

Testing Global Positioning System Telemetry to Study Wolf Predation on Deer Fawns

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ABSTRACT We conducted a pilot study to test the usefulness of Global Positioning System (GPS) collars for investigating wolf (*Canis lupus*) predation on white-tailed deer (*Odocoileus virginianus*) fawns. Using GPS collars with short location-attempt intervals on 5 wolves and 5 deer during summers 2002–2004 in northeastern Minnesota, USA, demonstrated how this approach could provide new insights into wolf hunting behavior of fawns. For example, a wolf traveled ≥ 1.5 –3.0 km and spent 20–22 hours in the immediate vicinity of known fawn kill sites and ≥ 0.7 km and 8.3 hours at scavenging sites. Wolf travel paths indicated that wolves intentionally traveled into deer summer ranges, traveled ≥ 0.7 –4.2 km in such ranges, and spent < 1 –22 hours per visit. Each pair of 3 GPS-collared wolf pack members were located together for $\leq 6\%$ of potential locations. From GPS collar data, we estimated that each deer summer range in a pack territory containing 5 wolves ≥ 1 year old and hunting individually would be visited by a wolf on average every 3–5 days. This approach holds great potential for investigating summer hunting behavior of wolves in areas where direct observation is impractical or impossible. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2767–2775; 2007)

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Most researchers who have studied wolf (*Canis lupus*) interactions with white-tailed deer (*Odocoileus virginianus*) in forested areas have done so in winter because such interactions are usually impossible to observe in summer. The sparse information that is available about wolf–deer interactions in summer indicates that wolves concentrate on fawns and take relatively few adult deer. However, little is known about the behavior of wolves hunting and killing fawns during summer.

Global Positioning System (GPS) radiocollars hold the potential for studying many wildlife behavior questions that researchers had been heretofore unable to explore. We used GPS collars on wolves and deer in a pilot study to 1) test the usefulness of GPS collars for investigating the movements of wolves hunting deer during summer, 2) obtain insights into the nature of summer wolf–deer interactions, and 3) gain at least a first approximation of the frequency with which individual deer are tested by wolves during summer.

STUDY AREA

We conducted our study during the summers of 2002–2004 in a 2,100-km² area in the Superior National Forest of northeastern Minnesota (48°N, 92°W). Nelson and Mech (1981) provide a detailed description of the study area. Wolves occurred throughout the study area at densities of

28–36/1,000 km² (L. D. Mech, United States Geological Survey, unpublished data). The area was near the northern limit of deer range, and density was an estimated 12–15 deer/10 km² (M. H. Dexter, Minnesota Department of Natural Resources, unpublished report). The major prey of wolves in the area were deer, primarily fawns during summer.

METHODS

During May–July 2002–2004, we live-trapped and anesthetized wolves with 250 mg of Telazol® (Fort Dodge Laboratories, Inc., Fort Dodge, IA) and 0.375 mg of xylazine administered via a pole syringe and reversed the xylazine with 0.15 mg/kg yohimbine. We sexed, weighed, and ear-tagged wolves, and we aged them by tooth wear (Gipson et al. 2000). We took testes and teat measurements to assess reproductive status and we administered antibiotics.

We fitted the wolves with GPS radiocollars programmed to obtain locations at regular intervals (Televilt, Lindesberg, Sweden, and Advanced Telemetry Systems, Inc. [ATS], Isanti, MN). During 2002, we programmed GPS collars to obtain locations at 60-minute intervals during 1000–1800 hours and 10-minute intervals during 1800–1000 hours. During 2003–2004, we programmed the collars to acquire locations at either 10-minute or 15-minute intervals, 24 hours per day. We expected locations to be within 5 m and 30 m of the true location 50% and 95% of the time, respectively (Moen et al. 1997, Dussault et al. 2001).

Televilt collars transmitted telemetry data at preprogrammed intervals, and all GPS collars stored the data for downloading upon collar recovery. The GPS collars

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Table 1. Background data on Global Positioning System (GPS)-collared wolves and deer monitored for the study in the Superior National Forest of northeastern Minnesota, USA, during 2002–2004.

Animal no. ^a	Species	Sex	Age (yr) ^b	GPS study period	Study duration (d)	No. GPS locations	\bar{x} location interval (min)	Min. convex polygon area (ha)
845 ^c	wolf	F	3	17 Jun–24 Jul 2002	38	2,664	15 ^d	
883	wolf	F	1	3 Jun–5 Jul 2003	33	1,669	28	
895	wolf	F	1	11 Jun–3 Jul 2003 ^e	23	1,009	29	
901	wolf	M	2	16 Jun–17 Jul 2003	32	2,281	20	
881 ^f	wolf	M	8	21 Jun–7 Aug 2004	48	2,880	24	
8084	deer	F	2	16 May–15 Aug 2003	92	803		132
8094	deer	F	3	15 May–15 Aug 2003	93	2,808		203
8104	deer	F	3	15 May–15 Aug 2003	93	1,359		87
8110	deer	F	2	15 May–15 Aug 2003	93	739		139
8158	deer	F	8	15 May–5 Aug 2004	83	1,403		133

^a All wolf GPS collars were Televilt (Lindesberg, Sweden) with location attempt rate of 1/10 min unless otherwise noted; all deer GPS collars were Advanced Telemetry Systems, Inc. (Isanti, MN) with location attempt rate of 1/30 min.

