

# Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Białowieża Primeval Forest in Poland

Włodzimierz Jędrzejewski, Krzysztof Schmidt, Jörn Theuerkauf,  
Bogumila Jędrzejewska, and Henryk Okarma

**Abstract:** Wolves (*Canis lupus*) (9 females and 2 males from 4 packs), were radio-tracked in a large Polish woodland in Białowieża Primeval Forest in 1996–1999. Based on 360 days of radio tracking with locations taken at 30- or 15-min intervals, daily movement distances (DMDs) of wolves and their utilization of territories were analyzed. DMDs averaged 22.1 km for females and 27.6 km for males. In reproductive and subadult females, DMDs varied seasonally, with the shortest daily routes in May and the longest in autumn–winter. Little seasonal variation was observed in nonbreeding and unsuccessfully breeding adult females. An adult male covered the longest DMDs in February (mating season). The mean speed of travelling wolves was 2.2 km/h. Wolves' hunting activity affected the length and speed of their movements, both of which were higher before than after a kill was made. With growing abundance of prey, DMDs of wolves became shorter. Snow cover and rainfall had a negligible effect on wolf travel. The mean straight-line distance between consecutive daily locations (SLD) was 4.4 km, i.e., on average, 21% of the actual route covered by wolves. Daily ranges utilized by wolves averaged 21.4 km<sup>2</sup>, or 9% of the whole territory. Variation in SLDs and daily ranges was shaped predominantly by mating, breeding, and pup rearing. The pattern of territory use by wolves differed between seasons. In spring–summer, their movements concentrated around the breeding den and rendezvous sites, and the areas used on consecutive days overlapped extensively. In autumn–winter, wolves moved widely and utilized their territory in a rotational way, returning to the same parts every 6 days, on average. Rotational use is related to intense patrolling and defense of territory, but may also help wolves to avoid behavioral depression of prey availability.

**Résumé :** Des Loups, *Canis lupus* (9 femelles et 2 mâles appartenant à quatre meutes), ont été suivis par radio-télémetrie dans un grand boisé polonais en 1996–1999. Des repérages radio-télémetriques à intervalles de 30 ou 15 min durant 360 jours ont permis d'analyser les distances parcourues chaque jour (DMD) et l'utilisation du territoire par les loups. La distance parcourue quotidiennement a été évaluée à 22,1 km chez les femelles et à 27,6 km chez les mâles. Chez les femelles reproductrices et sub-adultes, la distance DMD varie en fonction de la saison, les itinéraires les plus courts en mai, les plus longs en automne–hiver. Il y a peu de variation d'une saison à l'autre chez les femelles non reproductrices ou chez celles qui ont raté leur reproduction. Un des mâles adultes a fait ses plus longs parcours en février (saison des accouplements). La vitesse moyenne de déplacement des loups est de 2,2 km/h. L'activité de chasse affecte la longueur et la vitesse des déplacements, plus élevées avant qu'après la prise de la proie. Lorsque l'abondance des proies augmente, la distance DMD devient plus courte. La couverture de neige et l'abondance des précipitations ont peu d'influence sur les déplacements des loups. La distance quotidienne moyenne parcourue en ligne droite entre deux localités (SLD) a été estimée à 4,4 km, i.e., en moyenne 21 % de la distance totale parcourue par les loups. Les loups utilisent en moyenne 21,4 km<sup>2</sup> de territoire chaque jour, i.e., 9 % de leur territoire total. La variation des valeurs de SLD et de territoire chaque jour est surtout fonction des accouplements, de la période de reproduction et de l'élevage des petits. L'utilisation du territoire varie d'une saison à l'autre. Au cours de la période printemps–été, les mouvements se concentrent autour des terriers de reproduction et des points de rendez-vous et les zones utilisées au cours de jours consécutifs se recoupent largement. En automne–hiver, les loups se déplacent sur de grandes distances et utilisent leur territoire en faisant une rotation, retournant aux mêmes endroits tous les 6 jours en moyenne. La rotation est reliée au patrouillage et à la défense intensifs du territoire, mais aide probablement aussi les loups à éviter la surutilisation des proies.

[Traduit par la Rédaction]

Received February 23, 2001. Accepted August 21, 2001. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on November 9, 2001.

W. Jędrzejewski,<sup>1</sup> K. Schmidt, B. Jędrzejewska, and H. Okarma.<sup>2</sup> Mammal Research Institute, Polish Academy of Sciences, PL-17-230 Białowieża, Poland.

J. Theuerkauf. Mammal Research Institute, Polish Academy of Sciences, PL-17-230 Białowieża, Poland, and Wildlife Biology and Management Unit, Department of Ecosystem and Landscape Management, Munich University of Technical Sciences, D-85354 Freising, Germany.

<sup>1</sup>Corresponding author (e-mail: [wlodek@bison.zbs.bialowieza.pl](mailto:wlodek@bison.zbs.bialowieza.pl)).

<sup>2</sup>Present address: Institute of Nature Conservation, Polish Academy of Sciences, ulica Mickiewicza 33, PL-31–120 Kraków, Poland.

