

DAILY PATTERNS AND DURATION OF WOLF ACTIVITY IN THE BIAŁOWIEŻA FOREST, POLAND

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We studied the influence of human activity, hunting of prey by wolves, reproduction, and weather conditions on daily patterns and duration of activity of 11 radiotracked wolves (*Canis lupus*) in the Białowieża Forest (Poland) from 1994 to 1999. On average, wolves were active $45.2\% \pm 0.9 SE$ of the time and traveled 0.92 ± 0.05 km/h. The mean length of activity bouts was 0.76 ± 0.05 h, whereas inactivity bouts averaged 1.02 ± 0.07 h. Wolves were active throughout the day, but their activity peaked at dawn and dusk, which coincided with periods when they killed most prey. Periods of reproduction and high temperatures had less pronounced effects on activity patterns. Human activity and other factors did not significantly affect the wolves' daily activity patterns. The influence of humans may be indirect if hunting of ungulates by humans modifies activity patterns of the wolves' prey. We conclude that the daily activity patterns of wolves in our study area were mainly shaped by their pattern of hunting prey.

Key words: activity, breeding, *Canis lupus*, daily patterns, distance traveled, duration, human activity, prey, wolf

Radiotracking studies of wolves (*Canis lupus*) have suggested several factors that are likely to influence their activity patterns. These factors are human activity (Ciucci et al. 1997; Vilà et al. 1995), hunting of prey (Ballard et al. 1991; Harrington and Mech 1982; Mech and Merrill 1998; Murie 1944), reproduction (Ballard et al. 1991; Harrington and Mech 1982; Vilà et al. 1995), and weather (Fancy and Ballard 1995; Kolenosky and Johnston 1967). However, importance of each of these factors may vary according to geographic area. This causes dissimilarities in activity patterns of wolves

from different study sites: wolves were nocturnal in Italy (Ciucci et al. 1997); nocturnal with a tendency to bimodal activity in Spain (Vilà et al. 1995); active throughout day and night in Ontario, Canada (Kolenosky and Johnston 1967); and most active from 2200 to 0600 h in summer and from 0700 to 1600 h in winter in Alaska (Fancy and Ballard 1995). Wolves also show significant variation in daily activity patterns among individuals of a pack as observed at denning and rendezvous sites (Ballard et al. 1991; Harrington and Mech 1982).

We hypothesized that human and prey activities would have the most important influence on activity patterns of wolves. The

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activity patterns of wolves and their prey are theoretically dependent on one another because prey strive to avoid wolves, whereas wolves adapt their temporal hunting pattern to the times when prey are most vulnerable. Knowledge about temporal distribution of wolf kills could improve understanding of interactions between wolves and their prey, but information available is limited to data based on times when wolves leave den sites for hunting and times when they return afterward (Ballard et al. 1991; Harrington and Mech 1982; Mech and Merrill 1998; Murie 1944). The influence of humans on activity of wolves is especially important to determine. Wildlife managers need information about the potential influence of humans on behavior of wolves in areas where wolves are currently extending their range, such as Central Europe (Promberger and Schröder 1993) or the United States (Mech 1995). We expected that wolves living in areas with high human activity would either change their activity patterns to avoid encounters with humans or become used to the presence of people. In Central Europe, where hunting by humans strongly influences activity patterns of ungulates (Briedermann 1971; Georgii 1981; Georgii and Schröder 1983; Jeppesen 1989), hunting patterns of recolonizing wolves could cause a shift in activity patterns of their prey.

To obtain information about daily patterns of wolf activity, kills by wolves, and human activity, we radiotracked wolves, determined the time when wolves killed prey, and recorded human activity in the Białowieża Forest, Poland. This area lies on the western edge of the large wolf range that encompasses the boreal and temperate forest zone of Eurasia. The aim of our study was to determine how human activity, hunting for prey, reproduction, and weather conditions affect activity of wolves.

MATERIALS AND METHODS

Study area.—The Białowieża Forest straddles the Polish–Belarussian border (52°30′–53°00′N,

23°30′–24°15′E) in the transition zone between boreal and temperate climate. The forest consists of deciduous, coniferous, and mixed tree stands. Mean daily temperature is -5°C in January and 18°C in July, annual precipitation is 641 mm, and length of snow cover averages 92 days but ranges between 0 and 132 days (Faliński 1994). The maximum depth of snow during this study was 63 cm. Our study area was the Polish part of the Białowieża Forest (580 km²), which includes the Białowieża National Park (100 km²) and a commercial forest (480 km²). Timber harvest, reforestation, and hunting take place in the commercial forest. See Jędrzejewska and Jędrzejewski (1998) for a detailed description of the study area.

