July 2018

The usefulness of GPS telemetry to study wolf circadian and social activity

Samuel B. Merrill

New England Environmental Finance Center, smerrill@usm.maine.edu

L. David Mech

USGS, Northern Prairie Wildlife Research Center

The usefulness of GPS telemetry to study wolf circadian and social activity

Samuel B. Merrill and L. David Mech

Abstract This study describes circadian and social movement patterns of 9 wolves and illustrates capabilities and limitations of Global Positioning System (GPS) telemetry for analysis of animal activity patterns. Wolves were studied at the Camp Ripley National Guard Training Site in Little Falls, Minnesota, and were captured via helicopter net-gunning. All study wolves showed nocturnal movement patterns regardless of time of year. One wolf's movement pattern switched to diurnal when he conducted an extraterritorial foray from his natal territory. All data sets with GPS intervals ≤ 1 hour ($n=4$) showed crepuscular movement peaks. We identified patterns of den visitation and attendance, estimated minimum distances traveled and minimum rates of movement, and observed that GPS location intervals may affect perceived rates of wolf travel. Global Positioning System telemetry was useful in determining when pack members were traveling together or apart and how long a breeding female wolf spent near her pups (e.g., 10-month-old pups were left unattended by their mother for as long as 17 days).

Key words activity, *Canis lupus*, circadian, Global Positioning System, GPS, movements, telemetry, wolf

Global Positioning System (GPS) telemetry has great potential for providing information about wildlife (Rodgers and Anson 1994, Moen et al. 1996, Merrill et al. 1998, Mech and Barber 2002, Merrill 2002). Although wolves are among the species most studied, many areas of wolf biology include substantial gaps (Mech 1995). Circadian movement is one of these areas, and no previous study has examined such patterns in dispersing wolves or in wolves traveling on extraterritorial forays. We tested the utility of GPS telemetry for studying circadian and social movement patterns in gray wolves (Merrill 2002). Monitoring of dens and rendezvous sites during the pup-rearing season has provided information on attendance patterns (Carbyn 1975, Harrington and Mech 1982, Mech and Merrill 1998) and activities (Ballard et al. 1991, Theuerkauf et al. 2003) near these places, but little is known about circadian movement patterns away from them. Several studies have examined circadian wolf move-

ment patterns using conventional tracking techniques (Kolenosky and Johnston 1967, Peterson et al. 1984, Mech 1992, Vilà et al. 1995, Ciucci et al. 1997) in combination with activity sensors (Kunkel et al. 1991, Kreeger et al. 1996, Theuerkauf et al. 2003), but availability of GPS radiocollars provides an opportunity to fill in the gaps in greater detail than previously possible.

We used short-interval GPS telemetry to study circadian movement patterns in 9 wolves. Wolves studied included a 2-year-old male before and during an extraterritorial foray and a breeding female before, during, and after denning to identify how their circadian movement patterns changed with the onset of different stages in their life history.

Study area

We conducted this study at Camp Ripley, a 21,400-ha National Guard Training Site in Little

Address for Samuel B. Merrill: Environmental Office, Camp Ripley Headquarters, 15000 Highway 115, Little Falls, MN 56345-4173, USA; present address: New England Environmental Finance Center, Edmund S. Muskie School of Public Service, University of Southern Maine, 49 Exeter Street, #205, Portland, ME 04104, USA; e-mail: smerrill@usm.maine.edu. Address for L. David Mech: United States Geological Survey, Northern Prairie Wildlife Research Center, 8711 37th St. SE, Jamestown, ND, USA; mailing address: The Raptor Center, 1920 Fitch Avenue, University of Minnesota, St. Paul, MN 55108, USA.

Falls, Minnesota (46 N, 95 W) at the southern edge of wolf range within the state. The terrain was generally flat, and the major cover was northern hardwood forest (primarily oak [*Quercus* spp.], aspen [*Populus* spp.], and birch [*Betula papyrifera*], mixed with some conifers) interspersed with large open areas (grasslands, wetlands, and military firing ranges). Camp Ripley, located in the prairie-forest transition zone of central Minnesota, was surrounded on the east and south by agricultural lands and on the north and west by forest interspersed with agricultural development. Densities of white-tailed deer (*Odocoileus virginianus*) were about 10/km^2 (G. DelGiudice, Minnesota Department of Natural Resources, unpublished data), and deer were the main prey of the wolves, which have occupied the area since about 1994 (Merrill 1996).

Methods

We captured wolves via helicopter net-gunning (Barrett et al. 1982) from February 1997– September 1998. We weighed, measured, and ear-tagged wolves, fit them with a GPS radiocollar (Merrill et al. 1998), and released them. We aged wolves by tooth wear (Gipson et al. 2000) or by knowledge of each animal's history. We programmed each GPS collar to obtain a location at regular intervals from 15 minutes to 3 hours (Table 1). If no location was recorded, the collar tried again in 15 and 30 minutes. If all 3 tries failed, we made no further attempts until the next programmed interval.

After the GPS collars completed collecting all the data for which they had power, we triggered their release from the animals (Mech and Gese 1992) and downloaded the stored data into a computer (Merrill et al. 1998). In 2 of 13 cases, the release failed, so we retrieved the collars by live-trapping or helicopter capture of the wolves. We plotted data in Arc-View© (ESRI, Inc., Redlands, Calif.) and calculated distances between points and Minimum-Convex-Polygon home-range estimates using the Animal Movement Extension (Hooge and Eichenlaub 2000). We

measured circadian movement as mean distance traveled per GPS location interval. Distances and rates of travel are minimum estimates because they are straight-line measures of routes of unknown lengths between points. Thus, for example, 2 equal distances could represent different actual distances and rates of travel.

Although summation of distances between GPS-obtained locations would appear to accurately represent each wolf's movement pattern, this is not necessarily the case. Each time the GPS attempt and both retries were missed, the distances between locations before and after the missed interval(s) represents the minimum distance traveled in at least 2 intervals. If not removed from the data set, distances spanning missed intervals could substantially alter the description of a movement pattern. For example, with one wolf, the location attempt and both retries failed in 107 of 812 intervals (13%) before an extraterritorial foray and in 88 of 308 intervals (29%) during the foray. The pattern described below for that wolf was not apparent before we deleted lines spanning missed intervals from the analysis. We evaluated all our wolf movements and rates of travel using only distances associated with programmed intervals (±0.25 or 0.50 hour, including successful retry attempts).

Results

We obtained location data from 9 wolves of both genders and various ages and reproductive status during periods of 2-24 weeks, primarily during later winter, spring, and early summer (Table 1).

Table 1. Details about 10 wolves studied by Global Positioning System telemetry near Little Falls, Minnesota, from 20 February 1997–14 September 1998.

No.	Gender	Age	Dates of GPS collar activity	Location attempt interval	No. GPS locations	No. location pairs spanning one location attempt interval
850	F	2+ yr	2/20/97–3/9/97	1 hr	327	319
			recalculated:	4 hr	79	77
850	F	2+ yr	4/10/97–7/9/97	4 hr	254	120
840	M	Yearling	2/20/97–3/14/97	30 min	647	646
860	F	10 mo	2/20/97–3/10/97	1 hr	265	252
820	M	10 mo	2/21/97–3/13/97	15 min	1,477	1,358
133	M	2+ yr	1/31/98–7/9/98	3 hr	594	385
229	F	Yearling	1/31/98–6/18/98	3 hr	569	351
399	M	Yearling	2/3/98–7/27/98	3 hr	1,120	925
627	M	2+ yr	2/3/98–6/17/98	3 hr	715	552
134	F	2+ yr	9/14/98–11/15/98	3 hr	385	217

Except for one wolf traveling on an extraterritorial foray, all circadian movement patterns were nocturnal (Figure 1). Generally, wolves were more active from about 2000 hours to about 0800 hours, but there was no consistent sharp break in activity during night and day. Rather, activity tended to increase at 2000 hours and taper at 0800 hours (Figure 1). All 4 wolves with GPS collars programmed for intervals ≤1 hour showed standardized hourly movement peaks at dawn, dusk, and in the middle of the night. Mean minimum rates of travel per GPS interval varied from 269 m per hour for wolf 860 to 716 m per hour for wolf 820 after denning (Table 2). For the 2 breeding male wolves, straight-line distances per 3 hour were apparent between winter and summer for several 3-hour periods (Figure 1e and g).