^b For deer, on 1 Jun of yr studied.

^c Captured for kill and scavenging site study, we used all other wolves for studying use of deer ranges. Although collar life was 38 d, we attempted to gather kill-site data on 25 d and succeeded on 17 d.

^d Includes only location intervals during 1800–1000 hr when GPS location attempt rate was 1/10 min.

^e Dispersed from natal territory after 16 Jun 2003.

^f Advanced Telemetry Systems GPS collar with GPS location attempt rate of 1/15 min.

contained either drop-off mechanisms that we programmed to release after 110 days or 130 days post start-up (Televilt) or that we could release at will (ATS) by a remotely operated transceiver.

To locate wolf kills, we remotely downloaded data transmitted by GPS collars daily and plotted the locations on digital topographic maps of the study area (TOPO!, National Geographic Society, Hanover, PA). We identified potential kill sites by noting concentrations of GPS locations that were not known wolf home sites. We searched coordinates of potential kill sites and surrounding areas and recorded evidence of predation or scavenging (e.g., blood, animal remains, wolf scats).

We classified as kill sites or scavenging sites concentrations of locations where we found evidence of predation or scavenging during ground searches. Kill sites contained evidence of a kill having been made recently, such as fresh blood and prey remains, disturbed vegetation and soil, and fresh wolf scats. Scavenging sites, which were not necessarily wolf kills, included only sites associated with old ungulate carcass remains, such as desiccated hide and bones. One scavenging site contained remains of a deer carcass that humans had placed.

We captured deer during March 2003 and 2004 in collapsible Clover traps, anesthetized the animals with 1.1 mg/kg xylazine hydrochloride and 9.0 mg/kg ketamine hydrochloride (Kreeger 1996), and reversed the xylazine with 0.22 mg/kg yohimbine hydrochloride (Mech et al. 1985). We weighed, measured, and ear-tagged deer, and we extracted an I4 incisor for aging (Nelson 2001). We then attached a releasable GPS collar (ATS) programmed to obtain one location per week until 15 May and one location every 30 minutes thereafter. Positional accuracy was the same as with the wolf GPS collars. We remotely released the collars from the deer after the GPS battery level dropped below the threshold required to obtain fixes.

Our primary objective for the wolf GPS data was to

characterize wolf use of known kill sites and deer summer ranges. To minimize bias from capture, we excluded GPS locations during the first 5 days postcapture. We plotted GPS data in ArcMap and used Hawth's Analysis Tools (www.spatialecology.com) to calculate deer minimum convex polygons (MCPs; Mohr 1947) and wolf movement characteristics.

The intervals between successive locations in all wolf GPS datasets varied. We included all data associated with wolf use of known kill and scavenging sites and deer summer ranges to maximize sample sizes. Our analysis included data comprised of GPS-location-attempt intervals of both 10 minutes and 15 minutes. Because the actual intervals were similar at the different attempt rates, we could directly compare wolf movement characteristics among all datasets.

We used deer GPS data to determine locations and wolf use of deer summer ranges. We made no attempt to characterize individual wolf–deer interactions or wolf use of individual deer core-use areas because the time of deer and wolf GPS locations usually did not coincide, and some GPS location intervals could have included undetected interactions between wolves and deer or wolf use of deer core-use areas. For deer summer ranges we used MCPs of all GPS locations from 15 May to 15 August. The MCPs generally contained dense point clusters with a few outliers that we arbitrarily excluded if they were >200 m away. We used this common method because it is suitable to demonstrate the potential of GPS telemetry for studying wolf hunting behavior and because our deer MCPs included 739–2,808 locations (Table 1) without large voids, thus minimizing 2 of the main MCP biases (White and Garrott 1990).

All GPS-collared deer were adult females, and we assumed those ≥ 3 years old were accompanied by 1–3 fawns (Petra and Burcalow 1965). Daily movements of all GPS deer, except possibly for a 2-year-old, during late May–early June were characteristic of parturition (Nelson and Mech 1981, Huegel et al. 1985). Where data showed

that wolves were located within deer ranges, we assumed the wolves were hunting fawns rather than adult females because in our study area adult deer survival during summer was 0.99, whereas fawn survival was 0.66 (Nelson and Mech 1986).

We plotted wolf GPS locations at sites where we found kills and carcass remains during ground searches. We added lines connecting successive GPS points to approximate wolf travel paths, and we overlaid wolf locations and lines on the known kill and scavenging sites. We considered wolf locations to be associated with kill or scavenging site use if they occurred within 24 hours previous to site discovery by ground crews and if they were located within 200 m of the prey remains. We also included wolf locations 200–500 m from the prey remains if they indicated localized use occurring after arrival and before departure from the area (as characterized by directional travel). We calculated characteristics of wolf use of known kill and scavenging sites, including time of day, time spent at the site, and minimum distance traveled at the site.

We considered wolf locations and travel paths that overlapped deer MCPs as representing wolf use of a deer summer range. We estimated wolf use of deer summer range by using all wolf locations inside deer MCPs, and only included wolf locations outside deer MCPs if 1) they immediately preceded or followed a location that was inside the MCP, 2) most of the distance between the locations straddling the MCP boundary was within the MCP, and 3) the interval between the straddling locations was ≤ 10 minutes. We calculated the following characteristics of wolf use of deer summer ranges: time of day, time spent in the range, minimum distance traveled in the range (the total of all consecutive distances among all points used), and minimum travel rate.