Human density is about 7 inhabitants/km² in the Białowieża Forest and 70 inhabitants/km² in the region surrounding the study area (Białystok administration district). The density of forest roads suitable for 2-wheel drive cars is about 1.2 km/km² in the commercial forest, but only about 50 km of paved roads (0.1 km/km²) are intensively used by the public. Forestry is the main source of human activity in the commercial forest. Tourists contribute largely to human activity in summer, particularly in the National Park. Mushroom collectors and hunters are active seasonally. Traffic in the forest consists mostly of cars, trucks, or tractors. Tourists mainly move on foot or bicycle and usually remain on roads and trails.

Three wolf packs roamed the Polish part of the Białowieża Forest at the beginning of this study. The core area of 1 pack (National Park pack) was the strict reserve (50 km²) of the Białowieża National Park, where there is no motorized traffic and human access is restricted. Another pack inhabited the northwestern part of the Białowieża Forest (Ładzka pack). The 3rd pack lived in the southern part of the study area. This pack split in December 1997 into 2 packs (Leśna packs), but their home ranges overlapped nearly completely after the separation. Wolves have been protected since 1989 in the Polish part of the Białowieża Forest, but humans are still the main mortality factor. During our study, 6 of 12 radiocollared wolves were shot or died in snares set by poachers for wild boar (*Sus scrofa*). In the Belarussian part, hunters killed between 1975 and 1994 on average 80% of the wolf population per year (Jędrzejewska et al.

1996). Wolves usually flee when they meet humans in the forest.

The main prey of wolves in the Białowieża Forest (Jędrzejewski et al. 2000, 2002) are red deer (*Cervus elaphus*), followed by wild boar and roe deer (*Capreolus capreolus*). During this study, mean densities of prey for the whole study area were about 3–7 red deer/km², 1–6 wild boar/km², and 1–5 roe deer/km² (Jędrzejewski et al. 2000; Kossak 1997, 1999).

Radiotracking of wolves.—We captured 12 wolves from 4 packs, either with Aldrich foot snares equipped with radioalarm systems (3 wolves), as described in Okarma et al. (1998), or by the fladry-and-net method (9 wolves), as described in Okarma and Jędrzejewski (1997). Fladry are lengths of rope to which colored strips of cloth of about 40 by 15 cm are attached at intervals of about 50 cm. Wolves usually avoid crossing lines of fladry and can therefore be driven by a line of beaters toward nets set on 1 side of an area surrounded by fladry. We immobilized wolves with 1.2–1.8 ml of a xylazine–ketamine mixture (Okarma et al. 1998) and fitted them with radiocollars. The radiocollars of 5 wolves were equipped with activity sensors. The other transmitters were without activity sensors. We estimated the approximate age of wolves to range between 5 months and 9 years during the period of radiotracking, based on the date of capture, body mass, and tooth wear (Okarma et al. 1998).

During 24-h radiotracking sessions of usually 6 days (range 1–9 days), we noted activity and location of a radiocollared wolf continuously every 30 min (March 1994 to December 1996) or every 15 min (December 1996 to September 1999). We obtained locations of a wolf by triangulation from forest roads. We determined position of the wolf from at least 2 bearings taken from different places at intervals of no more than 5 min. The number of locations of 11 radiotracked wolves (9 females, 2 males) ranged from 557 to 8,336 locations/wolf during 3–42 months of radiotracking (total of 40,305 radiolocations).

From March 1994 to August 1997, we mapped locations of wolves using a grid of 267 by 267 m with a mean radiolocation error of 291 m (95% confidence interval (CI): 244–337 m). From September 1997 to September 1999, we estimated positions of wolves to the nearest 10 m, which reduced mean radiotracking error to

194 m (95% CI: 157–231 m). Daily patterns of mean distance traveled by wolves were not affected by the different levels of mapping precision (Theuerkauf and Jędrzejewski 2002). We calculated distances traveled by wolves as the straight-line distance between 2 consecutive locations. Because the sum of straight-line distances between radiolocations depends on interval length, we corrected straight-line distances obtained with an interval of 30 min by the factor 1.16 provided by Theuerkauf and Jędrzejewski (2002), which made the results comparable with those obtained with 15-min intervals.

We used 3 methods to determine whether a wolf was active or not during radiolocation. We considered wolves active if intensity of the signal was uneven or signal pulses were missed during 1 min, activity sensors indicated vertical movements of the wolf's head, or if the wolf had changed its location since the last radiolocation. We calculated mean time active by a wolf by assigning a value of 1 when the wolf was active (estimated by changes in signal strength) and changed its location, a value of 0 when the wolf was not active and did not change location, or a value of 0.5 when the wolf was active but did not change location or the wolf was not detected to be active during monitoring but changed its location. This provided an accurate estimate of wolf activity and did not require wolves to have radiocollars with activity sensors (Theuerkauf and Jędrzejewski 2002).

