudinal axes ≤ 50 m), we calculated the cluster centroids and entered the centroid positions into handheld GPS units. For larger clusters, besides centroids, we transferred other cluster locations to assure that the overall cluster area was checked. We visited all positions transferred to handheld GPS units in search of wolf signs and prey remains in a minimum radius of 100 m per position. Clusters were visited 1 to 7 days after remote downloading. We did not visit clusters when VHF signals indicated the wolves were still present.

The GPS collars were programmed to release 90 days after initialization, according to the expected battery life. We downloaded GPS data from the released collars and plotted them in Arcview 3.2, using the Animal Movement Analysis extension (Hooge and Eichenlaub 1997), to calculate wolf movements and cluster characteristics. We

Table 1 Variables measured for each GPS location cluster for wolves in the Superior National Forest during spring–summer 2007

Variable	Description
Duration	Time between the first and last location in the cluster
Prevdist	Minimum distance travelled from the previous cluster (adding linear distances between consecutive locations)
Postdist	Minimum distance travelled to the next cluster (adding linear distances between consecutive locations)
Prevtime	Time since the last location of the previous cluster until the first location of the current cluster
Posttime	Time since the last location of the current cluster until the first location of the next cluster
Area	Cluster minimum-convex-polygon area
Ldpp	Mean value of the linear distance from previous point
Perinact	Percent in a cluster of locations when both activity levels (x and y axis) = 0
Meanact	Mean value of activity levels (x+y) when x and y are distinct from 0

added lines connecting successive GPS points to estimate wolf travel paths. To minimize the possible effects of the capture, we excluded GPS locations during the first 3 days postcapture. To avoid errors due to missing locations during the remote downloading process, we conducted all the analyses from the released collars downloads.

For each cluster, we measured nine variables related to spatiotemporal characteristics and activity levels registered in the collars (Table 1). Moreover, we created a variable (daytime) related to the time of the day at which clusters occurred. Based on daylight and local time during the study, we divided the day into four periods (central daylight, 1000–1800; central night time, 2200–0600; and transition times, 0600–1000 and 1800–2200). Depending on the percentage of time spent at each interval, we assigned a value for each cluster, assigning value 1 to strictly diurnal clusters and value 5 with strictly nocturnal clusters (Table 2). Based on our field checks, we classified the clusters into three groups: resting clusters, when only wolf beds were found; feeding clusters, when prey remains or other food sources were found inside the minimum convex polygon (MCP) of the cluster; and unknowns. We used paired *t* test and Mann–Whitney *U* test to compare resting and feeding cluster characteristics.

At a broader scale, we defined events as a group of clusters and movements related to a prey/food item. Predation events were those when we found predation evidence as hematomas in the remains or when predation was the most probable option (depending on the type of prey, remains found, activity levels, and wolves' movements related with the findings), and scavenging events were those involving food resources not related to predation. We buffered prey remains and other food source positions with radii of 100 and 500 m. We considered the beginning of the event the first wolf location inside the buffer and the end of the event the last location inside the buffer. Because wolves sometimes return to food resources, we considered an event the same when locations within a buffered area occurred on consecutive days. We measured the number of consecutive days a wolf was inside the buffered areas related to the event, the number of locations related to the event inside the buffered areas, and the overall event duration considering the 100 and 500 m buffer radii. We also measured the number of days, weeks, and location a wolf was inside the buffered areas considering the whole period of study. We used paired *t* test and Mann–Whitney *U* test to determine if there were differences in these characteristics between scavenging and predation events. To explore possible relationships between event characteristics and the estimated prey weights, we used Pearson correlation coefficients.

For statistical analyses, we used SPSS (12.0) for Windows (SPSS Inc., Chicago, IL). Statistical significance in all analyses was assumed at $P \leq 0.05$.

Results

Data from the collars resulted in 12,194 locations for the female and 12,199 locations for the male, 5% of the overall

Table 2 Times of day used to define daytime values for GPS location clusters for wolves in the Superior National Forest during spring–summer 2007

Daytime value	Central daylight (1000–1800) % of cluster duration	Transition times (1800–2200 and 0600–1000) % of cluster duration	Central night time (2200–0600) % of cluster duration
1	100	0	0
2	50 to <100	<50	<50
3	<50	0–100	<50
4	<50	<50	50 to <100
5	0	0	100

scheduled locations being missed. Both wolves were together (<50 m apart) only 1.3% of the time (164 locations).