## Introduction

Although wolves (*Canis lupus*) are among the most thoroughly studied carnivores (Mech 1970; Harrington and Paquet 1982; Carbyn et al. 1995), information on their mobility, factors affecting its variation, and their pattern of territory utilization is scanty. This is due to the fact that the main method applied in ecological studies of wolves has been aircraft radio tracking, with locations recorded at intervals of a few days to several weeks and always during daylight (Fritts and Mech 1981; Messier 1985a; Potvin 1987). Details of wolves' daily movement routes and distances can only be investigated by means of continuous satellite radio tracking, following radio-collared wolves on the ground and recording locations as frequently as possible, or by using global positioning system (GPS) collars. While the first method has been developed recently and its application is still limited (Ballard et al. 1995), the second requires much human labor and can only be used in regions with good accessibility (a high density of roads and paths). Snow tracking both from aircraft and on the ground, the earliest and a still used method of following wolves, has an obvious deficiency: it can only be used at northern latitudes and during winter, therefore the seasonal variation related to the denning and pup-rearing period remains unknown. The third method (GPS collars) has only recently become available.

Our study was conducted in a large woodland in central eastern Europe, by year-round ground tracking of radio-collared wolves. Wolf density in the study area was 2–3 individuals/100 km<sup>2</sup> (Jędrzejewska et al. 1996; Okarma et al. 1998). Our objectives were to investigate (i) the daily movement distances (DMDs) covered by wolves and their variation in relation to seasonal phenomena of wolf biology as well as to ambient factors; (ii) the speed of travelling wolves; and (iii) the pattern of territory utilization by wolves, as shown by the sizes and overlaps of daily ranges in relation to the whole territory.

## Study area

The study was conducted in the Polish part of Białowieża Primeval Forest (BPF; 595 km<sup>2</sup>, 52°45'N, 24°E). BPF covers a total of 1450 km<sup>2</sup> and is located on the Poland–Belarus border. It is the best preserved woodland of its size in temperate Europe. The Polish part of BPF consists of managed (harvested and replanted) stands (495 km<sup>2</sup>) and a protected part (Białowieża National Park, covering 100 km<sup>2</sup>). Tree stands are composed of spruce (*Picea abies*), pine (*Pinus silvestris*), oak (*Quercus robur*), hornbeam (*Carpinus betulus*), black alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), and birches (*Betula verrucosa* and *B. pubescens*), with admixtures of several other tree species. The terrain is flat and the elevation 134–186 m asl. The only open areas within the woodland are marshes of sedge (*Carex* sp.) and reed (*Phragmites* sp.) in narrow river valleys (0.1–1 km wide) and several glades with small villages. There are five paved roads with a total length of about 50 km in the Polish part of BPF. During the study (1994–1999) the mean temperature was –2.9°C in January and 19.7°C in July. Annual precipitation averaged 611 mm and snow cover (maximal depths in various winters 10–63 cm) persisted for an average of 87 days per year. BPF

harbors five species of ungulates. The most numerous are red deer (*Cervus elaphus*) and wild boar (*Sus scrofa*); less common are roe deer (*Capreolus capreolus*), European bison (*Bison bonasus*), and moose (*Alces alces*) (Jędrzejewska et al. 1997). Wolves have been protected in the Polish part of BPF since 1989, but poaching does occur. More information on BPF was given by Jędrzejewska and Jędrzejewski (1998).