Male wolf 399

Wolf 399 conducted an extraterritorial foray 185 km (Merrill and Mech 2000) from his natal territory on 31 May 1998 and returned on 27 July 1998 (Figure 2; if he had not returned to his natal territory, it would have been a dispersal). Distances spanning 3 hours indicated that he traveled an average of 1,179 m per 3 hours prior to the foray and 1,055 m per 3 hours during the foray. The fastest rate of travel recorded before the foray was 10,439 m per 3 hours, and the fastest rate during the foray was 10,642 m per 3 hours. The wolf shifted his circadian movement pattern from nocturnal to diurnal during the foray (Figure 3a).

In the month before the foray, wolf 399 made at least 13 trips to and from the den site (Figure 4), at a rate of roughly one trip per 2 days. The longest duration of trips from the den during this period was 2.5 days, except for one absence that apparently lasted from 15-23 May 1998. The last recorded trip to the den area was on 24 May, one week prior to the foray.

Breeding female wolf 850 before and after whelping

We outfitted this wolf with a GPS collar twice (Table 1). Data from the first collar described the wolf's movements for 3 weeks before denning (327 locations, once per hour from 20 February-9 March 1997; Figure 5), and data from the second collar (254 locations once per 4 hour from 10 April-9 July 1997; Figure 6) recorded movement after denning (based on time of year and presence of only 2 of 76 GPS locations >1.5 km from the den during 11-30 April 1997). Prior to wolf 850's whelping, GPS data
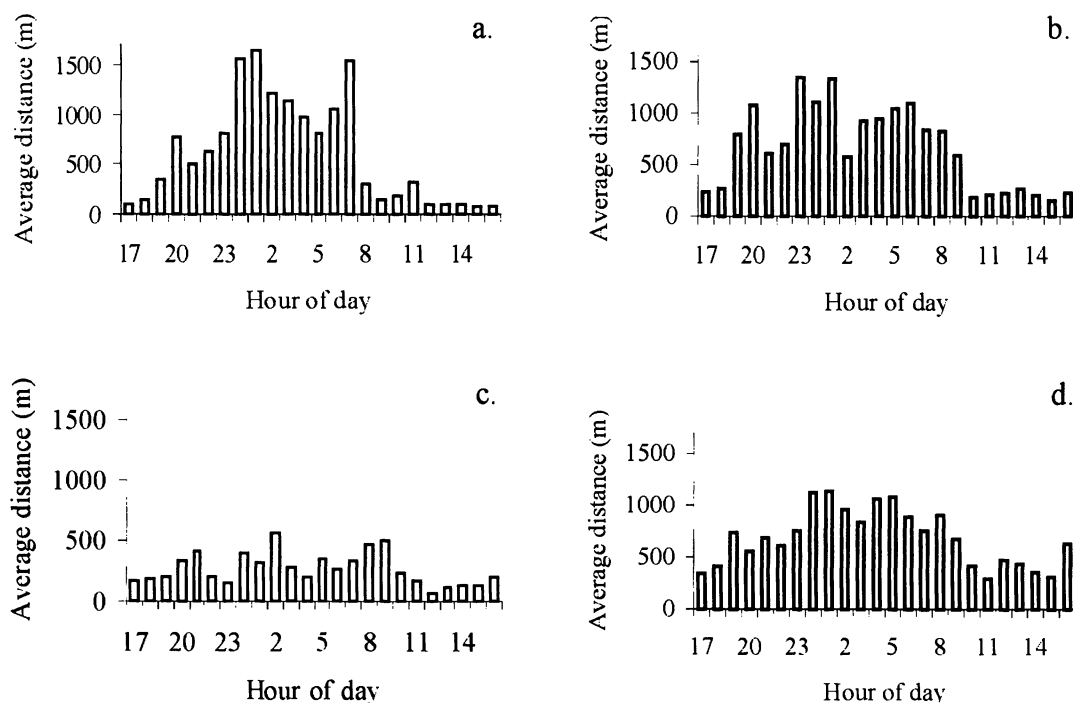

Figure 1. Activity (mean distance between locations) plots for all wolves studied, except male 399 (see Figure 3a); central Minnesota. a) Breeding female 850 (319 1-hour intervals, 20 February–8 March 1997). b) yearling male 840 (646 30-minute intervals pooled per hour, 20 February–14 March 1997). c) female pup 860 (252 1-hour intervals, 20 February–10 March 1997). d) male pup 820 (1,358 15-minute intervals pooled per hour, 21 February–13 March 1997). (*Continued next page*)
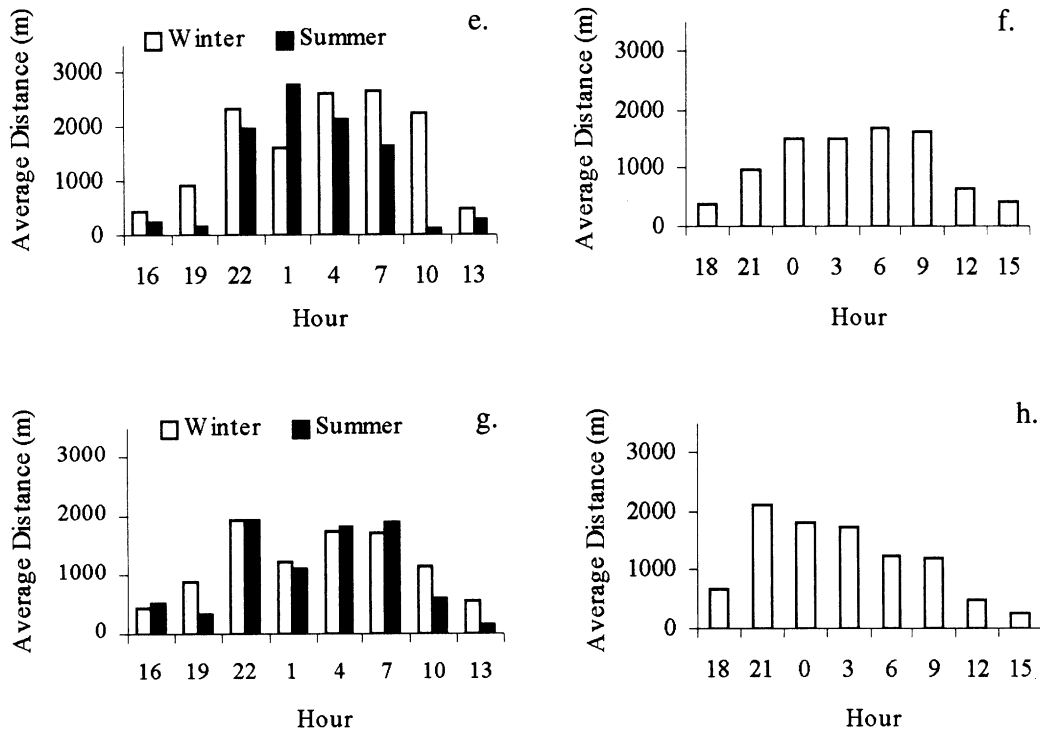
Figure 1 (*continued*). Activity (mean distance between locations) plots for all wolves studied, except male 399 (see Figure 3a); central Minnesota. e) breeding male 133 (385 3-hour intervals, 31 January–9 July 1998). f) yearling female 229 (351 3-hour intervals, 31 January–18 June 1998). g) breeding male 627 (552 3-hour intervals, 3 February–17 June 1998). h) breeding female 134 (217 3-hour intervals, 14 September–15 November 1998).

collected once per hour show that she moved at night with increases at dusk, dawn, and midnight (Figures 1a and 3b). Her mean minimum rate of travel was 583 ± 475 m per hour (Table 2). After converting data from one location per hour to one per 4

Table 2. Location attempt intervals and mean and maximum travel rates for wolves studied by Global Positioning System telemetry near Little Falls, Minnesota, from 20 February 1997–14 September 1998.