We conducted 76 remote downloads, with an average of 210 locations per download (35 h), and remotely downloaded 52% of the female and 60% of the male acquired locations. We checked 147 location clusters (31% of clusters resulting from the analysis of total collar data) and found signs of wolf activity in 88 clusters (60% of the clusters checked and 19% of the overall clusters). Clusters were checked 2.75±0.17 (SE) days after the wolf left the area.

We identified 75 resting clusters, 18 feeding clusters, and 59 unknowns (Table 3). We also considered as feeding clusters unchecked clusters related to the events when the remains/food position was inside the cluster MCP. Due to the small sample of kill sites found, we did not distinguish between predation and scavenging, considering only one class for feeding behavior.

Mean linear distances from previous points (Ldpp) were greater for feeding clusters than for resting clusters (t=-5.059, P<0.001). Wolf activity as measured by the collar (Meanact) was greater for feeding clusters (t=-4.462, P<0.001). When food remains were present, wolves were inactive (Perinact) 50% of the time, whereas in resting clusters, wolves were inactive a mean of 63% (t=-2.57, P=0.01). Feeding clusters were more nocturnal than resting clusters (Mann–Whitney U=326.0, P<0.001). Differences in the other measured variables were not significant (P>0.1) except that duration of resting clusters tended to be longer (t=1,777, P=0.08).

We defined 12 feeding events, five of them predation and the other seven scavenging. During the 3-month study, we found remains of one white-tailed deer fawn and a beaver (*Castor canadensis*) related to the male wolf and a white-tailed deer yearling, a ruffed grouse (*Bonasa umbellus*), and a fisher (*Martes pennanti*) related to the female wolf, which we considered as kill sites (Figs. 1a, b; 2a, b, and c). Based on the number of close beds found in the clusters (one single wolf bed found per cluster versus multiple beds and flattened vegetation), we assumed that with the fawn, grouse, and fisher kills, the wolf was alone, whereas the female was with pack mates at the yearling deer kill, and the male was with pack mates at least at the end of the beaver kill event. We found a correlation between estimated prey weight and the number of consecutive days the wolf used the 500-m-buffered areas (Pearson correlation coefficient r=0.96, n=5, P<0.001) and the overall event duration assuming a 500-m-buffer radius (Pearson correlation coefficient r=0.95, n=5, P=0.01).

The scavenging events included a road-killed adult deer ("road kill"), a pile of unidentified rotting meat, probably a bear-hunting (*Ursus americanus*) bait station, two bear-bait stations, and a pile of fish in a garbage dump. Both wolves visited the road kill (Fig. 3). The female and male were together at the road kill for 12 h. Event characteristics were similar for both the female and the male, although the male remained much longer inside the buffered area during successive visits (Table 4). The other food item visited by both wolves was the rotting meat (Fig. 4). During this event, the female and the male were together for 3 h. The use of this food source was completely different for both wolves based on the variables measured (Table 4) and the movements and clusters of the event (Fig. 4).

During one bear-bait station event, the female was alone, and during the dead-fish event, the male was alone. The male was with other pack mates during the other bait station event.

There were no significant differences between scavenging and predation event characteristics in the variables measured, although the small sample for this analysis needs to be considered for properly interpreting this result.

Table 3 Characteristics of feeding, resting, and unknown GPS location clusters for wolves in the Superior National Forest during spring–summer 2007

Variable	Cluster type					
	Feeding (n=18)		Resting (n=75)		Unknown (n=59)	
	Mean	2 SE	Mean	2 SE	Mean	2 SE
Ldpp (m)*	31.5	4.4	19.9	2.0	24.3	2.8
Perinact*	0.50	0.11	0.63	0.04	0.58	0.06
Meanact*	10.9	2.3	7.0	0.7	7.5	0.7
Daytime*	4.2	0.5	3.0	0.3	3.1	0.4
Duration (min)	310	134.2	448	68.7	401	89.1
Prevdist (m)	1,199	807.8	1,612	462.4	1,011	437.2
Postdist (m)	1,257	808.2	1,401	408.7	683	288.7
Prevtime (min)	127	48.0	144	35.1	98	30.0
Posttime (min)	100	56.1	129	34.7	79	19.6
Area (ha)	0.66	0.3	0.47	0.1	0.58	0.2