We calculated the frequency of wolf visits to each GPS deer summer range by dividing the number of GPS wolf visits by the number of GPS wolf days. We calculated GPS wolf days for each deer summer range by summing the study tenures of all GPS wolves whose summer territories overlapped the deer ranges. We considered wolf locations within deer summer ranges as visits, and we counted each visit as separate if wolf locations and paths indicated that the wolf left the deer MCP and had traveled >500 m away before revisiting or if it returned ≥ 12 hours later. We determined wolf-visit frequency in relation to individual summer deer MCP range boundaries as well as to boundaries created with the addition of 100-m and 200-m buffers to each MCP. We calculated wolf-visit frequency in relation to the buffered MCPs to provide a range of estimates to help offset the possibility that our deer MCPs were incompletely described (White and Garrott 1990).

We examined how frequently members of the same wolf pack were located near each other by plotting GPS locations of 3 members of the Pike Lake Pack whose GPS-collar tenures coincided for <1 –19 days. Time of GPS fixes usually did not coincide exactly between pack members, so

we assumed that they could be together when any 2 wolves were located within 1 hour and 100 m of each other.

RESULTS

We captured a nonbreeding female wolf (no. 845) from the Farm Lake Pack during summer 2002 for studying kill-site use. The wolf had a GPS study period of 38 days, with 2,664 GPS locations. Mean GPS location interval was 15 minutes (SD = 38) during 1800–1000 hours when the GPS collar was programmed to attempt fixes at a rate of one fix per 10 minutes (Table 1). We captured and instrumented 4 wolves from the Pike Lake Pack during early summer 2003 and 2004 for studying wolf use of deer ranges. The study animals consisted of 2 females and 2 males 1–8 years old. Mean GPS study period was 34 days (SD = 10, $n = 4$) and number of locations averaged 1,960 (SD = 804, $n = 4$). The actual mean location intervals from collars programmed for 10-minute fix attempts and the one programmed for 15-minute fix attempts were similar (25 min, $n = 4,956$ vs. 24 min, $n = 2,879$). Mean proportion of 3-dimensional (3D) fixes for the Televilt collars was 31% (range = 27–35%) versus 80% for the ATS collar. Mean horizontal dilution of precision of fixes was 3.6 (SE = 0.02) for the Televilt collars and 3.9 (SE = 0.08) for the ATS collar.

We captured and instrumented with GPS collars 4 deer in March 2003 and one deer in March 2004, each of which migrated to summer ranges that overlapped spatially and temporally with GPS wolf territories (Table 1). The GPS tenure of deer averaged 91 days (SD = 4) and mean number of GPS locations per deer was 1,422 (SD = 833). Mean area of summer MCPs, which included a nearby GPS-collared deer that did not overlap with any GPS-collared wolves, averaged 137 ha (SD = 37).

During 17 June to 24 July 2002 we attempted to remotely download wolf GPS collar data on 25 days and were successful on 17 days. We identified and searched 47 GPS location clusters that indicated possible locations of kill sites and were successful in locating 4 kill and 2 scavenging sites (Table 2). The search effort for each cluster ranged from approximately 0.25–1.5 hours and depended on denseness of vegetation, apparentness of the carcass, number of remaining clusters to examine, and remaining daylight. By late July we began to discover wolf rendezvous sites at some clusters so we ceased ground searches. Wolf 845's movements approaching and leaving kill and scavenging sites were generally directional with uniform distances between GPS locations. Movements representing kill and scavenging site use were characterized by short distances moved and many directional changes between successive locations. Wolf GPS location clusters occurred ≤ 20 –500 m from each location where we found evidence of predation (Fig. 1).

At kill site 1, we were able to determine from the GPS data that wolf 845 was present at the onset of the GPS study period. Thus the use characteristics of this site are minimums. At kill site 4, we found a mostly intact fawn carcass, and we detected the movement of a large animal upon arrival. The GPS locations from wolf 845 indicated

Table 2. Characteristics of deer fawn kill sites and scavenging sites used by a Global Positioning System (GPS)-collared wolf in the Superior National Forest of northeastern Minnesota, USA, during 17 June–1 July 2002.

Site no. ^a	Investigation date	Remains found	Site area (ha)	Time present (hr)	Min. distance traveled (m)
1 ^b	17 Jun 2002	jaw, teeth	1.0	9.7	985
2	19 Jun 2002	flesh, hair	13.3	21.8	2,998
3 ^c	20 Jun 2002	bones, hair	0.8	13.0	1,057
4 ^d	20 Jun 2002	carcass	4.1	11.5	1,306
5 ^e	24 Jun 2002	ankle, hoof	2.8	20.1	1,503
6 ^{c,f}	1 Jul 2002	bones, hair	0.3	3.7	366
\bar{x} ^g			8.1; 0.6	21.0; 8.3	2,251; 712

^a Sites are kill sites unless otherwise noted.

^b Wolf was at site at onset of GPS study period, so time present and distance traveled are min.

^c Scavenging site of ad deer or moose calf.

^d Wolf was at kill site when we arrived and was probably scared away from the carcass. Utilization characteristics are prior to disturbance so they are minimums.

^e Could be minimums; wolf was within 250 m of site while researchers were present.