Wolf	Location attempt interval	Max. Distance per location interval (m)	Travel rate (m/ interval)	Standard- ized travel rate (m/h)
850				
Before denning	1 hr	7,344	583	583
During denning	4 hr	9,370	1,423	356
After denning	4 hr	9,722	2,580	645
840	30 min	4,532	330	660
860	1 hr	2,983	269	269
820	15 min	3,660	179	716
133	3 hr	12,669	1,844	615
229	3 hr	10,906	1,198	399
627	3 hr	8,335	1,289	430
134	3 hr	6,725	1,229	410

hours (to compare fairly with data collected after she whelped), her mean minimum distance traveled before whelping was $1,889\pm1,334$ m per 4 hours. The observed nocturnal pattern was not altered by this conversion, although the peaks at dusk and dawn were lost. After whelping, 850's mean minimum distance traveled per 4 hours was $2,026\pm1,051$ m.

From 1 to 25 May 1997, wolf 850's amount of time >1.5 km from the den increased from 3% (2/76 locations) to 39% (25/64 locations). During this period she took 20 trips from the den, at one trip per 1.25 days. Of these trips 17 were represented by single GPS locations, 2 by 2 consecutive GPS locations, and one by 3 consecutive GPS locations. This pattern suggested that wolf 850's trips generally lasted <8 hours (the time spanned by 3 consecutive GPS locations). Most locations >1.5 km from the den were nocturnal (Figure 7), as would be expected based on the wolf's nocturnal pattern for distance traveled. We avoided bias in this estimate of temporal distribution of trips away from the den by including only one location for each trip. About 4 June, 850 moved her pups to rendezvous sites (Figure 6, "Locations from 0–6 weeks after pups").
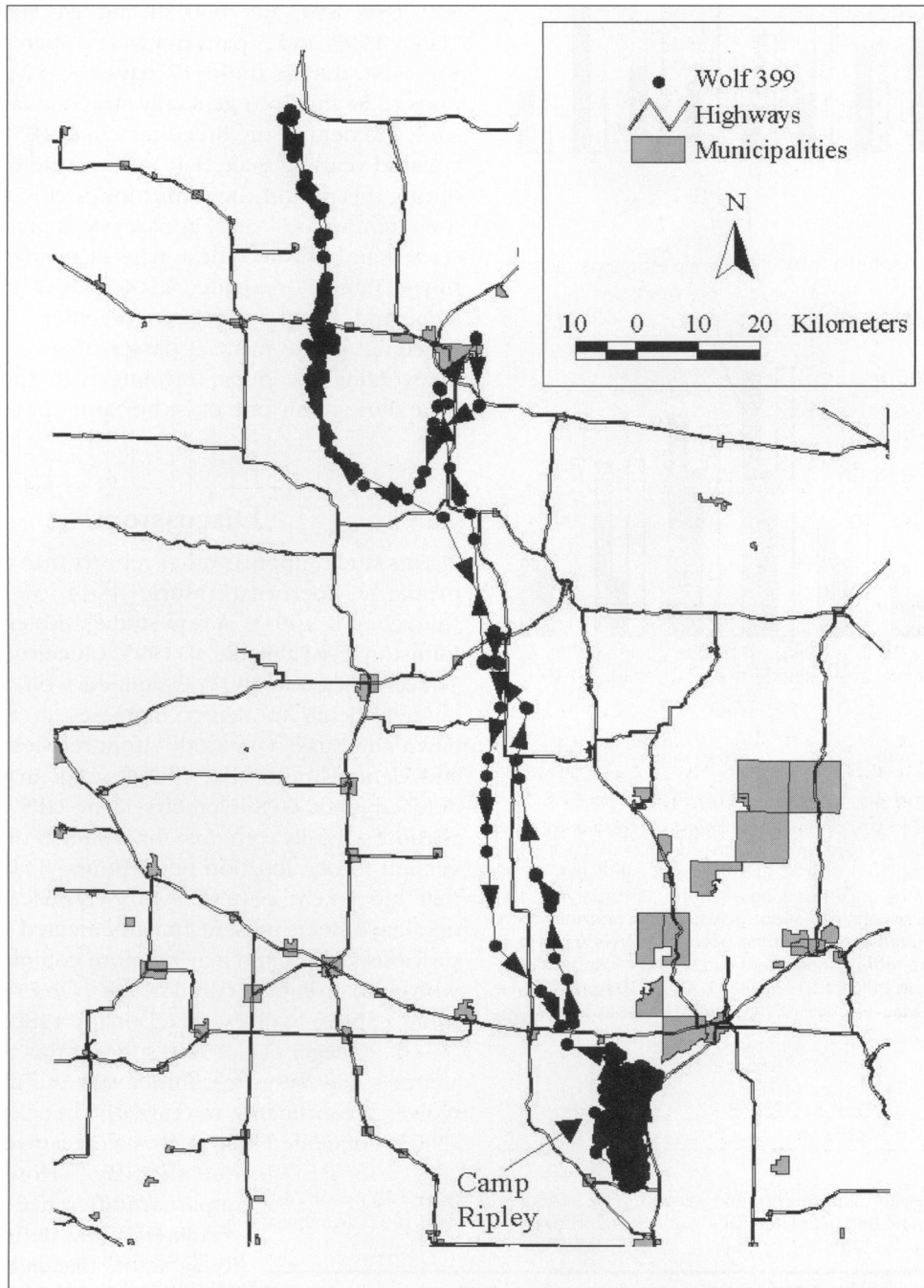
Figure 2. Locations of yearling male wolf 399 before and during an extraterritorial foray; location intervals once per 3 hours from 2 March 1998–27 July 1998; central Minnesota. The wolf commenced the foray on 31 May 1998 and returned on 27 July 1998, having spent about a month on both the outbound and inbound journeys. Lines connect 1,121 sequential locations and indicate direction of travel.
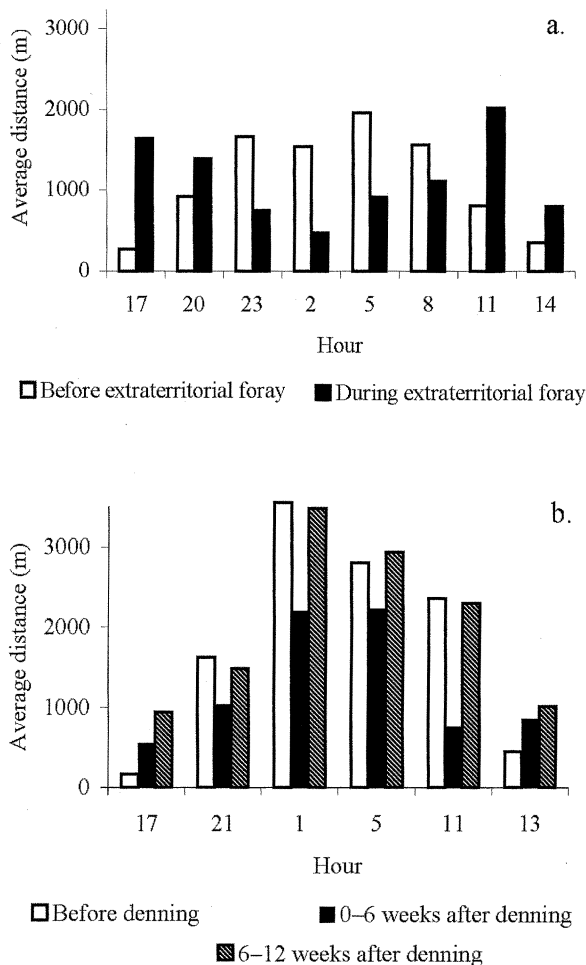
a.

b.