* Significant differences (P<0.05) between feeding and resting clusters found

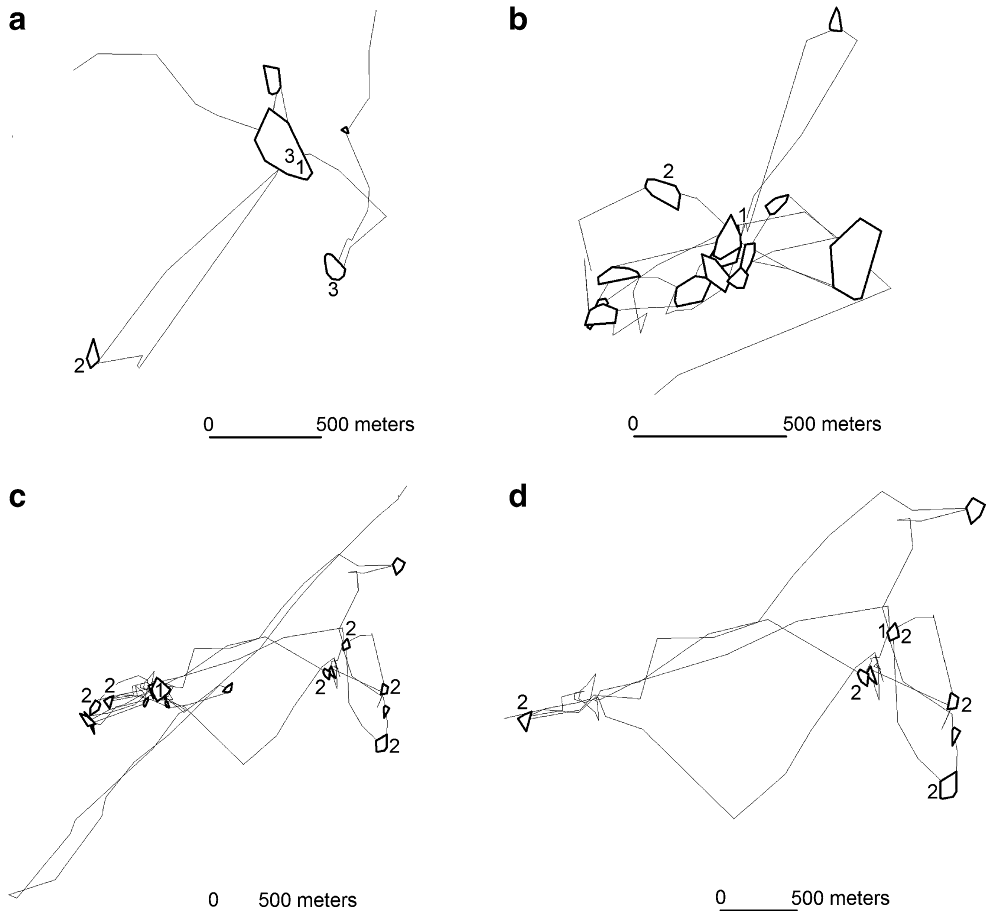

Fig. 1 GPS-collared male wolf feeding events in the Superior National Forest during spring–summer 2007. The figures represent all the MCPs of GPS location clusters and movements since the wolf arrived in the 500-m buffered area until the end of the event. **a** Deer fawn predation. **b** Beaver predation. **c** Dead-fish feeding. **d** Bear-bait station feeding. **c** and **d** events were chronologically consecutive. Based on our definition of an event, buffering fish and baiting station with 500-m radius, both events overlap in some extent. It implies that the collared wolf visited both food resources alternatively. Findings: (1) prey remains/food resources; (2) wolf beds; (3) wolf scats

Discussion

Programming collars to obtain locations at 10-min intervals provides information unobtainable a decade ago. However, we still found many problems in trying to study wolf predation on small prey in summer via GPS collars. The first problem is related to the specific equipment used and the field work needed for obtaining appropriate sample sizes. By terrestrial, remote downloading, we downloaded 50% to 60% of possible locations. The VHF-receiver data logger capacity was <2 days of information. Every download made after 2 days of the previous one resulted in real-time missing data. In other studies, collars were programmed for positioning at 30-min intervals (Sand et al. 2008), 15-min to 6-h intervals (Webb et al. 2008), and 60-min intervals (Franke et al. 2006), and remote-data downloading was conducted weekly or biweekly (Sand et al. 2005; Zimmermann et al. 2007). Demma et al. (2007) programmed one GPS collar for positioning at 10-min intervals during 1800 to 1000 h. They tried to remotely download the GPS collar data on 25 days, being 68% successful. In our study, we tried to locate the wolves almost every 2 days during the 89-day study; even so, we missed 40% to 50% of locations due to the fact that download trials were not always successful. Furthermore, the downloading in such circumstances (high fix rates and limited data logger capacity) directly reduced the time invested in checking clusters and, as a result, a smaller number of clusters checked.