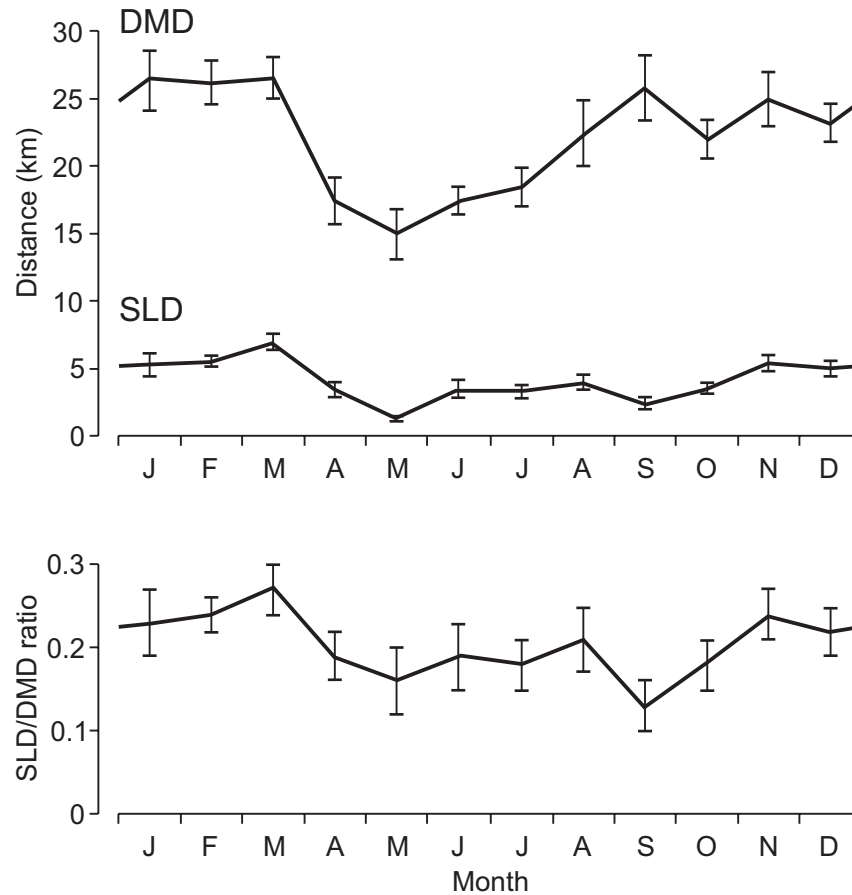
## Materials and methods

In 1994–1999, 12 wolves belonging to 4 packs were livetrapped and radio-collared. Data collected on 11 wolves (9 females and 2 males) were numerous enough for analysis. The pack in Białowieża National Park (the BNP pack) was formed by 4–7 wolves (numbers in midwinter in various years); 4 individuals were radio-collared. The Leśna I pack consisted of 4–7 wolves; 4 individuals were radio-collared but data on daily movements were gathered from 3 wolves. The Ładzka pack was formed by 3–6 wolves, of which 3 were radio-collared. The fourth studied pack, Leśna II, included 2–3 wolves of which 1 was radio-tracked. Wolves were captured in nets (Okarma and Jędrzejewski 1997) or with foot-snare traps (Aldrich foot-snare traps for black bears, modified by the authors). Foot-snare traps were equipped with radio-alarm systems (A. Wagener, Cologne, Germany), which allowed us to release the animal within 1–2 h after capture. Wolves were immobilized with 1.2–1.8 mL of a xylazine–ketamine mixture (583 mg of Bayer's Rompun dissolved in 4 mL of Parke–Davis Ketavet, 100 mg/mL) and fitted with radio collars (Telonics Inc., AVM Instrument Company, Telemetry Systems, Advanced Telemetry Systems). Five radio collars were equipped with head position activity sensors, which helped us to determine whether wolves were feeding, resting, or travelling. Radio-collared wolves were located by triangulation on 2–5 days per week by following forest roads with a vehicle or bicycle. In addition to daily locations, sessions of 2–9 (usually 4–6) days of continuous radio tracking were conducted. From March 1994 to August 1997, we mapped locations of wolves on forest maps with a 533 × 533 m square grid. Depending on the estimated location of wolves, their position was mapped as in the center of a square, in the middle of a side of two adjacent squares, or in the corner between four adjacent squares. From September 1997 to September 1999, we noted locations in the field using a metric system and measured the position of a wolf to the nearest 10 m.

During the continuous sessions of radio tracking, locations were taken at 30-min intervals (March 1994 – December 1996) or 15-min intervals (January 1997 – September 1999). Observers followed the wolves from a mean distance of 0.94 km (SD = 0.58 km) and the distance between wolf and observer had no effect on wolf activity (J. Theuerkauf and W. Jędrzejewski, in preparation). Since wolves moved more during the dark part of the day, all parameters of daily activities presented in this paper were calculated for the period 12:00–12:00 (i.e., from noon on day *n* to noon on day *n* + 1). During a total of 584 days of continuous radio tracking, contact with wolves was sometimes lost for some hours. In such cases, we calculated the straight-line distance between the last location before contact with a wolf was lost and the first location after it was reestablished. We plotted DMD against the duration of daily tracking and, by applying Lowess methods (Cleveland 1979), found that DMD increased with duration of daily tracking, levelled off at 19 h, and did not increase further. Thus, we included in the analysis all days when continuous radio tracking covered 19–24 h (*n* = 360 days). The mean duration of a day's tracking for the whole sample was 23.1 h.

The following four parameters of wolf travel were calculated: (1) DMD (km/day); the sum of straight-line distances between

**Fig. 1.** Month-to-month variation (mean  $\pm$  SE) in daily movement distances (DMDs), straight-line distances between consecutive daily locations (SLDs), and SLD/DMD ratios for radio-collared wolves (*Canis lupus*) in Białowieża Primeval Forest (BPF) in eastern Poland from January to December. Data for all wolves and years are pooled. The sample size for each month ranged from 16 to 69 days. Seasonal (between-month) changes are statistically significant for DMDs (ANOVA,  $F_{[11,348]} = 4.19$ ,  $P < 0.0005$ ) and SLDs (Kruskal–Wallis ANOVA,  $H_{[11]} = 71.82$ ,  $P < 0.0005$ ).



consecutive locations taken at 30- or 15-min intervals during a day of continuous radio-tracking; the distances are minimal because they are based on straight-line distances between points. (2) Straight-line distance between daily locations (SLD; km/d), i.e., between the beginning and end points of daily movement routes of wolves. (3) Daily range (km<sup>2</sup>); a minimum convex polygon embracing the daily movement route of a wolf. (4) Index of intensity of wolf movement,  $I$ , measured as metres of route travelled per day per 1 km<sup>2</sup> of the whole territory, after Goszczyński (1986):  $I = \text{DMD}/T_{\text{year}}$ , where  $T_{\text{year}}$  is the size of a pack's territory estimated for the whole year as minimum convex polygon with 100% of locations.

DMDs, SLDs, daily ranges, and overlaps of daily ranges on consecutive days were calculated with the program Tracker (A. Angerbjörn, Radio Location Systems AB, Huddinge, Sweden). We compared the four parameters of wolf travel calculated on the basis of locations taken at 30- and 15-min intervals and mapped with different levels of precision. To avoid the effect of variation among individual wolves, for this comparison we used the data for 2 adult females (breeding females in their respective packs) that were radio-tracked both before and after 1 January 1997. We found no statistical differences between the two datasets (Mann–Whitney  $U$  test,  $U = 1064.0$ – $1568.5$ ,  $P = 0.06$ – $0.7$ ,  $n_1 = 34$ ,  $n_2 = 81$ ), so we pooled all the data. The influence of hunting activity on wolf DMD and speed of movement was assessed based on 47 days for which the exact time and location of kill were known from continuous

radio tracking, and we found prey remains during the following days, after the wolves had left the kill site.