Figure 3. a) Mean distance between successive location attempt intervals versus time of day for Global Positioning System (GPS)-collared male wolf 399 prior to an extraterritorial foray; locations once per 3 hours (from 3 February–27 July 98; central Minnesota). b) Mean distance between successive GPS location intervals versus time of day for breeding female wolf 850 before, during, and after bearing pups; locations once per 4 hours (from 20 February–9 March 1997, 10 April–24 May 1997, and 25 May–9 July 1997; central Minnesota).

Social activities of pack members during late winter

We analyzed a subset of GPS data from wolves 820, 840, 850, and 860 during 24 February–13 March 1997, and 3 patterns were apparent (Figure 8). First, during these 17 days the 10-month-old pups (820 and 860) generally stayed at rendezvous sites, and neither the breeding female (850) nor the collared yearling male (840) visited them. Second, during this period, the pups took 3 trips away from their rendezvous sites, apparently together. They started and finished these trips at nearly the same times (Table 3), remained <100 m apart during the trips, and could have been together. Third, the breeding female made 2 passes of several km circumventing the pups, traveling with the yearling male during only one pass (her inner pass in Figure 8).

Discussion

This study supports other reports that wolves are primarily nocturnal (Murie 1944, Mech 1970, Kunkel et al. 1991). A few studies (Kolenosky and Johnston 1967, Vilà et al. 1995, Ciucci et al. 1997, Theuerkauf et al. 2003) examined wolf activity in enough detail to detect increases in activity at dawn and dusk. Our study supports these findings and demonstrates that these peaks may not be detectable via GPS telemetry if the GPS interval is >3 hours. Peaks were lost for wolf 850 during conversion to one location per 4 hours. This suggests that movement patterns with crepuscular peaks may have been present but undetected in several previous studies and may be more common among wolves than is generally known. Observations of some captive wolves (MacDonald 1980) but not others (Kreeger et al. 1996) support this possibility.

One study seems to conflict with our results that wolves are primarily nocturnal. Theuerkauf et al. (2003) concluded that wolves were active throughout the day. However, the apparent difference probably results from our defining activity as actual distance traveled. The wolves in Theuerkauf et al's (2003) study also traveled least during daylight, so in that respect our findings are in agreement. Apparently, wolves are active during the day without generally traveling as far as

Table 3. Onset and cessation of excursions from 2 rendezvous sites by 10-month-old wolf pups 820 and 860 near Little Falls, Minnesota, February and March 1997. Numbers indicate month/day hr:min.

Wolf	Trip 1		Trip 2		Trip 3	
	Onset	Cessation	Onset	Cessation	Onset	Cessation
820*	2/28 04:01	2/28 12:31	2/28 20:45	3/01 09:46	2/25 20:16	2/26 09:45
860**	2/28 04:01	2/28 13:02	2/28 21:00	3/01 10:01	2/25 21:01	2/26 09:46

* GPS data collection interval: 1 location per 15 min.
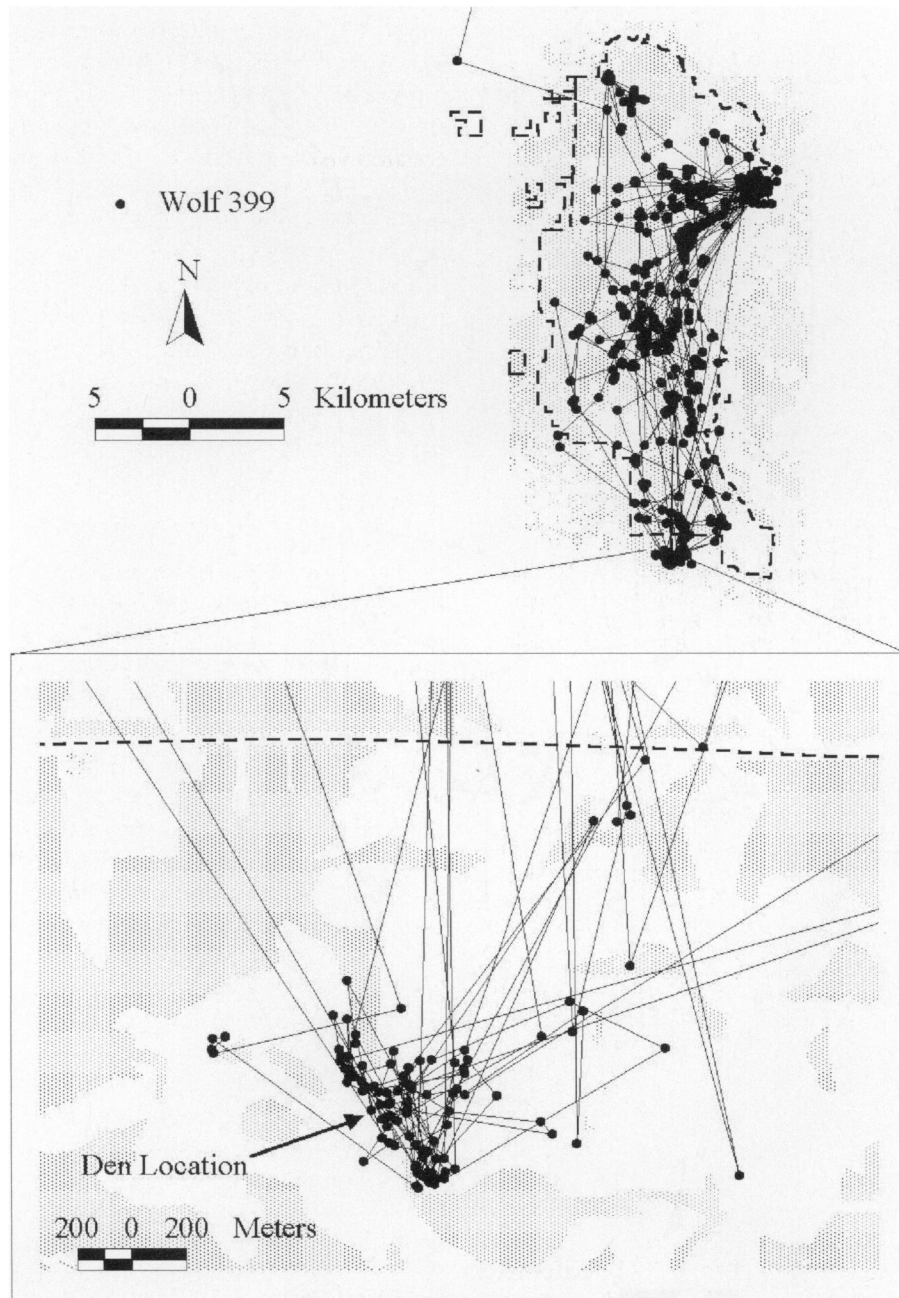** GPS data collection interval: 1 location per hr.