We also found other problems that would be unrelated to the type of GPS collar or technology used. We classified 40% of the checked clusters as unknowns because we did not find wolf sign or predation evidence. In spite of being difficult to find small-prey remains itself, summer conditions and habitat characteristics, often swampy and with dense thicket, could affect the percentage of unknown clusters. A possible solution to increase the percentage of *knowns* in future studies could be the use of well-trained dogs for checking clusters. Dogs have been used for carnivore scat detection (Mackay et al. 2008) and for checking clusters in wolf kill-rate studies as well (Sand et al. 2008).

We classified known clusters as resting and feeding clusters. Although it might be simplistic to reduce wolf behavior at clusters to resting and feeding, these results could serve to decide in future studies which clusters to check, avoiding diurnal clusters with low linear distance between consecutive locations, a high percentage of inactive time, and low activity levels if the purpose of the study is to estimate kill rates. We did not further evaluate

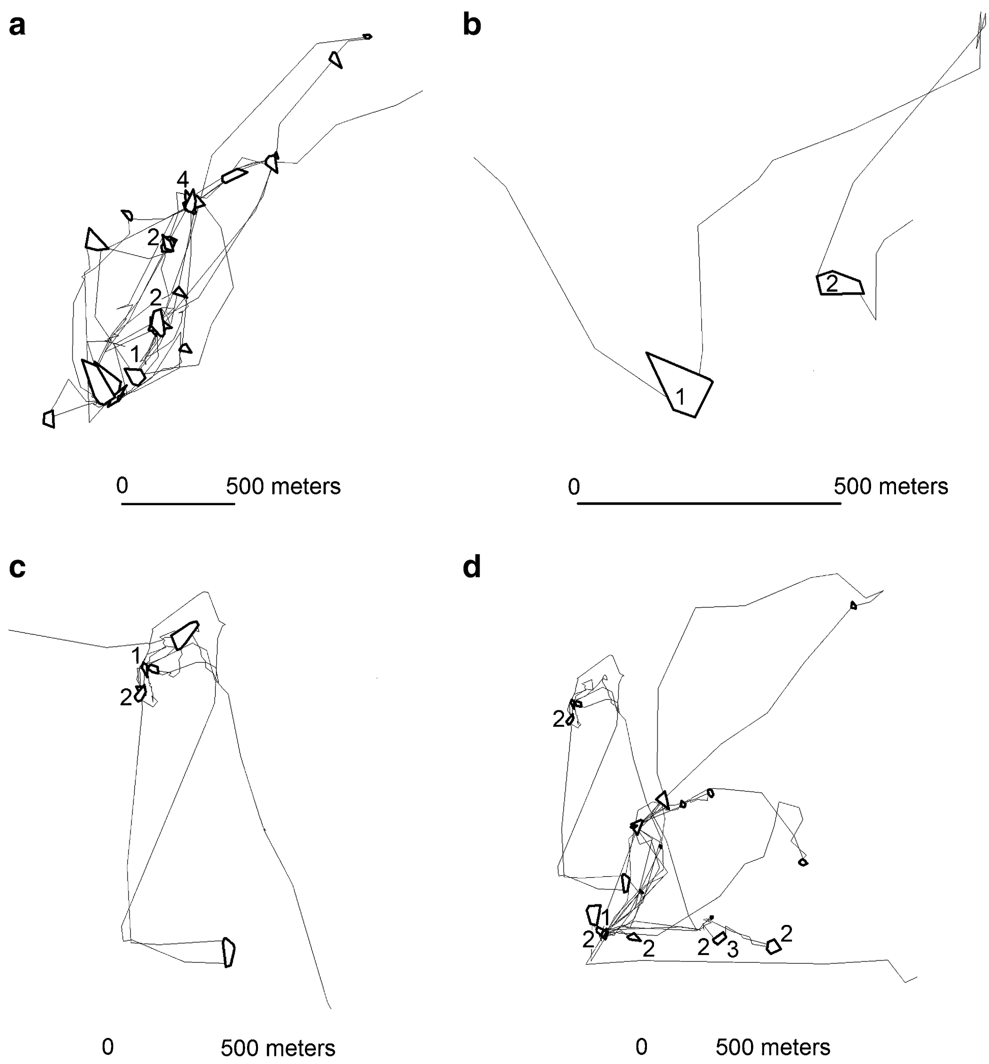

Fig. 2 GPS-collared female wolf feeding events in the Superior National Forest during spring–summer 2007. The figures represent all the MCPs of GPS location clusters and movements since the wolf arrived in the 500-m buffered area until the end of the event. **a** Yearling deer predation. **b** Grouse predation. **c** Fisher predation. **d** Bear-bait station feeding. Findings: (1) prey remains/food resources; (2) wolf beds; (3) wolf scats; (4) digging

the accuracy of the activity levels or try to determine which behaviors could be related with different activity levels, but this type of study could be very useful in the future for understanding wild wolves' behavior.