We calculated duration of activity bouts with uninterrupted series of 15-min intervals for which we had data on activity sensors, estimated activity, and change of location (2,607 bouts during 2,334 h radiotracking of 5 wolves). We defined length of an active (or inactive) bout as an uninterrupted block of radiolocations during which the animal was active (or inactive) and that was preceded and followed by an interval in which the wolf was inactive (or active). Short activity changes between 2 radiolocations (i.e., rising up for a moment while resting) were not detected with this method unless they happened to occur during the radiolocation.

Data on animal activity gathered by 24 h radiotracking are often not temporally independent (Salvatori et al. 1999). Temporal independence can be obtained by analyzing radiotracking data in time series (Doncaster and Macdonald 1997) or by assessing interval of independence (Salvatori et al. 1999). We did not use time series to

analyze our data because we were not able to follow wolves without short breaks during which we lost contact. Time intervals that ensure temporal independence are often large, which can lead to an important underestimate of home range size and movements of radiotracked animals (Rooney et al. 1998). We therefore decided not to reduce our radiotracking data to temporally independent locations, which would have resulted in a lower accuracy of results, but instead to eliminate autocorrelation among consecutive radiolocations by calculating 1 value for each wolf. Accordingly, we used the variation among wolves and not among radiolocation data for statistical testing.

For 15% of the time during which we followed the 4 wolf packs, we radiotracked 2 wolves in a pack simultaneously instead of 1 wolf. Activity and movement of the radiotracked wolves of a pack could therefore have been partly autocorrelated. However, wolf packs are not fixed units, and wolves show significant variation in daily activity patterns among individuals in a pack at denning and rendezvous sites (Ballard et al. 1991; Harrington and Mech 1982). In our study, we noted both activity and location of radiotracked wolves separately because wolves often did not show the same behavior at the same time, and packs regularly separated. Nonetheless, to test whether activity patterns of wolves in our study area were more often correlated within than among packs, we calculated correlation coefficients among the 11 radiotracked wolves (55 comparisons). The daily activity patterns were not more often significantly correlated (1-sided Fisher's exact test, $P = 0.448$), and the correlation coefficients were not higher among wolves of the same pack than among wolves of different packs (t -test, $t = 1.14$, $d.f. = 53$, $P = 0.260$). We therefore decided to use the individual wolf rather than the wolf pack as the sample unit. Otis and White (1999) also recommend using individual animals as sample units for studies on resource selection.

We defined dawn and dusk as beginning 1 h before and ending 1 h after sunrise or sunset. Moonlit night hours were the 5 lightest hours of the night in the week around the full moon, whereas dark nights began 1 h after sunset and lasted until 1 h before sunrise (excluding moonlit night hours). We defined the denning period as the time during which breeding females stayed mostly at the den site (from 2 weeks be-

fore a birth until 6 weeks after the birth) and the postdenning period as the time when wolves had left the den site but still met at rendezvous sites (from 6 weeks until 5 months after the birth).

Prey of wolves and activity of humans.—From 1997 to 1999, we made an effort to find the remains of all prey killed during continuous radiotracking sessions. We tracked wolf trails in snow to find prey remains or, if there was insufficient snow cover, organized a search party that included a dog whenever possible. If we found the place where wolves had killed their prey, we defined the time at which wolves killed the prey as the moment when they were 1st radiolocated at this point. Although we think that we found most prey when conditions were favorable (snow cover), we probably missed some prey remains in summer, especially during periods when wolves also take small prey such as calves of deer or young wild boar. We therefore did not compare differences in the time wolves killed prey among seasons.

To document the daily pattern of human activity in the study area, we observed vehicular and foot traffic either visually or with a magnetic count card at 39 counting points on roads in the forest from 1997 to 1999. During visual counts, which lasted for units of 2–24 h (total of 569 h), volunteers counted people and vehicles that passed a given counting point. In addition, a magnetic traffic counter card (NC-30, Nu-Metrics, Uniontown, Pennsylvania) placed in forest roads recorded number of passing vehicles for continuous periods of 1 week (total of 5,712 h). We checked reliability of the card during 150 h of direct observations, and it appeared that the card had registered 144 vehicles when 142 vehicles had actually passed. We therefore considered that the card recorded the number of vehicles precisely enough and pooled these data with those gathered visually (together 1,440 h for winter and 4,841 h for summer). We defined each counting hour as an hour with or without human presence, according to whether or not a human or vehicle had passed the observation point during that hour. We used this measure of human presence as an expression of human activity.