Figure 4. Locations of Global Positioning System-collared yearling male wolf 399 before an extraterritorial foray; location intervals once per 3 hours from 2 March 1998–31 May 1998; central Minnesota. Inset shows the wolf made at least 13 trips to the den in the month prior to the foray (30 April–31 May 1998). Lines connect sequential locations. Stippled area represents forest. Dashed line represents Camp Ripley border.
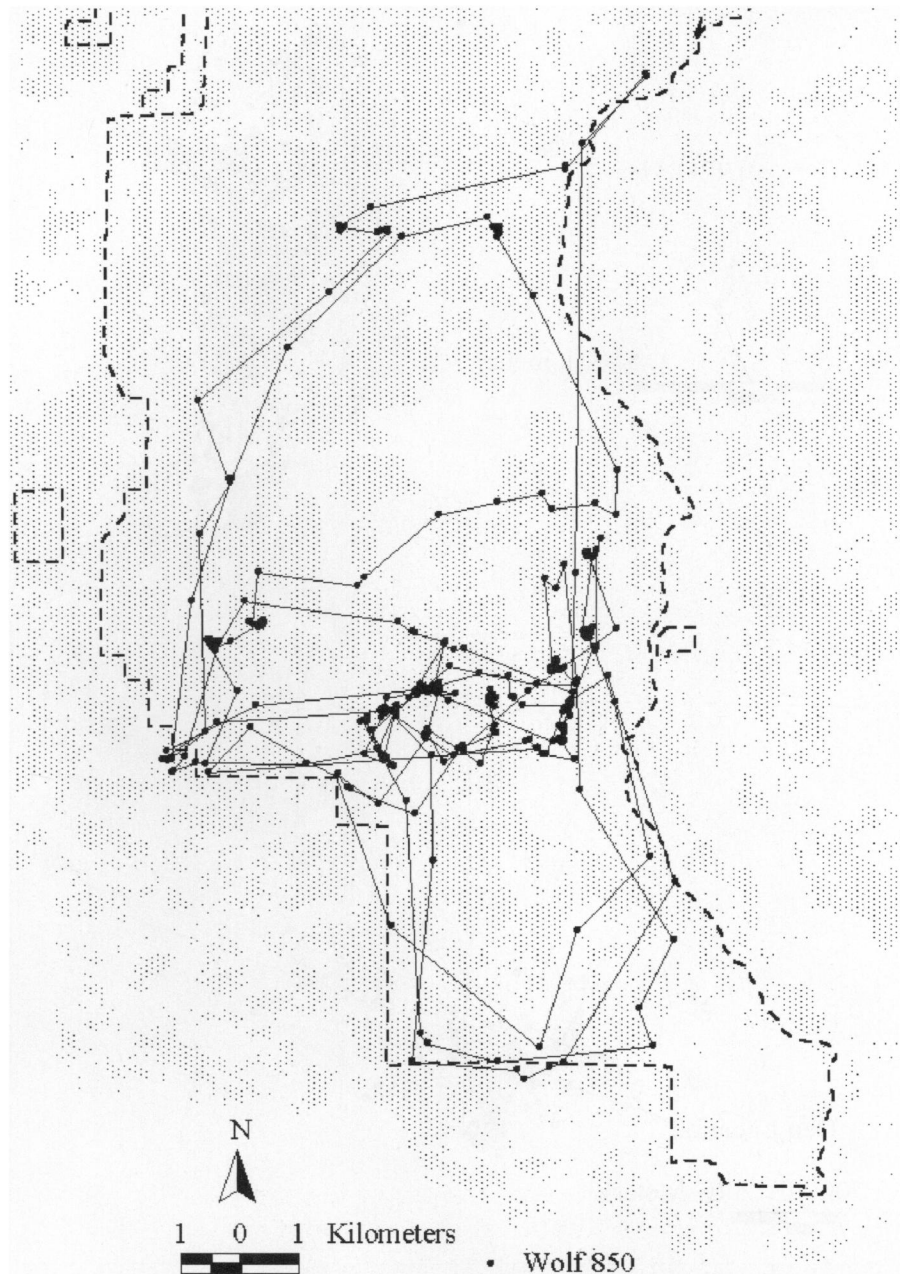
Figure 5. Movement data collected by Global Positioning System collar on breeding female wolf 850; locations once per hour from 20 February–9 March 1997; central Minnesota. Lines connect sequential locations and show the movement pattern before pups were born (compare with Figure 6). Stippled area represents forest. Dashed line represents Camp Ripley border.
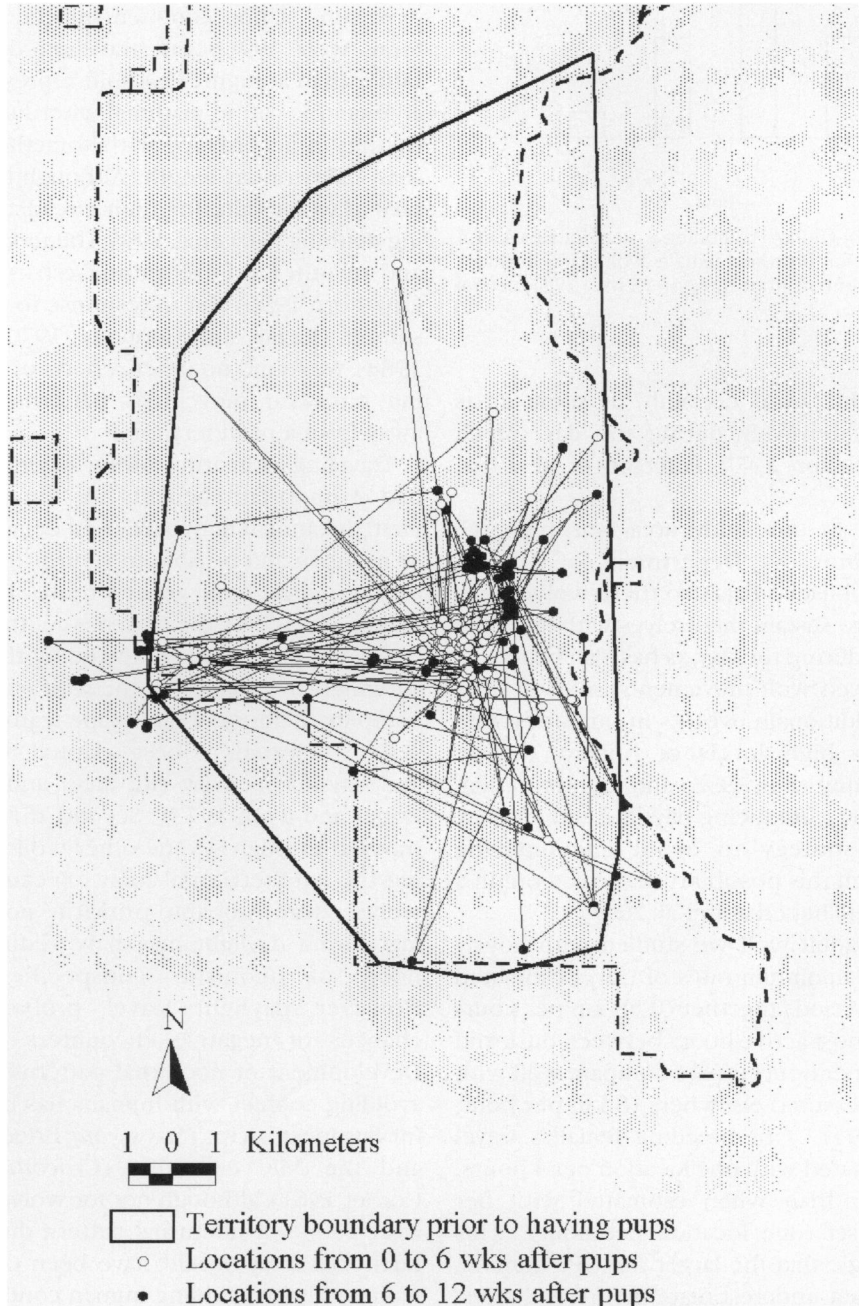
Figure 6. Movement data collected by Global Positioning System collar on breeding female wolf 850; locations once per 4 hours from 10 April–9 July 1997; central Minnesota. Lines connect sequential locations and show the movement pattern after pups were presumed born (compare with Figure 5). Stippled area represents forest. Dashed line represents Camp Ripley border. Location clusters indicate rendezvous sites.
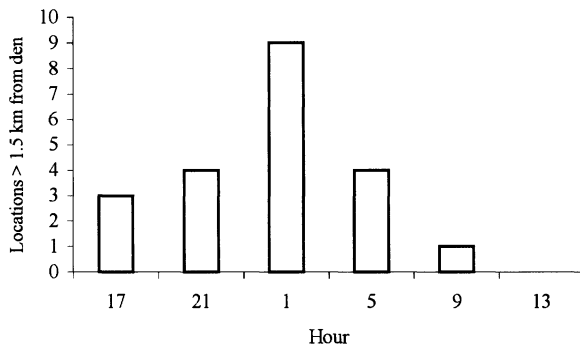
Figure 7. Number of Global Positioning System locations >1.5 km from the den for breeding female wolf 850; locations obtained once per 4 hours from 10 April–25 May 1997; central Minnesota.