In this study, we found that wolves fed on carrion and bear-bait stations, and killed two deer, a beaver, a fisher, and a grouse. As it has been reported, wolves can kill large prey and small prey and eat carrion and garbage, taking advantage of a variety of resources (Peterson and Ciucci 2003). Four of the five preys we found were small and medium. Other studies reported that wolves preyed on grouse and beavers (Zimmermann et al. 2007; Sand et al. 2008), similar to our results. We know of no other reports of wolves killing fishers. Although only minor scavenging was reported in the Canadian Rocky Mountains (Webb et al. 2008), our wolves spent considerable time scavenging. Thus, attempts to estimate kill rates in such a multiprey/food resources system become difficult.

Other problems in determining summer kill rates include the fact that wolves of the same pack do not travel together

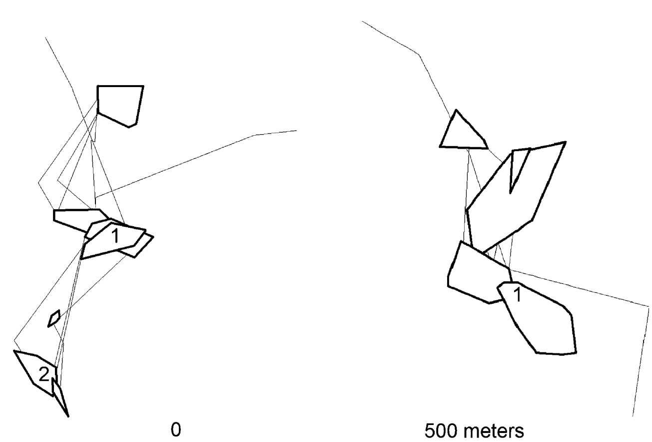

Fig. 3 MCPs of location clusters and movements of GPS-collared male wolf (left) and female wolf in the Superior National Forest during spring–summer 2007 within 500 m of road kill. The figures represent only the first event, not the consecutive visits to the area. Findings: (1) prey remains/food resources; (2) wolf beds

Table 4 Characteristics of visits to food items by both collared wolves in the Superior National Forest during spring–summer 2007 assuming a variable 500-m buffer

Event	Wolf		Week of Study													Total
			1	2	3	4	5	6	7	8	9	10	11	12	13	
Road kill[a]	Female	*N* days	1						3	4	1	5	2	3		19
		N locations	1						260	52	1	44	3	56		417
	Male	*N* days					1	3	4	7	4			1		20
		N locations					2	117	289	737	318			1		1,464
Rotting meat[b]	Female	*N* days						1	2			2				5
		N locations						3	2			70				75
	Male	*N* days	2	1	1	1	1		1			6	3	1		17
		N locations	121	24	1	7	3		23			546	8	2		735

Highlighted weeks reflect the event dates.

[a] Based on both a 100- and 500-m buffer, the female spent 44 h near the road kill, and the male spent 27 h.