^f Deer carcass placed by humans.

^g First value includes only kill no. 2 and no. 5. Second value includes only scavenging sites.

that 30 minutes before we arrived at the kill site she was close to where we discovered the carcass and she remained nearby while we were present. Because we likely disturbed wolf 845 at this kill, the only data that were usable were from before the disturbance. Thus the use characteristics of this site are minimums and probably represent primarily hunting and killing behavior because we apparently disturbed the wolf in the early stages of feeding.

We were able to calculate that the areas used at the 2 kills comprising complete use periods were 2.8 ha and 13.3 ha and averaged 8.1 ha (Table 2), and the mean minimum distance the wolf traveled at the sites was 2,251 m. The average time spent at the 2 sites was 21.0 hours. Mean area used around all kill sites was 5.3 ha (SD = 5.5, $n = 4$), and minimum distance traveled at the sites averaged 1,698 m (SD = 893, $n = 4$). Wolf 845 spent an average of 15.8 hours (SD = 6.1, $n = 4$) at all kill sites and used the 2 scavenging sites less. The animal's GPS data showed that the mean area used at the scavenging sites was 0.6 ha, minimum distance traveled averaged 712 m (Table 2), and time spent at scavenging sites averaged 8.3 hours. Wolf 845 arrived and departed all kill and scavenging sites between 2400 hours and 1200 hours.

During summer 2003, 3 GPS-collared wolves used areas that overlapped 4 GPS-collared deer summer ranges, and in 2004, one GPS-collared wolf overlapped one GPS deer summer range. Thus we had sufficient GPS data to characterize wolf use for 8 visits to deer summer ranges and the overall mean wolf GPS location interval in GPS-collared deer summer ranges was 59.7 minutes (SE = 15.0, $n = 43$).

The wolf GPS collar data allowed us to determine that the wolves' locations and travel patterns varied in relation to known deer summer ranges. Several times wolf travel direction changed markedly ($\geq 90^\circ$) as the wolf approached or entered the deer summer range (Fig. 2). Mean minimum distance wolves traveled in radioed-deer summer ranges was 1,894 m (SE = 385, $n = 8$). Mean interval travel speeds of wolves during each deer summer-range visit ranged from 7.0

m/minute to 51.2 m/minute (Table 3). The overall mean interval speed of wolves in radioed-deer summer ranges was 14.0 m/minute (SE = 2.5, $n = 43$). The highest observed interval speed was 57.9 m/minute between successive GPS locations 10 minutes apart. Minimum time spent in GPS-collared deer summer ranges averaged 5.9 hours (SE = 3.0, $n = 8$). In 5 of 8 deer summer range visits, wolves spent ≤ 1.0 hour, whereas in the remaining 3 visits wolves were present for ≥ 5.5 hours (Table 3). Wolves arrived in GPS-collared deer summer ranges throughout the day and departed between 0800 hours and 2300 hours.

By combining data from both wolf and deer GPS collars we were able to tell that each GPS-collared wolf visited a GPS-collared deer summer range a mean of once per 17–24 days, depending on the buffer size around the deer MCP (Table 4). By extrapolating these data to a wolf pack size of 5 wolves ≥ 1 year old and hunting individually (see below), we could estimate that each deer summer range was visited by a wolf an average of once per 3–5 days.

We applied Geographic Information System (GIS) analysis to the wolf GPS data to determine information about wolf associates. The 3 wolves in the Pike Lake Pack whose GPS tenures overlapped were infrequently found together. The GPS locations of wolves 883 and 895, which were 1-year-old female littermates with an overlapping GPS period of 6 days, were within 100 m of each other during the same hour for 20 of 315 (6%) and 12 of 345 (3%) of possible locations respectively. Wolf 883 and a 2-year-old male pack mate, wolf 901, had overlapping GPS tenure of 19 days and may have been together for 20 of 909 (2%) and 29 of 1,451 (2%) locations respectively. The MCPs of wolves 883 and 901 overlapped 70% during the period when both were monitored. Wolf 895 and wolf 901 overlapped GPS periods for < 1 day and were never together.

DISCUSSION

Deducing wolf hunting behavior from GPS collar data comprising locations with sub-30-m accuracy and intervals