they do at night. And certainly in some areas wolves travel extensively during the day (Mech 1966, 1992, Peterson 1977, Peterson et al. 1984, Boitani 1986).

Deer density in our study area was high (G. DelGiudice, Minnesota Department of Natural Resources, unpublished data), so these wolves may have been able to sustain themselves with less time spent traveling during the day, as has also been suggested for reduced wolf movements in Spain (Vilà et al. 1995). Additionally, wolves in our study area coexisted with high levels of human activity (Merrill 1996,Thiel et al. 1998) and high road density (Merrill 2000). Reducing daytime activity may have been a strategy to avoid encountering humans, although this possibility was ruled out in a study in Poland (Theuerkauf et al. 2003).

For the only adult wolf we studied with hourly GPS data, mean minimum rates of travel estimated for all 24-hour periods together (0.58 km per hour) or for only the most active hours between dusk and dawn (0.94 km per hour) do not compare well with rates actually measured elsewhere (8 km per hour; Mech 1970, 1994). Our breeding female's travel rate, when estimated with one location per 4 hours, was 19% lower than when estimated with her complete data set (one location per hour). This confirms the logic that the larger the GPS interval, the more the data underestimate wolf travel rates. Even hourly locations obviously underestimate wolf speed, except when the wolf is traveling for prolonged periods in a straight line.

Male wolf 399

Global Positioning System data from this wolf show a change in his circadian movement pattern

associated with his extraterritorial foray. His nearly complete cessation of visits to the den one week prior to the extraterritorial foray suggests that he ceased participating in pup-rearing prior to his departure. Upon commencing the extraterritorial foray, wolf 399 began traveling during the day rather than at night. This shift represents an unusual example of a mammal altering its circadian rhythm in accordance with something other than seasonality or day length. Although there are examples of wolves altering their circadian rhythms during denning (Vilà et al. 1995,Theuerkauf et al. 2003) and of other animals during estrus (Cushing and Cawthorn 1996) and in response to different social stimuli (Regal and Connolly 1979, Mrososovsky 1988), we found no other reports of animals changing circadian movement patterns during travel away from a natal territory.

Traveling primarily during daylight might have had 2 important benefits for the traveling wolf. First, the animal may have used detailed visual cues to navigate and be able to return to his natal territory using the same general route. This hypothesis was supported by the closeness of the inbound and outbound travel ways followed by the wolf (Figure 2), which also suggested the wolf might have had a complex memory of landscape features. The visual system of canids is best adapted for crepuscular and daytime activity (Kavanau and Ramos 1975, Roper and Ryon 1977). Second, the wolf probably traveled through several other wolf territories during the extraterritorial foray. Because these other wolves were probably primarily nocturnal, traveling during daylight may have reduced the likelihood of agonistic conspecific encounters. However, daylight travel probably increased chances of negative encounters with humans. Development of nocturnal patterns as a means of avoiding contact with humans has been suggested for European swine (*Sus scrofa*;Briedermann 1971) and the Nile crocodile (*Crocodilus niloticus*; Corbet 1961), although not for wolves (Theuerkauf et al. 2003). A nocturnal pattern during the extraterritorial foray would have been expected if the wolf had been avoiding human contact; the diurnal pattern suggests it was not.

Dispersing wolves in some areas show significantly lower survival rates than wolves of the same age that remain in packs (Peterson et al. 1984, Messier 1985). In one study 90% (18/20) of mortalities among dispersing wolves resulted from human causes (Boyd and Pletscher 1999).
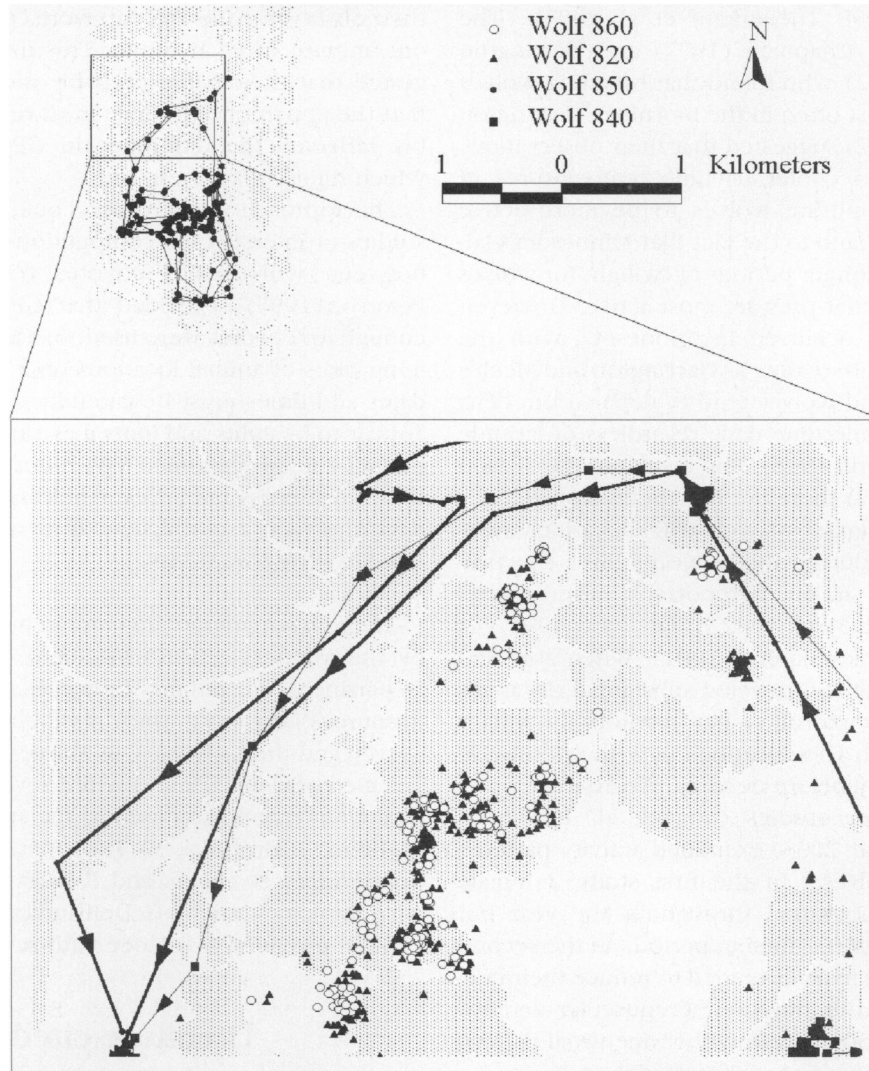
Figure 8. Movement data collected by Global Positioning System collars on wolf pups 860 and 820 (locations once per 15 minutes and once per hour), breeding female wolf 850 (locations once per hour), and yearling male wolf 840 (locations once per 30 minutes) from 24 February–12 March 1997; central Minnesota. Lines connect sequential locations and show the breeding female circumvented her pups during this period. Stippled area represents forest. Lower map is an expanded view of the upper map; upper map has locations only from wolf 850. We assumed her territory boundaries (based on 327 locations) were represented by her outermost points.