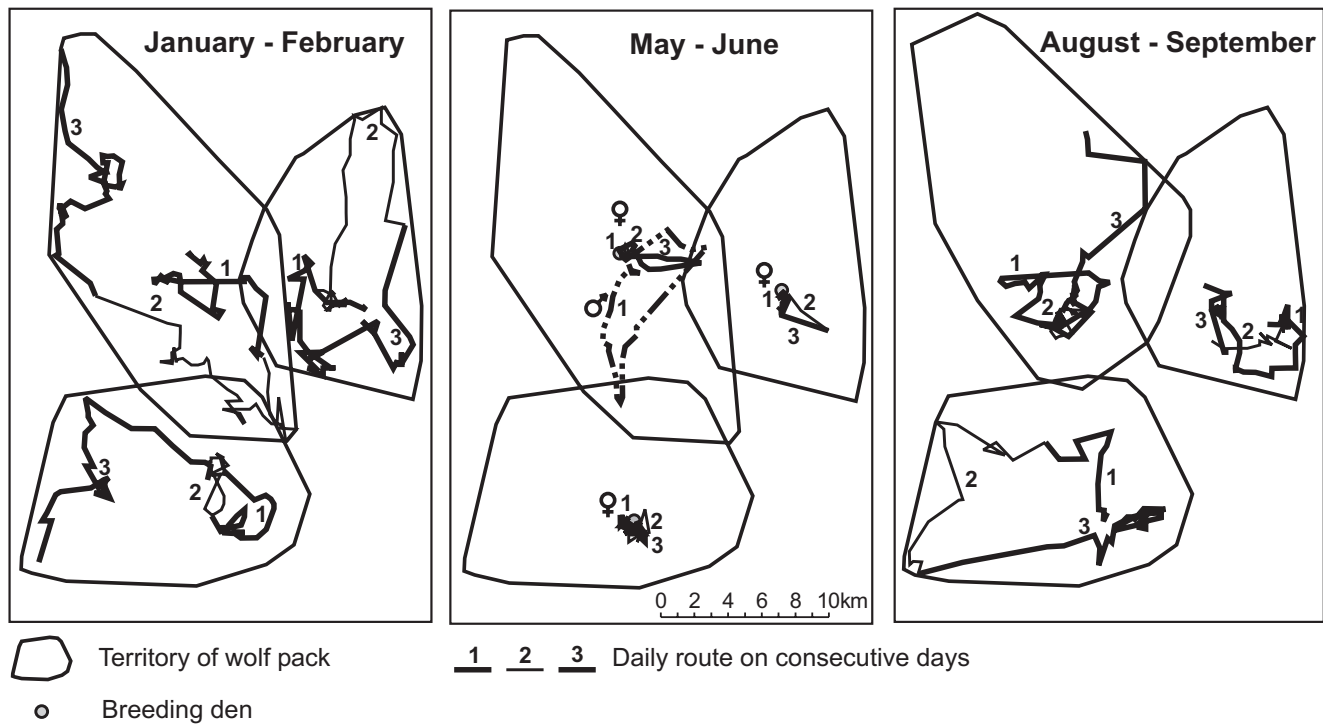
We obtained an index of ungulate abundance by documenting all observations of animals encountered during our fieldwork. Having recorded the time spent in the forest by human observers, we were able to calculate encounter rates with ungulates (the number of animals seen per 1 h spent in the forest by a human observer). In 1996–1999, a total of 4889 ungulates were seen during 8722 h in the forest. Meteorological data (snow depth, rainfall) were obtained from a meteorological station located in the village of Białowieża, which lies in the center of BPF.

## Results

### Factors affecting DMD and speed of wolves

DMDs varied from 0.4 to 64 km and averaged 22.8 km (SE = 0.62 km,  $n = 360$  days). There was clear seasonal variation in wolf travel (Fig. 1). Monthly mean DMDs for all wolves ranged from 26.2 to 26.6 km in January–March to 15 km in May, when pups were very small and stayed in the natal den. DMDs increased again through summer and autumn (Fig. 1). There were manifest differences in wolf travel that were related to sex and age of wolves (Table 1). Very long DMDs (nearly 34 km/day, on average) were typical for

**Fig. 2.** Examples of daily movement routes of wolves from three packs in January–February (mating season), May–June (small pups in the den), and August–September (pups begin to travel with other pack members) in their annual territories.



**Table 1.** Daily movement distances (DMDs; km) of radio-collared wolves (*Canis lupus*) in Białowieża Primeval Forest (BPF) in 1994–1999.

	Young nonbreeding females (5)	Adult breeding females (5)	Adult females with litters lost (2)	Old nonbreeding female (1)	Young nonbreeding male (1)	Adult breeding male (1)
January	—	25.7 ± 4.0	25.9 ± 6.8	—	29.1 ± 2.7	—
February	21.1 ± 12.3	25.4 ± 2.1	23.2 ± 7.3	18.7 ± 5.1	—	33.8 ± 4.1
March	20.7 ± 3.5	27.7 ± 2.0	22.7 ± 1.7	25.4 ± 5.5	—	31.4 ± 4.7
April	—	17.1 ± 2.1	—	—	—	—
May	11.3 ± 3.2	9.8 ± 2.3	—	22.5 ± 1.9	—	25.7 ± 5.4
June	14.2 ± 1.4	18.9 ± 1.7	14.5 ± 3.8	—	—	—
July	16.0 ± 1.7	20.0 ± 2.5	17.2 ± 4.8	—	—	—
August	26.6 ± 3.7	20.2 ± 3.1	—	—	—	—
September	27.3 ± 3.0	29.3 ± 3.8	17.2 ± 2.0	—	—	—
October	22.5 ± 3.9	22.1 ± 3.0	23.5 ± 3.1	—	19.1 ± 3.8	—
November	26.8 ± 5.3	29.8 ± 4.2	18.6 ± 1.7	—	20.4 ± 3.0	—
December	24.6 ± 2.3	22.1 ± 2.2	—	—	—	—
Whole year	20.9 ± 1.2	22.8 ± 0.9	20.8 ± 1.3	—	27.6 ± 1.8	—
Range	0.7–45.4	0.4–64.0	6.6–51.3	—	7.4–59.3	—
No. of days	59	202	57	—	42	—