If human activity modified the activity pattern of wolves, wolves in regions with higher human activity should reduce their activity and movement during the time of human presence compared with wolves in regions with lower human

TABLE 1.—Activity of wolves during different parts of the day in the Białowieża Forest (Poland), 1994–1999, as shown by time active, time moving, distance traveled ($n = 11$ wolves), and duration of activity ($n = 5$ wolves with activity sensors).

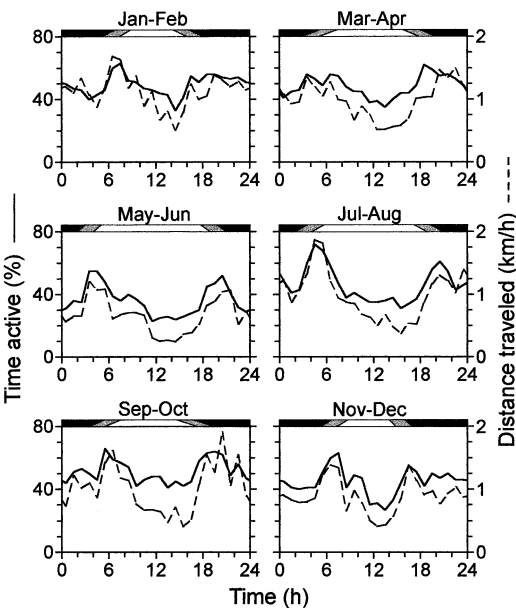
Variable	Whole day (24 h)		Daylight (10 h)		Dawn and dusk (4 h)		Night (10 h)	
	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE	\bar{X}	SE
Time active (%)	45.2	0.9	39.2	2.6	50.8	1.6	48.9	1.5
Time active (h)	10.8	0.2	3.9	0.3	2.0	0.6	4.9	0.1
Time moving (%)	35.9	1.6	30.7	2.4	40.6	2.1	39.2	1.8
Time moving (h)	8.6	0.4	3.1	0.2	1.6	0.1	3.9	0.2
Distance traveled (km/h)	0.92	0.05	0.67	0.07	1.06	0.09	1.10	0.06
Length of active bout (h)	0.76	0.05	0.68	0.06	0.93	0.12	0.81	0.04
Length of inactive bout (h)	1.02	0.07	1.05	0.08	0.75	0.09	1.06	0.11

activity. We therefore compared mean activity and movement of wolf packs during the time of highest human activity to assess effect of humans on activity patterns of wolves. We did not compare human and wolf activity patterns directly because a mere correlation would not prove an effect of humans on wolf activity. Data are presented as mean \pm SE.

RESULTS

General activity patterns of wolves and humans.—Wolves were active 45% of the day on average, but bouts of activity and inactivity were relatively short (Table 1). Most active and inactive bouts lasted only 15 min (46% and 37% of bouts, respectively) or 30 min (18% and 16%, respectively), whereas only 19% of active and 30% of inactive bouts were longer than 1 h. The longest activity bout lasted 7 h and the longest bout of inactivity 9.5 h. Activity of wolves was highest at dawn and dusk, which also coincided with the longest activity bouts (Table 1). Activity bouts decreased in length (linear regression, 0.03 h/year) with increasing age of wolves ($r^2 = 0.649$, $d.f. = 7$, $P = 0.009$) but length of inactive bouts ($r^2 = 0.050$, $d.f. = 7$, $P = 0.562$), time active ($r^2 = 0.002$, $d.f. = 25$, $P = 0.847$), or distance traveled ($r^2 = 0.002$, $d.f. = 25$, $P = 0.820$) did not. In all months, wolves in the Białowieża Forest were active throughout the day but with peaks at dawn and dusk and troughs in the middle of the day and middle of the night (Fig. 1). Peaks of wolf activity followed seasonal changes in time of sunrise and sunset (Fig. 2).

FIG. 1.—Daily patterns of mean time active and distance traveled by 11 wolves for periods of 2 months in the Białowieża Forest (Poland), 1994–1999. Bars indicate length and variation of night (black), dawn and dusk (gray), and day (white) during the 2-month periods.