Although the diurnal pattern for our wolf cannot necessarily be extrapolated to other wolves, possibly other wolves disperse or travel on extraterritorial forays more during the day. If so, this could be maladaptive in human-dominated landscapes and could have contributed to the high dispersal mortality reported by Boyd and Pletscher (1999).

Breeding female wolf 850

Location data obtained from this wolf parallel changes in her life-history stage as well. When she produced pups, her movement pattern changed from nomadism within a territory with no obvious center of activity to making numerous trips away from her den. This spoke-like pattern of movement away from a center of activity supports previous observations (Zimen 1978, Ciucci et al. 1997, Mech et al. 1998). Data collected during the second 6 weeks after denning demonstrate the ability to identify rendezvous sites using GPS telemetry data.

The nocturnal pattern of 850's trips away from the den is consistent with most studies (Murie 1944, Kolenosky and Johnston 1967, Haber 1977, Ballard et al. 1991, Williams and Heard 1991, Mech

and Merrill 1998, Theuerkauf et al. 2003). The exceptions are Chapman (1977) and Harrington and Mech (1982), who found that breeding wolves left the den most often in the morning. Harrington and Mech (1982) suggested that their observations were related to cooler daytime temperatures in Minnesota, permitting wolves to be more active during daylight, and to the fact that Minnesota's latitude provides longer periods of twilight for wolves to hunt when their prey are most active. However, our study also occurred in Minnesota, with the same temperature regime as Harrington and Mech's (1982) study, and wolves tend to depart from dens at about the same time daily regardless of latitude (Mech and Merrill 1998). The results of Harrington and Mech (1982) therefore remain unexplained.

The small number of wolf 850's locations away from the den during the 6 weeks after she produced pups is similar to reports in other studies (Harrington and Mech 1982, Ballard et al. 1991, Vilà et al. 1995, Jedrzewski et al. 2001). When wolf 850 left her den, she still traveled substantial distances and apparently patrolled her territory boundary (compared with GPS locations near the perimeter of her boundary before denning; Figure 6).

Only 2 other studies (Vilà et al. 1995 and Theuerkauf et al. 2003) examined activity patterns of nursing wolves. In the first study, 2 female wolves were nocturnal throughout the year but diurnal for a 6-week nursing period. In the second study, 5 nursing females tended to reduce their nocturnal activity but not their crepuscular activity. Nursing wolf 850 maintained her nocturnal pattern through the 6-week nursing period.

Social aspects of wolf activity

Data collected from breeding female 850, male yearling 840, and pups 820 and 860 demonstrate the usefulness of GPS telemetry data in determining when members of a social group travel together and apart. When the pups were 10 months old, their mother had suspended visiting them. Presumably other pack members had helped provide food, for the pups remained at the rendezvous site most of the time and hunted little themselves.

Different GPS intervals for collars worn by different animals could have obscured some patterns. This possibility was reflected visually in the easternmost of the 3 trips taken by the pups (Figure 8; trip 3 in Table 3). Although it appears one pup traveled directly back to the rendezvous site while the other took a more circuitous route (traveling in a clockwise loop), GPS locations at the next place

their observed paths overlap were collected within one minute of each other. This information suggested that their paths probably did not split but that the apparent difference in travel routes probably reflected the difference in GPS intervals for which their collars were set.

The approach we used also could be valuable in studies of interspecific competition—for example, between wolves and coyotes (*Canis latrans*, Peterson 1995)—provided that GPS collars light enough for coyotes were used. In addition to examining plots of animal locations on a map, however, dates and times must be carefully compared; what appear to be splits and joins may simply reflect differences in programmed GPS intervals or in GPS location success rate. Nevertheless, GPS telemetry data represent a useful new approach to studying wildlife activity patterns.
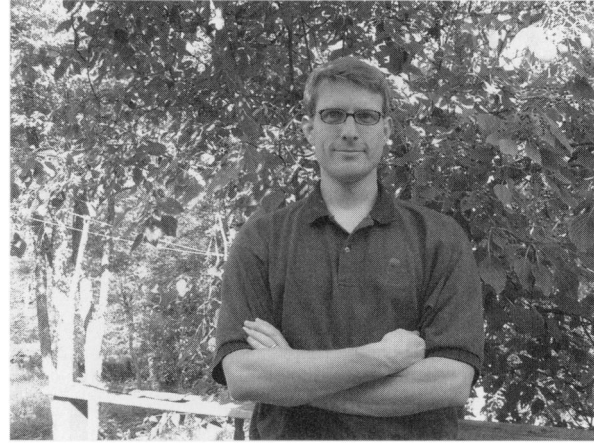
Literature cited

BALLARD, W. B., L. A. AYRES, C. L. GARDNER, AND J. W. FOSTER. 1991. Den site activity patterns of gray wolves, *Canis lupus*, in south-central Alaska. Canadian Field-Naturalist 105:497-504.

BARRETT, M. W., J. W. NOLAN, AND L. D. ROY. 1982. Evaluation of a hand-held net-gun to capture large mammals. Wildlife Society Bulletin 11:184-187.

BOITANI, L. 1986. Dalla parte del lupo. L'Airone di G. Mondadori and Association, Milan, Italy.

BOYD, D. K., AND D. H. PLETSCHER. 1999. Characteristics of dispersal in a colonizing wolf population in the central Rocky Mountains. Journal of Wildlife Management 63:1094-1108.

BRIEDERMANN, L. 1971. Ermittlungen zur Aktivitätsperiodik des mitteleuropäischen Wildschweines (*Sus s. scrofa* L.). Zoologische Garten 40:302-327.

CARBYN, L. N. 1975. Wolf predation and behavioural interactions with elk and other ungulates in an area of high prey diversity. Dissertation, University of Toronto, Ontario, Canada.

CHAPMAN, R. C. 1977. The effects of human disturbance on wolves (*Canis lupus* L.). Thesis. University of Alaska, Fairbanks, USA.

CIUCCI, P., L. BOITANI, F. FRANCISCI, AND D. ANDREOLI. 1997. Home range, activity and movements of a wolf pack in central Italy. Journal of the London Zoological Society 243:803-819.

CORBET, P. S. 1961. Discussion contribution. Page 354 *in* A. Chovnick, editor. Biological Clocks—Cold Spring Harbor Symposia on Quantitative Biology.