**Note:** Values are given as the mean ± SE. Monthly samples in various sex and age groups of wolves were obtained during 3–44 days of continuous radio tracking. Numbers in parentheses show the number of wolves studied in each sex and age group (4 females changed their status during the study). Mean estimates for the whole year were calculated for four sex and age groups of wolves (males were pooled and nonbreeding or unsuccessfully breeding adult females were also pooled). A dash denotes a lack of data or that samples were too small to calculate a mean value.

a dominant male in February (mating season). Adult breeding females reduced their travel in May. Interestingly, however, by June–July females were moving, on average, 19–20 km/day (Table 1). Young nonbreeding females often remained at the den with pups. Therefore, their travel in May–July was relatively short and increased in August–

September. An old nonbreeding female and a reproducing male did not reduce their movements in May (Table 1). Examples of wolves' daily movements in various seasons are shown in Fig. 2.

On an annual basis, DMDs differed significantly between the sexes, the mean for females being 22.1 km (SE =

**Table 2.** Straight-line distances between consecutive daily locations (SLD; km) of radio-collared wolves in BPF.

	Young nonbreeding females	Adult breeding females	Adult females with litters lost	Old nonbreeding female	Young nonbreeding male	Adult breeding male
January	—	4.5 ± 0.8	4.5 ± 1.4	—	7.3 ± 2.7	—
February	4.3 ± 1.2	5.7 ± 0.6	4.3 ± 1.9	5.1 ± 2.2	—	6.2 ± 1.3
March	4.8 ± 0.5	6.9 ± 1.1	2.7 ± 1.0	10.1 ± 2.2	—	11.1 ± 3.6
April	—	3.7 ± 0.9	—	—	—	—
May	1.7 ± 1.1	1.0 ± 0.4	—	1.7 ± 1.1	—	1.1 ± 0.4
June	2.3 ± 0.8	3.6 ± 1.1	6.1 ± 3.1	—	—	—
July	2.5 ± 0.7	2.9 ± 0.7	6.8 ± 3.2	—	—	—
August	3.3 ± 0.9	4.4 ± 1.2	—	—	—	—
September	0.6 ± 0.2	2.3 ± 0.4	4.1 ± 1.4	—	—	—
October	3.4 ± 0.9	3.1 ± 0.6	7.4 ± 1.7	—	1.5 ± 0.3	—
November	4.0 ± 1.9	4.9 ± 1.0	4.5 ± 0.4	—	8.1 ± 2.5	—
December	6.9 ± 1.0	3.6 ± 0.9	—	—	—	—
Whole year	3.4 ± 0.4	4.2 ± 0.3	—	4.9 ± 0.5	—	6.2 ± 1.0
Range	0–10.4	0–17.9	—	0.3–15.3	—	0.4–23.3

Note: Values are given as the mean ± SE. For further details see Table 1.

**Table 3.** DMDs of females from the four wolf packs in relation to indices of red deer abundance in their territories.

	Pack or pack territory			
	BNP	Leśna I	Leśna II	Ladzka
Index of deer abundance*	0.506	0.136	0.125	0.101
DMD (km)	19.8 ± 0.9	21.4 ± 1.0	23.5 ± 1.4	27.5 ± 2.2
No. of days of radio tracking	129	90	42	57

Note: DMD values are given as the mean ± SE.

\*Encounter rate with deer by human observers (number of deer seen per hour spent in the forest).

0.6 km) and that for males 27.6 km (SE = 1.8 km) (ANOVA,  $F_{[1,358]} = 8.36, P = 0.004$ ). Also, the age and reproductive status of wolves significantly differentiated their DMDs ( $F_{[3,356]} = 3.505, P = 0.02$ ). Pairwise comparisons among the four groups of wolves (see Table 1) showed that again the most pronounced differences were those between the sexes, i.e., between males and each of the three groups of females (Tukey’s HSD test,  $P = 0.02–0.07$ ), and not among females of various ages and differing in reproductive status ( $P = 0.7–1.0$ ).

SLDs varied from 0 to 23.3 km, with an average of 4.4 km (SE = 0.2 km), i.e., 21% of the actual daily routes covered by wolves. Monthly variation in SLD (Fig. 1) resembled that in DMD, except that SLDs remained short not only in May–June, when pups stayed in the den, but also in summer and early autumn until they attained the full capacity to travel with other pack members. There were some differences, though not statistically significant, in SLD among various sex and age groups of wolves (Kruskal–Wallis ANOVA,  $H_{[3]} = 5.96, P = 0.1$ ). SLDs were shortest in subadult females, longer in breeding females, still longer in nonbreeding or unsuccessfully breeding females, and longest in males (Table 2). On an annual basis, the mean SLD for all females was 4.2 km (SE = 0.2 km) and that for males 6.2 km (SE = 1.0 km); the difference was not significant (Mann–Whitney  $U$  test,  $U = 5667.5, P = 0.1, n_1 = 318, n_2 = 42$ ). The SLD/DMD ratio is an index of tortuosity of a wolf’s daily

route. It can vary from 0, when the wolf returns to the same place at the end of its daily route, to 1, when it moves directionally along a straight line. The SLD/DMD ratios (monthly means) were lower in April–October (0.13–0.21) than in November–March (0.22–0.24; Fig. 1).