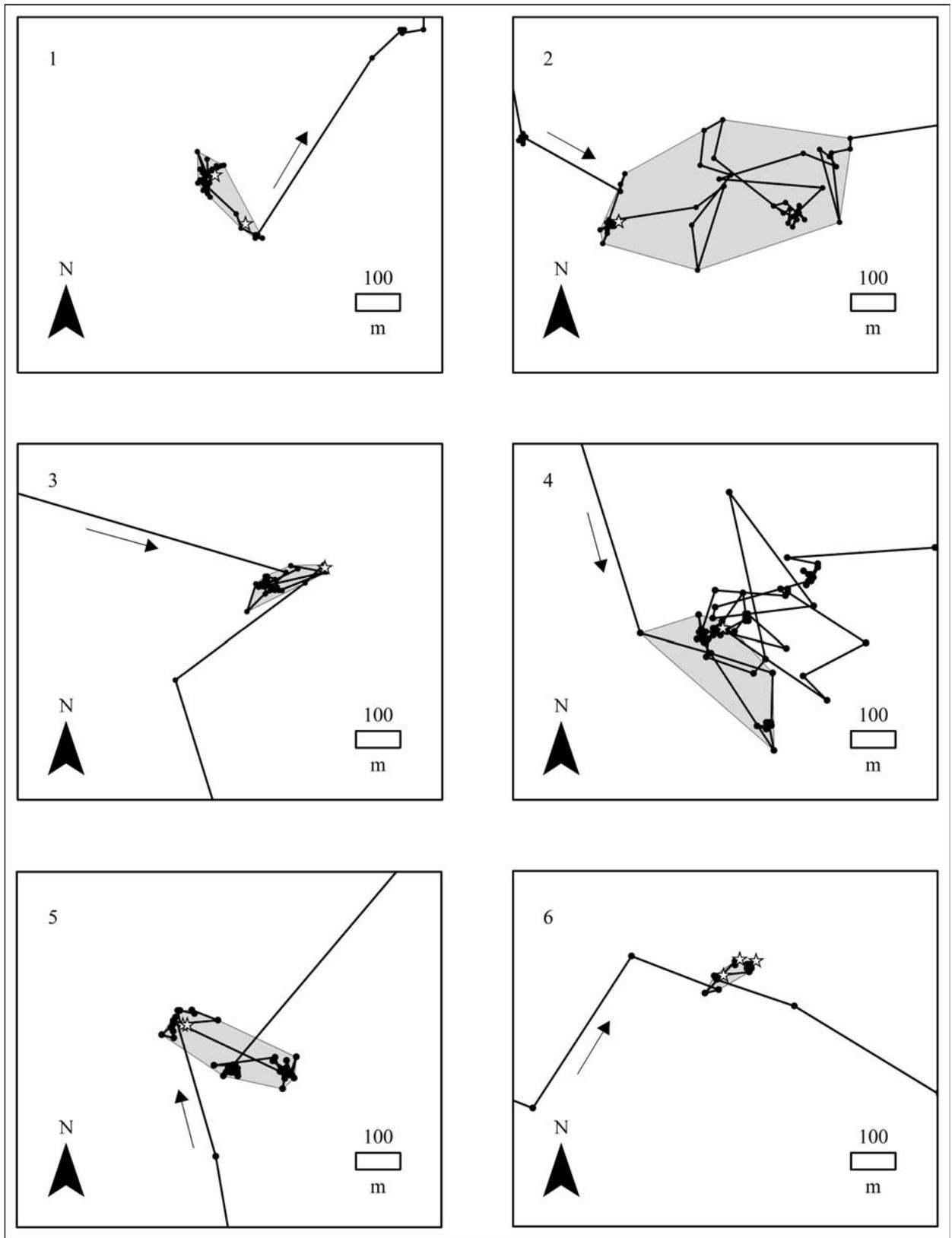


Figure 1. Wolf locations and direction of travel (arrows) in relation to locations of prey remains (stars) found at known kill and scavenging sites (shaded) utilized by a Global Positioning System-collared wolf in the Superior National Forest of northeastern Minnesota, USA, during 17 June–1 July 2002. The shaded area of site number 4 represents the wolf utilization area before researchers disturbed it.