CUSHING, B. S., AND J. M. CAWTHORN. 1996. Species differences in activity patterns during oestrus. Canadian Journal of Zoology 74:473-479.

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.

HABER, G. C. 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. Dissertation, University of British Columbia, Vancouver, Canada.

HARRINGTON, F. H., AND L. D. MECH. 1982. Patterns of homesite attendance in two Minnesota wolf packs. Pages 81-105 *in* F. H. Harrington and P. C. Pacquet, editors. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes, Park Ridge, New Jersey, USA.

HOOGE, P. N., AND B. EICHENLAUB. 2000. Animal movement extension to ArcView v. 2.2. Alaska Biological Science Center, United States Geological Survey, Anchorage, USA.

JEDRZEWSKI, W., K. SCHMIDT, J. THEUERKAUF, B. JEDRZEJEWSKA, AND H. OKARMA. 2001. Daily movements and territory use by radiocollared wolves (*Canis lupus*) in Bialowieza Primeval Forest in Poland. Canadian Journal of Zoology 79:1993-2004.

KAVANAU, J. L., AND J. RAMOS. 1975. Influences of light on activity and phasing of carnivores. The American Naturalist 109:391-418.

KOLENOSKY, G. B., AND D. H. JOHNSTON. 1967. Radio-tracking timber wolves in Ontario. American Zoologist 7:289-303.

KREEGER, T. J., D. L. PEREIRA, M. CALLAHAN, AND M. BECKEL. 1996. Activity patterns of gray wolves housed in small vs. large enclosures. Zoo Biology 15:395-401.

KUNKEL, K. E., R. C. CHAPMAN, L. D. MECH, AND E. M. GESE. 1991. Testing the Wildlink activity-detection system on wolves and white-tailed deer. Canadian Journal of Zoology 69:2466-2469.

MACDONALD, K. B. 1980. Activity patterns in a captive wolf pack. Carnivore 3:62-64.

MECH, L. D. 1966. The wolves of Isle Royale. National Parks Fauna Series, United States Government Printing Office 7:1-210.

MECH, L. D. 1970. The wolf: the ecology and behavior of an endangered species. Natural History Press, Garden City, New York, USA.

MECH, L. D. 1992. Daytime activity of wolves during winter in northeastern Minnesota. Journal of Mammalogy 73:570-571.

MECH, L. D. 1994. Regular and homeward travel speed of arctic wolves. Journal of Mammalogy 75:741-742.

MECH, L. D. 1995. What do we know about wolves and what more do we need to learn? Pages 537-545 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and Conservation of wolves in a changing world. Canadian Circumpolar Institute, Occasional Publication 35.

MECH, L. D., L. G. ADAMS, T. J. MEIER, J. W. BURCH, AND B. W. DALE. 1998. The Wolves of Denali. University of Minnesota Press, Minneapolis, USA.

MECH, L. D., AND S. M. BARBER. 2002. A critique of wildlife radio-tracking and its use in National Parks. United States National Park Service, Fort Collins, Colorado, USA.

MECH, L. D., AND E. M. GESE. 1992. Field testing the Wildlink Capture Collar on wolves. Wildlife Society Bulletin 20:249-256.

MECH, L. D., AND S. B. MERRILL. 1998. Daily departure and return

patterns of wolves, *Canis lupus*, from a den at 80 N latitude. Canadian Journal of Zoology 112:515-517.

MERRILL, S. B. 1996. The wolves of Camp Ripley. International Wolf 6:7-9.

MERRILL, S. B. 2000. Road densities and Gray Wolf, Canis lupus, habitat suitability: an exception. Canadian Field-Naturalist 114:312-313.

MERRILL, S. B. 2002. An evaluation of the use of global positioning system telemetry in studying wolf biology. Dissertation, University of Minnesota, Minnesota, USA.

MERRILL, S. B., L. G. ADAMS, M. E. NELSON, AND L. D. MECH. 1998. Testing releasable GPS radiocollars on wolves and white-tailed deer. Wildlife Society Bulletin 26:830-835.

MERRILL, S. B., AND L. D. MECH. 2000. Details of extensive movements by Minnesota wolves. American Midland Naturalist 144:428-433.

MESSIER, F. 1985. Social organization, spatial distribution, and population density of wolves in relation to moose density. Canadian Journal of Zoology 63:1068-1077.

MOEN, R. J., J. PASTOR, Y. COHEN, AND C. C. SCHWARTZ. 1996. Effects of moose movement and habitat use on GPS collar performance. Journal of Wildlife Management 60:659-668.

MROSOSOVSKY, N. 1988. Phase response curves for social entrainment. Journal of Comparative Physiology 162:35-46.

MURIE, A. 1944. The wolves of Mount McKinley. University of Washington Press, Seattle, USA.

PETERSON, R. O. 1977. Wolf ecology and prey relationships on Isle Royale. National Park Service Scientific Monograph Series, United States Government Printing Office 11:1-210.

PETERSON, R. O. 1995. Wolves as interspecific competitors in canid ecology. Pages 315-324 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and Conservation of wolves in a changing world. Canadian Circumpolar Institute, Occasional Publication 35.

PETERSON, R. O., J. D. WOOLINGTON, AND T. N. BAILEY. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88.

REGAL, P. J., AND M. S. CONNOLLY. 1979. Social influences on biological rhythms. Behaviour 72:171-199.

RODGERS, A. R., AND P. ANSON. 1994. Animal-borne GPS: tracking the habitat. GPS World 5:20-32.

ROPER, T. J., AND T. RYON. 1977. Mutual synchronization of diurnal activity rhythms in groups of red wolf/coyote hybrids. Journal of the London Zoological Society 182:177-185.

THIEL, R., S. B. MERRILL, AND L. D. MECH. 1998. Tolerance by denning wolves, *Canis lupus*, to human disturbance. American Midland Naturalist 112:340-342.

THEUERKAUF, J., W. JEDRZEWSKI, K. SCHMIDT, H. OKARMA, I. RUCZYNSKI, S. SNIEZKO, R. GULA. 2003. Daily patterns of wolf activity in the Bialowieza Forest, Poland. Journal of Mammalogy 84:127-137.

VILÀ, C., V. URIOS, AND J. CASTROVIEJO. 1995. Observations on the daily activity patterns of the Iberian wolf. Pages 335-340 *in* L. N. Carbyn, S. H. Fritts, and D. R. Seip, editors. Ecology and Conservation of wolves in a changing world. Canadian Circumpolar Institute, Occasional Publication 35.

WILLIAMS, T. M., AND D. C. HEARD. 1991. Predation rates, movement and activity patterns, pup survival and diet of wolves associated with dens on the range of the Bathurst caribou herd, June-August 1991. Northwest Territories Department of Renewable Resources Wildlife Management Division Progress Report.

ZIMEN, E. 1978. Der Wolf: Mythos und Verhalten. Meyster Verlag, Munich, Germany.

Samuel B. (Sam) Merrill (photo) is Projects Director at the New England Environmental Center, through the Muskie School of Public Service at the University of Southern Maine. For 6 years he worked for the Minnesota Department of Natural Resources as Animal Survey Coordinator at the Camp Ripley National Guard Training Site. He now works on smart-growth policy and research in the six New England states. He received a B.A. in zoology from the University of Maine at Orono and an M.S. in conservation biology and a Ph.D. in wildlife conservation from the University of Minnesota. **L. David (Dave) Mech** is a senior research biologist with the Biological Resources Division of the United States Geological Survey and an adjunct professor at the University of Minnesota. He holds a Ph.D. from Purdue University. He has studied wolves and their prey for 45 years and published several books and numerous articles.

Associate editor: *Applegate*