Although snow reached a maximum depth of 63 cm during the study, our data on wolves’ movements in winter were collected on days with snow 1–23 cm deep. Within this range, snow hampered wolves’ mobility slightly and not significantly (DMD =  $27.306–0.244 \times$  snow depth;  $R^2 = 0.02, P = 0.2, n = 94$  days). Similarly, rainfall, which varied from 0 to 32 mm/day, had only a weak negative effect on DMD (DMD =  $22.96–0.186 \times$  rainfall;  $R^2 = 0.003, P = 0.3$ ).

Significant differences in DMD were recorded among the four wolf packs studied (ANOVA,  $F_{[3,314]} = 6.536, P < 0.0005$ ) (Table 3). For this analysis, data on males were excluded, as males in only one pack were radio-tracked. There was some indication that interpack variation in wolves’ daily movements was related to differences in red deer abundance among territories (Table 3): the BNP pack enjoyed densities of red deer over 5 times higher and covered shorter DMDs than the Ladzka pack.

The influence of hunting activity and prey consumption on wolf mobility was assessed on the basis of 47 kills for which the time of kill was known. DMD was calculated for 24 h preceding the kill ( $n = 37$ ) and 24 h after the kill ( $n = 43$ ). Wolves usually consumed an ungulate prey item over

**Table 4.** Average minimum speeds of travelling wolves.

	No. of travelling bouts	Speed (km/h)	
		Mean $\pm$ SE	Range
January–February	150	2.24 $\pm$ 0.09	0.3–4.9
March–April	127	2.24 $\pm$ 0.10	0.7–7.0
May–June	79	2.01 $\pm$ 0.12	0.4–5.0
July–August	115	2.19 $\pm$ 0.14	0.7–5.4
September–October	91	2.18 $\pm$ 0.12	0.4–5.1
November–December	79	2.36 $\pm$ 0.12	0.6–5.9
Whole year	596	2.21 $\pm$ 0.05	0.3–7.0

**Note:** Only bouts of uninterrupted movements were used for calculations.

1–2 days and killed new ones at 2-day intervals (Jędrzejewski et al. 2002b). On the day preceding a kill, DMDs ranged from 5.7 to 54.7 km, the average being 25.5 km (SE = 1.6 km), and were significantly longer than those on the day after a kill was made (mean = 18.9 km, SE = 1.1 km, range = 5.8–33.9 km) (ANOVA,  $F_{[1,78]} = 12.935$ ,  $P = 0.001$ ). On average, wolves reduced their mobility by 26% after making a kill.

The rate of movement approximates the “speed” with which wolves utilize their territories, including actual movements as well as bouts of resting, feeding, and other stationary activities. For BPF wolves, the mean rate of movement was 0.95 km/h, varying from an average of 0.41 km/h for breeding females in May to 1.41 km/h for an adult male in February. The actual speed of wolves was calculated on the basis of bouts of uninterrupted movements. Speeds of travelling wolves ranged from 0.3 to 7 km/h, with an average of 2.2 km/h (Table 4). Mean bimonthly values increased by only 15% from a minimum observed in May–June to a maximum in November–December and seasonal changes were not significant (ANOVA,  $F_{[5,590]} = 0.84$ ,  $P = 0.5$ ). Greater variation was observed when speed was analyzed in relation to prey killing. Within 12 h before killing new prey, the wolves moved significantly faster (mean = 2.5 km/h, SE = 0.23 km/h, range = 0.5–5.9 km/h,  $n = 31$ ) than during the 12 h after they made a kill (mean = 1.0 km/h, SE = 0.19 km/h, range = 0.1–2.3 km/h,  $n = 13$ ) (Mann–Whitney  $U$  test,  $U = 337.0$ ,  $P < 0.0005$ ). Moreover, in 18 out of 31 cases (58%) wolves remained stationary for 12 h after making a kill. If these 18 cases are included in the whole sample, the mean speed of wolves during the 12 h after they made a kill would be 0.5 km/h (SE = 0.12 km/h,  $n = 31$ ).

#### Pattern of territory utilization by wolves

In BPF, wolf-pack territories, estimated for each year as minimum convex polygons with 100% of locations, averaged 232 km<sup>2</sup> (SE = 15 km<sup>2</sup>, range = 154–343 km<sup>2</sup>,  $n = 15$ ). Daily ranges of wolves, calculated as minimum convex polygons enclosing the daily route, varied from 0 to 132.4 km<sup>2</sup>, with an average of 21.4 km<sup>2</sup> (SE = 1.2 km<sup>2</sup>). Examples of daily ranges utilized by wolves on consecutive days in spring–summer and autumn–winter are shown in Fig. 3. For all wolves, daily range was smallest in May (9.3 km<sup>2</sup>, on average) and largest in January–February (29.5–30.4 km<sup>2</sup>) and seasonal changes in daily range were statistically significant

(Kruskal–Wallis ANOVA,  $H_{[11]} = 48.26$ ,  $P < 0.0005$ ) (Fig. 4). Again, there were clear sex- and age-related differences in daily range, which were manifested especially during the mating (February) and pup-rearing seasons (from May onwards) (Table 5). In May–June, daily ranges of breeding and subadult females were markedly smaller than those of males and nonbreeding adult females.