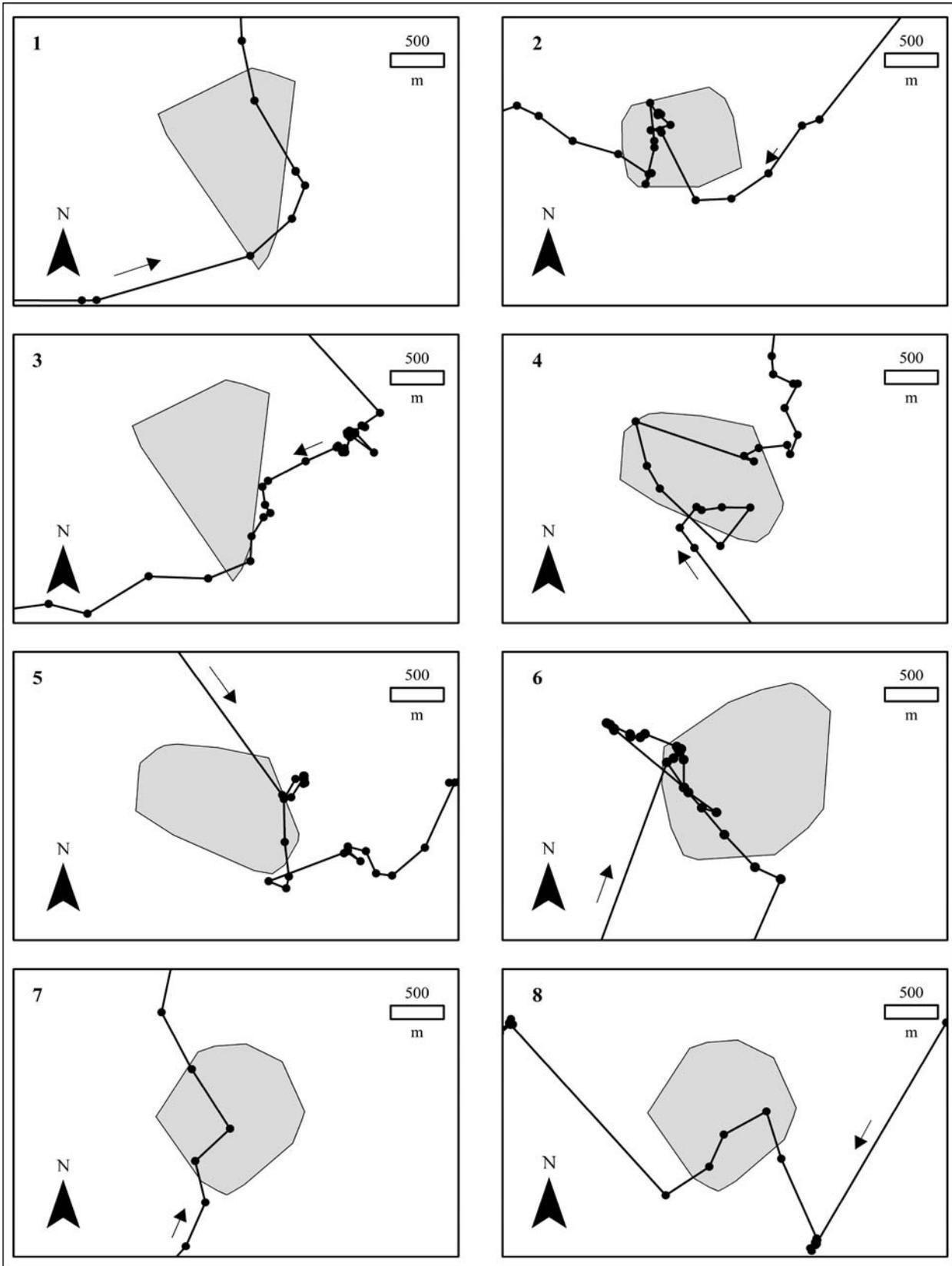


Figure 2. Wolf locations and direction of travel (arrows) in relation to Global Positioning System-collared deer summer range minimum convex polygons (shaded) in the Superior National Forest of northeastern Minnesota, USA, during 2003–2004. Overall mean wolf location interval within ranges was 60 minutes, but for any map, some location intervals were much longer.

Table 3. Characteristics of wolf use of Global Positioning System–collared deer summer ranges in the Superior National Forest of northeastern Minnesota, USA, during 2003–2004.

Visit no.	Wolf no.	Deer no.	Deer min. convex polygon area (ha)	Wolf visit period date(s)	Time present (hr)	Min. distance traveled (m)	\bar{x} interval travel rate (m/min)
3	883	8110	139	1 Jul 2003	0.3	669	33.8
5	901	8084	132	4 Jul 2003	0.5	744	29.2
1	883	8110	139	11 Jun 2003	0.7	1,892	51.2
7	881	8158	133	10 Jul 2004	0.8	1,534	32.9
8	881	8158	133	21 Jul 2004	1.0	1,761	29.3
4	901	8084	132	3 Jul 2003	5.5	4,153	18.1
2	883	8104	87	26 Jun 2003	16.7	2,049	7.0
6	901	8094	203	5–6 Jul 2003	21.8	2,346	10.0

as short as 10 minutes was a considerable improvement over previous studies using conventional collars where obtaining such accuracy and location rates was impractical. Our GPS data allowed us to estimate time spent, distance traveled, and movement rates for wolves at sites where they were hunting, killing, and consuming white-tailed deer fawns. In addition, we were able to obtain the first approximations of the rate at which deer are tested by wolves during summer.

Due to the nature of our wolf data (i.e., only GPS locations, no direct observations of wolves), we could not determine the actual hunting behavior of the wolf. We could infer that the kill-site use characteristics represented a variety, and probably the entire continuum, of activities related to hunting white-tailed deer fawns including searching, capturing and killing, consuming, caching, and resting or sleeping after the initial feeding. Wolf 845 used kill sites for long periods. In the immediate areas where we found evidence of recent fawn kills and had both arrival and departure information, wolf 845 spent 20–22 hours and traveled minimum distances of 1.5–3.0 km near the sites. At known scavenging sites, wolf 845 spent less time, covered less area, and moved shorter distances, as expected because there was less to eat (presumably only skeletal remains) and no time or effort was needed to find, pursue, or kill prey.

Wolf visits to deer summer ranges appeared purposeful in most cases based on changes in travel direction as the wolves approached or entered deer ranges. Time spent and distance traveled by wolves in deer summer ranges varied considerably and these characteristics probably comprised a range

of hunting behaviors, search effort, and success. In 5 of 8 such visits, wolves spent ≤ 1 hour there, whereas in the other 3 visits, wolves spent an estimated 6 hours, 17 hours, and 22 hours. Although we could not determine whether wolves actually killed fawns during any of the 8 documented visits to deer summer ranges, 2 of the visits, where wolves remained ≥ 17 hours, were most similar to those of known fawn kills. If the wolves were indeed hunting fawns of the GPS-collared deer, and actually made 2 kills, these data would constitute a hunting success rate of 25% of attempts.