Human activity was lowest both in intensity and length in the home range of the National Park pack, especially in winter (Fig. 3). However, during the main period

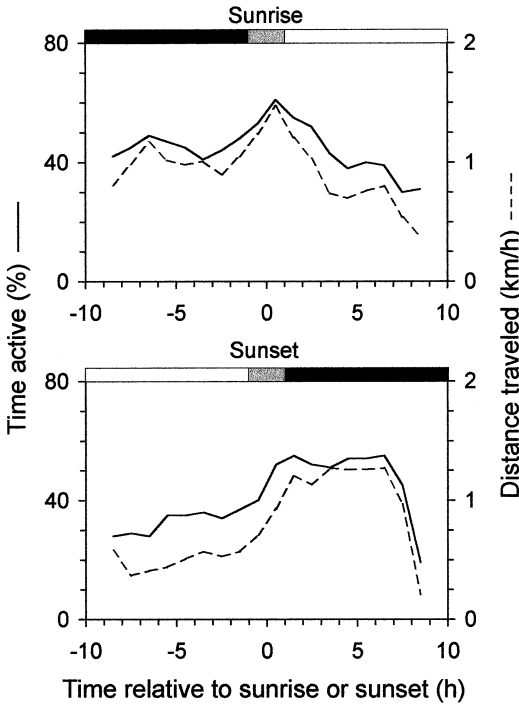


FIG. 2.—Patterns of mean time active and distance traveled by 11 wolves in relation to sunrise and sunset in the Białowieża Forest (Poland), 1994–1999. Bars indicate night (black), dawn and dusk (gray), and day (white).

of human activity (0700–1700 h), distances traveled by wolves of the National Park pack were not greater than those traveled by wolves living in the commercial forest in winter ($t = 0.12$, $d.f. = 9$, $P = 0.906$) or summer ($t = 1.87$, $d.f. = 7$, $P = 0.104$). During the same part of the day, wolves from the National Park pack were not more active than wolves from the commercial forest in winter ($t = 0.95$, $d.f. = 9$, $P = 0.365$) but were even less active in summer ($t = 2.77$, $d.f. = 7$, $P = 0.028$).

Prey.—Wolves killed most of the prey that we found and for which we could estimate time of killing ($n = 54$) in the 6 h around sunrise (on average 2.3 ± 0.5 h before sunrise) and in the first 4 h after sunset (on average 2.7 ± 0.6 h after sunset). They killed less often in the night and rarely in the middle of the day (Fig. 4). Compared

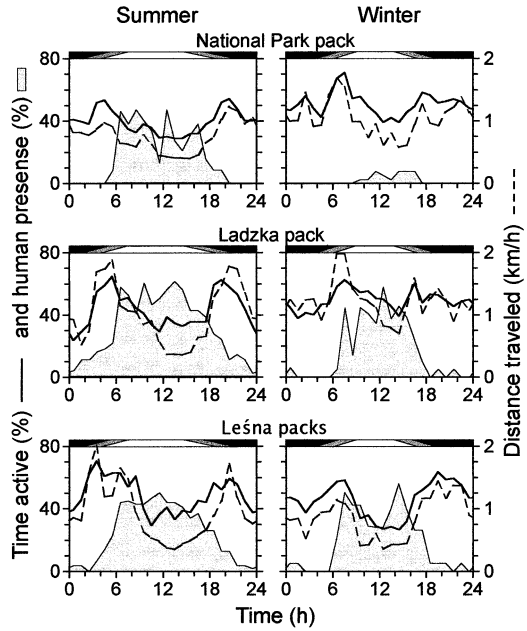


FIG. 3.—Daily patterns of mean time active and distance traveled by wolves compared with patterns of mean time with human presence in home ranges of the National Park pack (4 wolves), Ladzka pack (3 wolves), and Leśna packs (4 wolves) in the Białowieża Forest (Poland), 1994–1999. Bars indicate length and variation of night (black), dawn and dusk (gray), and day (white).

with length of each period of day during days of hunts, wolves killed 1.8 times more than expected at dawn, dusk, and during moonlit nights (1-sided Fisher's exact test, $P = 0.047$) but not significantly more than expected during night ($P = 0.282$). Daylight hours accounted for 33% of the time during days for which we could estimate time of killing, but wolves killed only 9% of their prey during daylight, which was less than expected ($P = 0.002$).