When data were pooled for the whole year, the mean daily range for all females was 19.9 km<sup>2</sup> (SE = 1.2 km<sup>2</sup>) and that for males 31.0 km<sup>2</sup> (SE = 4.3 km<sup>2</sup>), the difference being statistically significant (Mann–Whitney  $U$  test,  $U = 4870.5$ ,  $P = 0.004$ ,  $n_1 = 318$ ,  $n_2 = 42$ ). In pairwise comparisons of the four classes of wolves, which varied in sex, age, and reproductive status (data were pooled for all months; see Table 5), the largest differences were between males and subadult females ( $U = 734.0$ ,  $P = 0.001$ ) and between males and breeding females ( $U = 5288.5$ ,  $P = 0.01$ ). Nearly significant differences were detected between daily ranges of breeding and subadult females ( $U = 1453.0$ ,  $P = 0.07$ ).

The cumulative area utilized by wolves on consecutive days increased fast in autumn–winter, from an average of 29.2 km<sup>2</sup> on day 1 to 115.0 km<sup>2</sup> on day 4 to 174.7 km<sup>2</sup> after 8 days, i.e., from 13 to 45 to 67% of the whole territory (Fig. 5). In spring–summer, when the life of a pack was concentrated around the den with pups, daily ranges utilized by wolves were smaller and the cumulative area covered by wolves’ movements increased slowly, from 13 to 50 km<sup>2</sup>, on average (i.e., from 6 to 20% of the annual territory) during 4 consecutive days (Fig. 5).

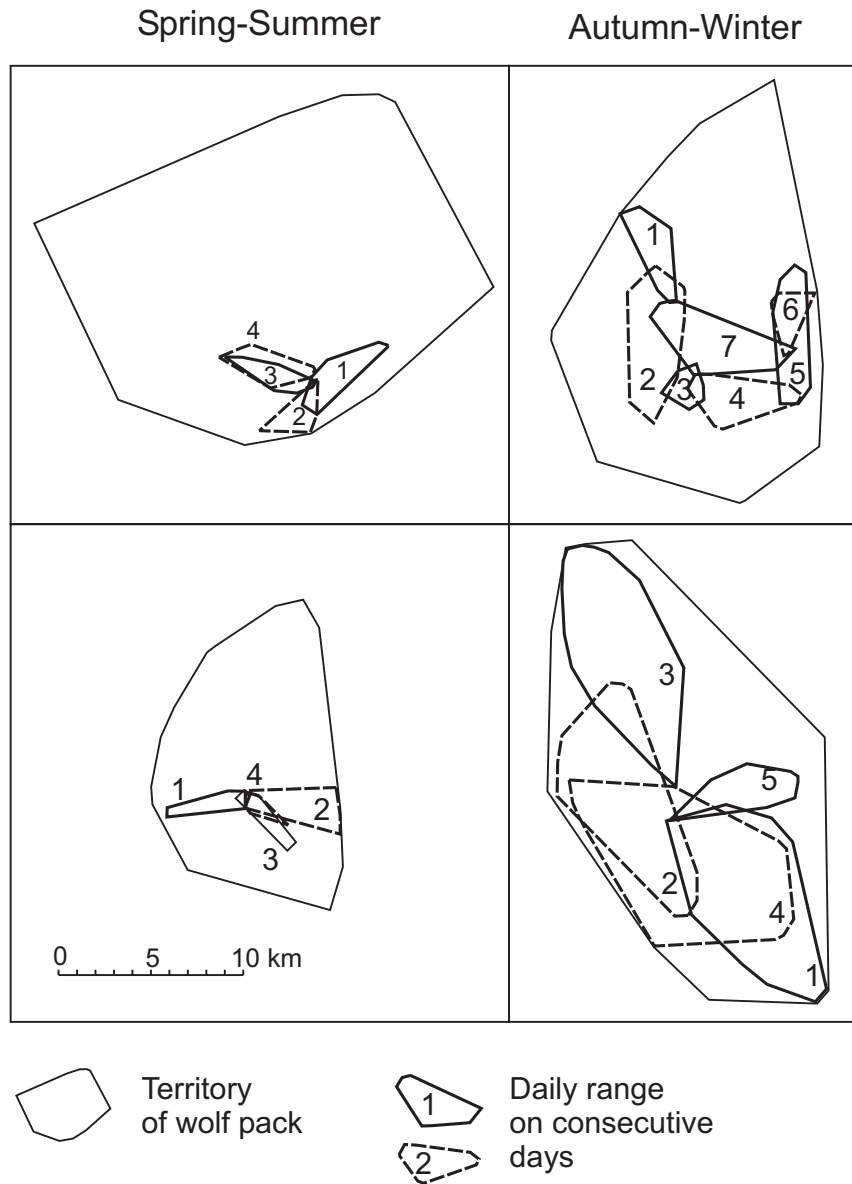
The index of intensity of territory use ( $I$ ) ranged from 1 to 294 m per 1 km<sup>2</sup> of territory per day, an average of 97 m/km<sup>2</sup> (SE = 2.7 m/km<sup>2</sup>). Seasonal changes in  $I$  were statistically significant (ANOVA,  $F_{[11,348]} = 4.04$ ,  $P < 0.0005$ ) and were similar to those observed in DMD, with the lowest values in April–May (66–68 m/km<sup>2</sup>) and the highest in January–March (107–123 m/km<sup>2</sup>) (Fig. 6).