Our GPS location data also provided information about wolf visitation of deer. All GPS-collared deer summer ranges within the Pike Lake Pack territory were visited by ≥ 1 GPS-collared pack member (Fig. 3). With an average pack size of about 5 adult-sized wolves in our study area, we estimated that some wolf would visit each deer summer range an average of about every 3–5 days, or 18–30 times during June–August. We could not determine the distribution of deer summer ranges throughout the entire Pike Lake Pack territory, but it is reasonable to assume that in areas where we had no GPS-collared deer, our wolves were likely visiting other deer summer ranges hunting fawns in the same manner as we observed in known deer ranges. The number of wolf visits to deer summer ranges increased with the addition of the buffers around deer ranges. Most of the wolf visits were within the original MCPs of GPS-collared deer and comprised 71% of total visits in the 200-m-buffered MCPs. Thus we believe that the addition of the 200-m buffers (and corresponding wolf visits) to the deer

Table 4. Estimated frequency of Global Positioning System (GPS)–collared deer summer range visits by GPS-collared wolves in the Superior National Forest of northeastern Minnesota, USA, during 2003–2004.^a

Deer no.	GPS wolf d	GPS wolf visits	Time/wolf visit (d)	Total visits if corresponding buffer area added			
				100 m		200 m	
				Total visits	Time/wolf visit (d)	Total visits	Time/wolf visit (d)
8084 ^b	64	2	32	3	21	3	21
8094 ^b	32	1	32	1	32	1	32
8104 ^b	32	2	16	2	16	2	16
8110 ^b	69	3	23	4	17	5	14
8158 ^c	47	2	24	2	24	3	16
Total	244	10		12		14	
\bar{x}			24		20		17

^a Time/wolf visit frequency rounded to nearest whole day.

^b Summer 2003.

^c Summer 2004.

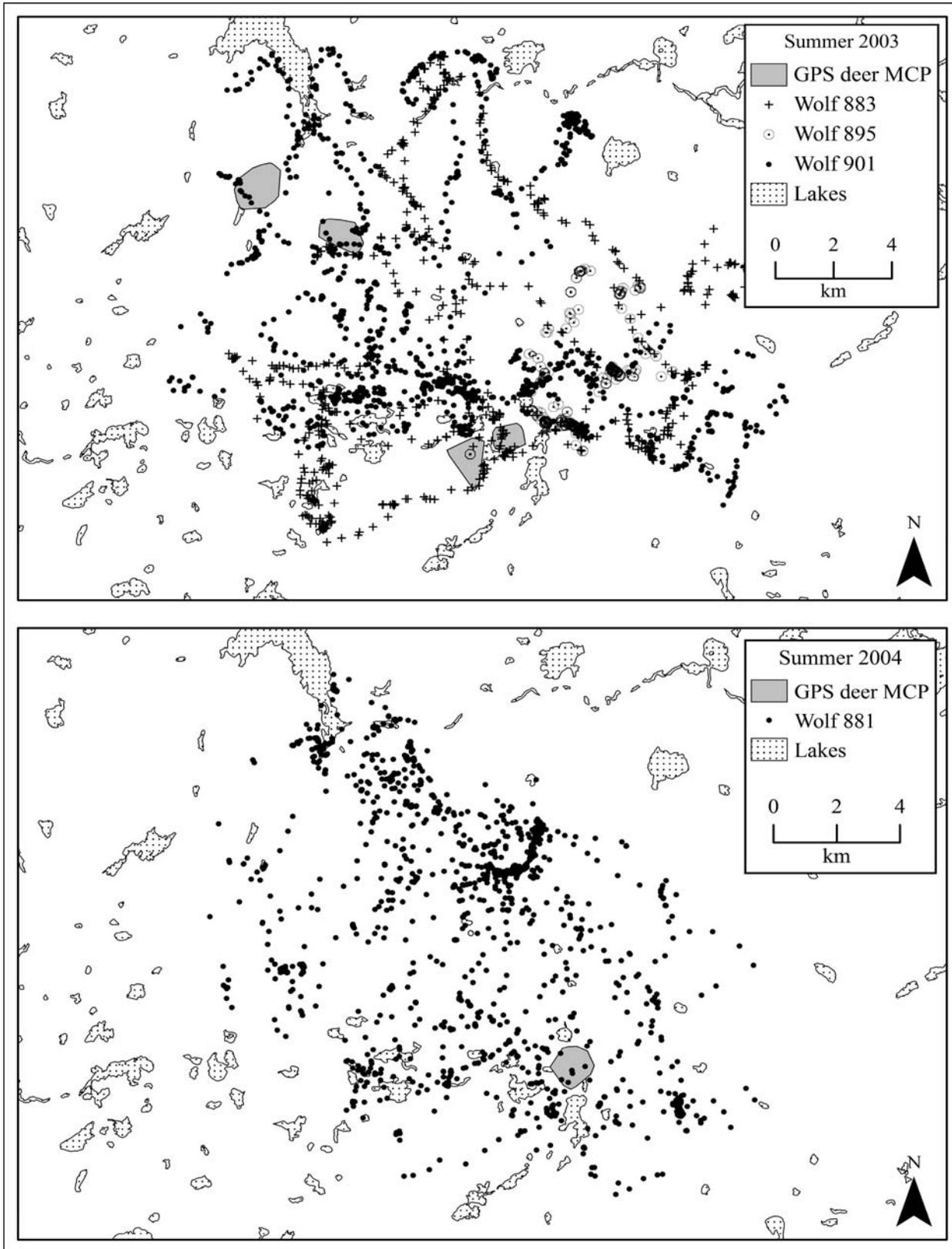


Figure 3. Global Positioning System (GPS)-collared wolf locations and GPS-collared deer summer range minimum convex polygons (MCPs; shaded) within the Pike Lake Pack territory in the Superior National Forest of northeastern Minnesota, USA, during 2003–2004.

ranges was a reasonable approach to estimate wolf visits to deer ranges that were likely underestimated by our methods.