Wolves were active and moved 1.7 ± 0.2 h before they made a kill. Accordingly, hourly activity and distance traveled by wolves were highest during the 2 h before a kill (Fig. 5). Distance traveled dropped immediately after wolves made a kill, but wolves remained mostly active and moved short distances in the hour after a kill. We

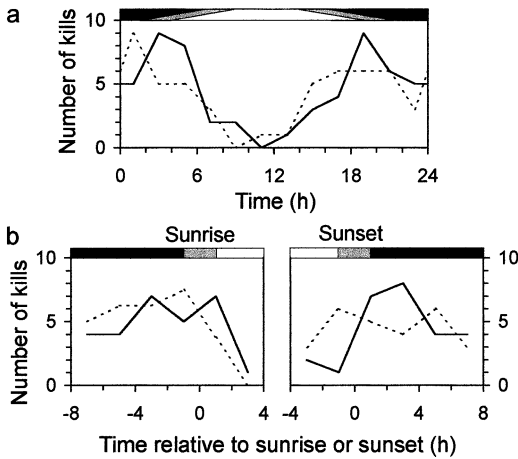


FIG. 4.—Temporal distribution of 54 wolf kills in the Białowieża Forest (Poland), 1994–1999, shown as a) time of day and b) time relative to sunrise and sunset. Continuous lines indicate number of prey killed in 2-h periods, broken lines start of hunting, and bars length and variation of night (black), dawn and dusk (gray), and day (white).

compared activity and movement of wolves the day before a kill with the day after for 2 parts of the day. From evening to morning (3 h before sunset to 3 h after sunrise), wolves were less active ($45.9 \pm 2.1\%$) and traveled shorter distances (0.79 ± 0.06 km/h) the day after a kill compared with their activity ($58.1 \pm 2.5\%$) and distance traveled (1.37 ± 0.13 km/h) the day before the kill (t -test for paired samples, $t = 4.53$, $d.f. = 9$, $P = 0.001$ for activity; $t = 4.20$, $d.f. = 9$, $P = 0.002$ for distance traveled). However, in the middle of the day (3 h after sunrise to 3 h before sunset), wolves did not reduce their activity ($49.4 \pm 7.2\%$ before and $44.2 \pm 3.2\%$ after a kill, $t = 0.69$, $d.f. = 8$, $P = 0.507$) or movement (0.84 ± 0.16 km/h before and 0.85 ± 0.13 km/h after a kill, $t = 0.06$, $d.f. = 8$, $P = 0.950$). Length of active ($t = 1.15$, $d.f. = 3$, $P = 0.241$) and inactive bouts ($t = 0.79$, $d.f. = 3$, $P = 0.487$) did not differ between the days before and after a kill.

Breeding season.—Wolves were least active and mobile during the period of raising

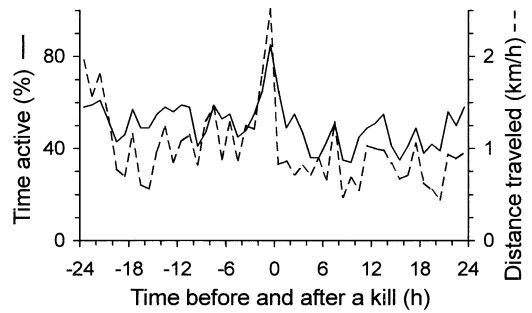


FIG. 5.—Mean time active and distance traveled by 10 wolves 24 h before and after time of 54 kills in the Białowieża Forest (Poland), 1994–1999.

young (April–July). Activity and movement were highest in August and in February and March during the mating season (Fig. 6). Breeding females reduced their activity and movement at night during the period of denning compared with nonbreeding females but not from dawn to dusk (Table 2). The 1 adult male that we radiotracked during the denning period was no more active ($t = 0.48$, $d.f. = 4$, $P = 0.655$) but traveled longer distances (1.04 km/h, $t = 6.41$, $d.f. = 4$, $P = 0.003$) than did the breeding females. Breeding females stayed near the den $67 \pm 4\%$ of the time during the 8-week-long denning period ($37 \pm 18\%$ of time the 2 weeks before birth; $86 \pm 3\%$ during the first 2 weeks after birth; $73 \pm 6\%$ during 3rd and 4th week after birth; $32 \pm 10\%$ during 5th and 6th week after birth).

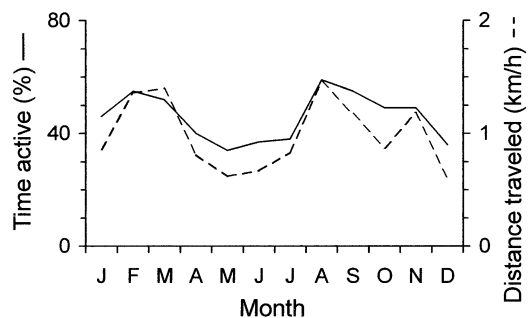


FIG. 6.—Monthly means of time active and distance traveled by 11 wolves in the Białowieża Forest (Poland), 1994–1999.

TABLE 2.—Time active and distance traveled by breeding female wolves compared with nonbreeding females in the Białowieża Forest (Poland), 1994–1999, during the denning and postdenning periods, at night and from dawn to dusk (including the day). Mean time active and distance traveled by breeding ($n = 5$) and nonbreeding females ($n = 2$) were compared by a t -test ($d.f. = 5$).