[b] Based on a 100-m buffer, the female spent 17 h, and the male 109 h near the meat; based on a 500-m buffer, the female spent 24 h and the male 161 h.

all the time during summer. Our wolves belonged to the same pack, and their home ranges overlapped 89% (unpublished data), but they travelled separately almost throughout the study, similar to other packs near our study area (Demma and Mech 2008; Demma et al. 2007). Demma and Mech (2008) suggested that this pattern could be due to the fact that while they seek food independently, pack mates visit each other's kill remains. In our study, the most time the wolves were together was at the road kill and rotting meat. One wolf arrived at the area first, and the other joined it. Travelling separately but remaining loosely associated could increase the chance of finding as many different food sources as possible for all the pack mates. On the other hand, our results suggest that predation on small prey tends to be related to wolves travelling alone. Hence, pack member independence can be a problem for estimating kill rates when few animals per pack are radiocollared (Webb et al. 2008). Moreover, as we found at the road kill and rotting meat, for the same event, different wolves can behave differently, making it more complex to build predictive models of predation patterns in such circumstances.

Despite our small sample, we found a strong correlation between the time a wolf is near a kill and the prey's weight, similar to Webb et al. (2008). However, Zimmermann et al. (2007) reported great variability in handling times, due to pack member independence and stochastic factors such as human disturbance and others. Spending more time around large prey should be normal especially for wolves travelling alone and with no disturbance.

A final problem to consider is the fact that during summer, most wolf packs have pups. We did not find evidence of pups in our Perch Lake pack during the study. The pups' feeding needs should affect handling time at kill sites, as wolves commonly carry food to the pups (Packard 2003).

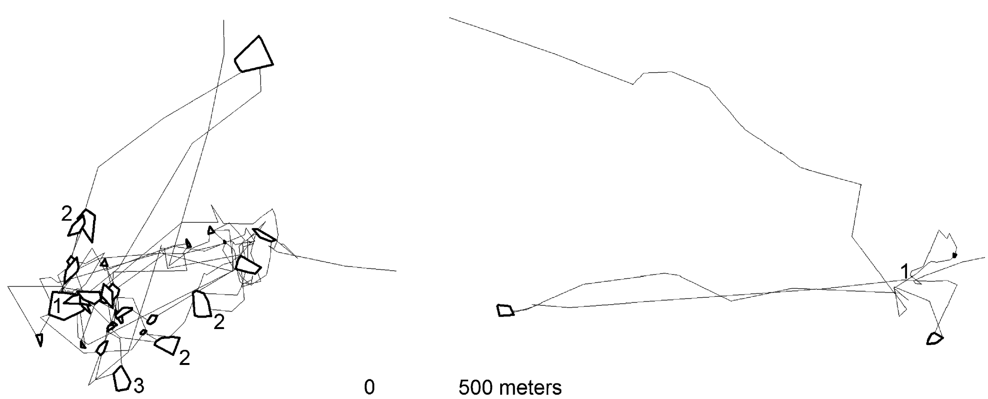

Fig. 4 GPS-collared male wolf (left) and female wolf rotting meat feeding events in the Superior National Forest during spring–summer 2007. The figures represent all the MCPs of GPS location clusters and movements since the wolf arrived in the 500-m buffered area until the end of the event. The male arrived 31 July and left 6 August. The female arrived 4 August and left 6 August. In this case, we could infer that the female spent less time because there was less/no remains left at the site. Findings: (1) prey remains/food resources; (2) wolf beds; (3) wolf scats

Thus, during summer, the movement patterns depending on the prey species, presence of pups, and the pack role of the radioed wolf could vary considerably.

We conclude that it is difficult to get an accurate account of the number and type of small prey via GPS collars even with the high location acquisition rates we used. Despite obtaining positions at 10-min intervals, we found the same problems as others studying wolf predation, especially on small prey such as deer fawns. Although Demma et al. (2007) located four deer fawn kill sites checking clusters of one GPS-collared wolf for a 37-day-period, they reported the need for improving the detection of kills as well. There are multiple factors (prey size, prey availability, presence of other food sources, presence of pups, pack role, stochastic factors, human disturbances, whether the study animal is alone or with other pack mates, among others) that increase the variability of predation patterns, making it difficult to estimate accurate kill rates and modeling predation patterns for wolves.

However, our results could be useful for future studies of wolf predation on deer fawns. Improving the data-downloading process, increasing the chance of finding wolf signs and prey remains, and rejecting resting clusters could be helpful to increase the number of small-prey kill sites found. This type of study still provides valuable information for the understanding of wolf predation, although extensive field work must still accompany it.

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