Our GIS comparison of wolf GPS-collar data among concurrently monitored pack members yielded valuable information about wolf associations. We found our pack members together $\leq 6\%$ of locations during summer. This low degree of association is less than that found in other summer studies, which tend to report associations of about 15–40%. However, most of those studies were biased toward daytime data when wolves tend to congregate around dens and rendezvous sites (Van Ballenberghe et al. 1975, Peterson et al. 1984, Ballard et al. 1991, Mech and Merrill 1998). Similar to our results, Kolenosky and Johnston (1967), who tracked wolves day and night, found that 2 pack members tended to move independently during summer in Ontario, Canada. These findings emphasize the advantage that GPS collars have of providing data day and night.

A final example of the type of information that using GPS telemetry to study wolf use of known fawn kills and deer summer ranges in forested areas provided involved characteristics of general wolf foraging behavior. Our radiocollared wolf pack members tended to forage separately throughout their pack territory and frequently visit the known deer ranges. The wolves spent a substantial amount of time around fawn kill sites, even though the body mass of fawns would be about 7–13 kg at that time (Rawson et al. 1992, Kunkel and Mech 1994). This could be due in part to long searching and capturing time, as well as an attempt to completely consume the prey and defend it from scavengers.

MANAGEMENT IMPLICATIONS

By improving detection rate of kills and increasing the sample of both GPS-radiocollared pack members and adult female ungulates within a pack territory, future studies using GPS collars in forested areas during summer may be able to estimate wolf kill rates and handling times of ungulate neonates. Further, this approach can be used to gain insights into the movements and hunting behavior of multiple wolf pack members as well as their interactions with prey. To improve detection rates of kills, we recommend locating and omitting pack dens and rendezvous sites from the wolf GPS location clusters being considered as candidate kills and using the maximum number of personnel feasible for searching the potential kill sites.

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LITERATURE CITED

- Ballard, W. B., L. A. Ayres, C. L. Gardner, and J. W. Foster. 1991. Den site activity patterns of gray wolves, *Canis lupus*, in southcentral Alaska. *Canadian Field Naturalist* 105:497–504.
- Dussault, C., R. Courtois, J.-P. Ouellet, and J. Huot. 2001. Influence of satellite geometry and differential correction on GPS location accuracy. *Wildlife Society Bulletin* 29:171–179.
- Gipson, P. S., W. B. Ballard, R. M. Nowak, and L. D. Mech. 2000. Accuracy and precision of estimating age of gray wolves by tooth wear. *Journal of Wildlife Management*. 64:752–758.
- Huegel, C. N., R. B. Dahlgren, and H. L. Gladfelter. 1985. Use of doe behavior to capture white-tailed deer fawns. *Wildlife Society Bulletin* 13: 287–289.
- Kolenosky, G. B., and D. H. Johnston. 1967. Radio-tracking timber wolves in Ontario. *American Zoologist* 7:289–303.
- Kreeger, T. J. 1996. Handbook of wildlife chemical immobilization. International Veterinary Services, Laramie, Wyoming, USA.
- Kunkel, K. E., and L. D. Mech. 1994. Wolf and bear predation on white-tailed deer fawns. *Canadian Journal of Zoology* 72:1557–1565.
- Mech, L. D., G. D. DelGiudice, P. D. Karns, and U. S. Seal. 1985. Yohimbine as an antagonist to xylazine-ketamine immobilization of white-tailed deer. *Journal of Wildlife Diseases* 21:405–410.
- Mech, L. D., and S. B. Merrill. 1998. Daily departure and return patterns of wolves, *Canis lupus*, from a den at 80° latitude. *Canadian Field Naturalist* 112:515–517.
- Moen, R., J. Pastor, and Y. Cohen. 1997. Accuracy of GPS telemetry collar locations with differential correction. *Journal of Wildlife Management* 61:530–539.
- Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. *The American Midland Naturalist* 37:223–249.
- Nelson, M. E. 2001. Tooth extraction from live-captured white-tailed deer. *Wildlife Society Bulletin* 29:245–247.
- Nelson, M. E., and L. D. Mech. 1981. Deer social organization and wolf predation in northeastern Minnesota. *Wildlife Monographs* 77.
- Nelson, M. E., and L. D. Mech. 1986. Mortality of white-tailed deer in northeastern Minnesota. *Journal of Wildlife Management* 50:691–698.
- Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildlife Monographs* 88.
- Petraborg, W. H., and D. W. Burcalow. 1965. The white-tailed deer in Minnesota. Pages 11–48 in J. B. Moyle, editor. *Big game in Minnesota*. Minnesota Department of Conservation Technical Bulletin 9, St. Paul, USA.
- Rawson, R. E., G. D. DelGiudice, L. D. Mech, and H. E. Dziuk. 1992. Energy metabolism and hematology of white-tailed deer fawns. *Journal of Wildlife Diseases* 28:91–94.
- Van Ballenberghe, V., A. W. Erickson, and B. Byman. 1975. Ecology of the timber wolf in northeastern Minnesota. *Wildlife Monographs* 43.
- White, G. C., and R. A. Garrott. 1990. Analysis of wildlife radio-tracking data. Academic Press, San Diego, California, USA.

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