Variable	Denning period				Postdenning period			
	Night		Dawn to dusk		Night		Dawn to dusk	
	\bar{X}	<i>SE</i>	\bar{X}	<i>SE</i>	\bar{X}	<i>SE</i>	\bar{X}	<i>SE</i>
Time active (%)								
Breeding	37.5	4.0	36.0	3.0	46.8	2.9	43.9	4.7
Nonbreeding	72.1	11.2	34.1	9.0	40.5	12.2	38.7	4.7
<i>P</i>	0.012		0.788		0.467		0.553	
Distance (km/h)								
Breeding	0.77	0.37	0.55	0.03	1.05	0.14	0.83	0.08
Nonbreeding	1.18	0.12	0.50	0.22	0.83	0.21	0.49	0.01
<i>P</i>	0.006		0.854		0.441		0.011	

Breeding females were the least active ($28.7 \pm 1.5\%$) and mobile (0.42 ± 0.10 km/h) during the first 2 weeks after birth.

In the postdenning period, time active and distances traveled by breeding females increased compared with those of nonbreeding females (Table 2). From dawn to dusk, breeding females moved even more than did nonbreeding females (Table 2). In the postdenning period, activity ($t = 0.61$, $d.f. = 4$, $P = 0.573$) and distance traveled ($t = 1.68$, $d.f. = 4$, $P = 0.168$) by breeding females were not significantly higher than those of the male. During the rest of the year, activity and distance traveled by breeding females did not differ from those of nonbreeding females ($t = 0.25$, $d.f. = 9$, $P = 0.804$ for activity; $t = 1.15$, $d.f. = 9$, $P = 0.278$ for movement) or males ($t = 0.53$, $d.f. = 5$, $P = 0.619$ for activity; $t = 0.78$, $d.f. = 5$, $P = 0.472$ for movement).

Weather.—Wolves reduced their mean activity from $44.1 \pm 1.4\%$ on days with no or light rain (≤ 10 mm/day) to $32.6 \pm 3.8\%$ on days with >10 mm/day (t -test for paired samples, $t = 2.80$, $d.f. = 8$, $P = 0.023$). Simultaneously, they reduced their movement from 0.89 ± 0.05 km/h to 0.55 ± 0.11 km/h ($t = 2.41$, $d.f. = 8$, $P = 0.043$) and length of their activity bouts from 0.79 ± 0.06 h to 0.39 ± 0.06 h ($t = 8.26$, $d.f. =$

2 , $P = 0.014$); wolves increased length of inactive bouts from 1.09 ± 0.09 h to 1.51 ± 0.06 h ($t = 4.59$, $d.f. = 2$, $P = 0.044$). In contrast, activity ($t = 0.00$, $d.f. = 10$, $P = 0.998$) and distance traveled ($t = 0.81$, $d.f. = 10$, $P = 0.437$) by wolves were not different on days with and without snowfall. However, wolves decreased time active by 0.6% and distance traveled by 0.02 km/h for every centimeter of increasing snow depth (linear regression, both $P < 0.001$) for snow depths of 1–63 cm.

We tested the influence of extreme weather conditions (high and low temperatures, heavy rainfall, heavy snowfall, and deep snow) on daily patterns of wolf activity, but the animals only significantly modified their activity patterns on days when mean daily temperatures were $\geq 20^\circ\text{C}$. On such warm days, wolves reduced their movement from that on cooler summer days ($10\text{--}19^\circ\text{C}$ from May to August) during the evening (1800–2400 h) from 1.15 ± 0.19 km/h to 0.57 ± 0.12 km/h (t -test for paired samples, $t = 2.76$, $d.f. = 7$, $P = 0.028$). In the morning (0400–0800 h), differences in movement rates (1.09 ± 0.11 km/h on cooler days, 1.33 ± 0.21 km/h on warm days) were not significant (t -test for paired samples, $t = 0.84$, $d.f. = 6$, $P = 0.432$).

DISCUSSION

Wolves in Europe had to adapt to >1,000 years of heavy persecution by humans, whereas they were hunted intensively during shorter periods in many areas of North America. If wolves adapted their behavior to avoid direct contact with humans, they might have become less active during the day. Indeed, wolves studied in mountainous agricultural regions of Spain and Italy with human densities of 20–30 inhabitants/km² hardly moved during daylight (Ciucci et al. 1997; Vilà et al. 1995). In Alaska, where human density is low, wolves moved during 50% (Peterson et al. 1984) of the daylight. In forests of Minnesota, where human density in the wolf range was 1.5 inhabitants/km² (Mladenoff et al. 1995), wolves moved during 28% of the daylight in winter (Mech 1992). In the Białowieża Forest, persecution does not seem to have caused wolves to reduce their activity and movement in daylight, perhaps because our study area is mostly covered by forest. In Italy and Spain, where <40% of the area in the wolves' home ranges was forested (Ciucci et al. 1997; Vilà et al. 1995), there may not have been enough cover for daylight movement. Human activity therefore does not seem to significantly influence temporal activity patterns of wolves in regions where they have the opportunity to avoid direct contact with humans. Our hypothesis that wolves would adapt their activity patterns to human activity was insufficient to explain behavior of wolves in our study area. We suggest that humans and wolves are spatio-temporally separated; i.e., wolves do not change their temporal activity patterns under human influence, but they avoid being in the same place at the same time as humans. In Romania, a wolf pack regularly visited a dump site at night in a town of 300,000 inhabitants but remained in the forest in the day (C. Promberger et al., in litt.).

There may have been other reasons why wolves reduced their activity and movement during the day. On warm days, wolves

in our study area moved less in the evening but more in the morning, when ambient temperatures were usually lowest. Mech (1970) reported that wolves quickly get overheated in summer and usually reduce their daylight movement. Temperature may therefore have partly caused the nocturnal activity patterns of the wolf radiotracked in Italy from June to November by Ciucci et al. (1997). Human influences, however, can act indirectly through prey. Ungulates under human hunting pressure often reduce their daytime activity (Briedermann 1971; Jepsen 1989), which could drive wolves to be more nocturnal and hunt more at night than they would in areas without human activity. Although it is possible that human activity caused the nocturnality of wolves in Spain and Italy, the influence of humans may be confounded with factors such as temperature and prey activity. It is therefore difficult to clearly determine the effect of human activity on the temporal patterns of wolf activity.

In our study, the number of prey taken by wolves was highest when light was dim, i.e., at dawn, dusk, and on moonlit nights. Vision of canids is best adapted to daylight and the phase between day and night (Kavanau and Ramos 1975; Roper and Ryon 1977). Wolves that are kept in enclosures and do not have to hunt are almost exclusively active during daylight (Kreeger et al. 1996). We therefore think that the crepuscular and nocturnal activity of wolves is probably caused by the need to hunt. We suggest that dim light provides the best hunting chances for wolves and that prey are more readily available during this period. Red deer (*C. elaphus*) in the Białowieża Forest are active throughout the day with a tendency to activity peaks at dawn and dusk (E. Kaniowska and B. Jędrzejewska, in litt.).

Peaks in activity and, especially, movement of wolves were closely related to the hunting pattern, and after a successful hunt, wolves reduced their activity. However, wolves did not decrease their activity and

movement in the middle of the day after a kill in comparison with the day before a kill. This time may be used to eat, socialize, play, or keep diurnal scavengers such as ravens away from their kill.

During the period of reproduction, wolves (especially breeding females) spend much of their time at denning and rendezvous sites (Ballard et al. 1991; Harrington and Mech 1982). Because other wolves from the pack usually assure the feeding of breeding females during this time (Mech 1999; Mech et al. 1999; Murie 1944), females do not have to maintain an activity pattern based on hunting. In our study, breeding females reduced their activity and movement at night during the denning period, which indicated that other wolves may have provided them with food. If other wolves cannot supply the breeding female with enough food, her activity pattern should be shaped both by hunting and by the need to attend pups. In Spain, such a situation caused breeding females to leave the den mainly in the day, whereas they were mainly active at night in other periods of the year (Vilà et al. 1995). Vilà et al. (1995) assumed that in Spain, where packs are usually small, it would be the safest for females to leave the den for hunting during the day when sunlight would help keep the unattended pups warm and potential predators are less active. Activity patterns of breeding females therefore seem to depend greatly on the ability of other pack members to provide them with food.

We conclude that daily activity patterns of wolves in our study area were mainly shaped by their pattern of hunting prey. Human activity appeared to have no significant influence on temporal activity patterns of wolves. The influence of humans may be indirect if hunters of ungulates modify the activity patterns of the wolves' prey. Rearing of young had a temporary influence on activity patterns and length of time active. Weather markedly modified behavior of wolves only under extreme situations such as high temperature and heavy rain. Al-

though information on daily activity patterns of wolves has been gathered (Ballard et al. 1991; Ciucci et al. 1997; Fancy and Ballard 1995; Harrington and Mech 1982; Kolenosky and Johnston 1967; Vilà et al. 1995; this study), it is still not possible to completely explain activity patterns of wolves in different sites.

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