Wolves had a strong tendency to utilize their territory in a rotational way. Areas utilized on 2 consecutive days usually overlapped very little; in 41% of cases the overlap was below 10% and in 27% of cases 10.1–30% overlap was found. Furthermore, we analyzed the overlaps of daily ranges used on days 2–8 with that covered by wolves on day 1 (Fig. 7). In spring–summer, the mean overlap was 26–35% and did not decline on days 2–4 (Kruskal–Wallis ANOVA,  $H_{[3]} = 2.83$ ,  $P > 0.4$ ). In contrast, in autumn–winter, wolves most often utilized new areas each day, so the overlap with the range on day 1 declined on days 2–5 (to 10–12%) but then markedly increased on day 6, to decline again on days 7 and 8 (Fig. 7). The temporal pattern of daily-range overlaps (days 2–8 with day 1) is highly heterogeneous ( $H_{[6]} = 33.32$ ,  $P < 0.0005$ ) and shows that, on average, wolves returned to the same part of their territory every 6th day. In other words, in autumn–winter, the rotation cycle in utilization of the territory by wolves lasted, on average, 6 days.

#### Discussion

The mean DMD of BPF wolves (22.8 km) is similar to DMDs reported for wolves from other regions of Europe and North America. Based on 15 daily routes of wolves snow-tracked in Alaska, Burkholder (1959) reported an average

**Fig. 3.** Examples of daily ranges of wolves in spring–summer and autumn–winter in the annual territories of wolf packs. Daily ranges are minimum convex polygons embracing the daily movement routes of wolves.



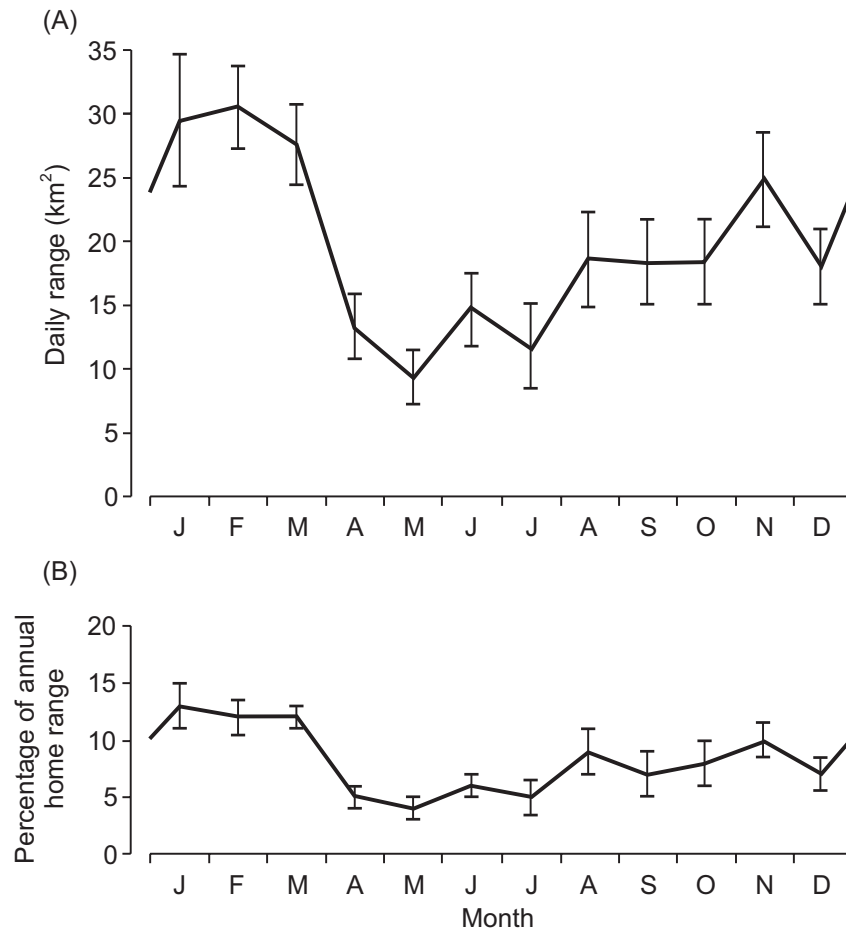
DMD of 24.9 km (range = 9.7–72.4 km). In the montane region of Italy, Ciucci et al. (1997) followed 10 daily routes of radio-collared wolves in summer and autumn and found that DMDs varied from 17 to 38 km, with an average of 27.4 km. Studies conducted by Russian researchers, who followed wolves by snow tracking, yielded shorter DMDs. During a large-scale census in 1966–1981, 857 daily routes of wolves were snow-tracked in various regions of the European part of Russia (S.G. Prikloński, unpublished data cited by Bibikov et al. 1985). DMDs estimated mostly in February and early March averaged 18.5 km. The mean SLDs obtained by radio tracking were 3.1 km (Mech et al. 1971) and 4.0 km (Fuller 1991) in Minnesota, U.S.A., and 3.3 km in Italy (Ciucci et al. 1997). Again, these estimates are similar to the mean SLD obtained in our study (4.4 km).

Wolves move in order to search for and kill prey, to mark their territories, and, if temporarily separated from other pack members, to join them at the den, kill, or other place.

In our study, data covering the whole year and several wolves varying in sex, age, and reproductive status made it possible to show how the mobility of wolves was related to the biological phenomena in their annual life cycle as well as to ambient factors. First and foremost, DMDs of wolves were closely related to the stage of reproduction: mating, denning, and pup rearing. During the mating season in January–February, wolves’ DMDs were longest and those of reproducing males and females were 20–80% longer than daily movements of nonbreeding (young and very old) pack members. This was also observed in the Russian study (Bibikov et al. 1985): during the mating period, DMDs of pairs of wolves were longer (mean = 20.2 km), than those of lone wolves (17.1 km) and whole packs (18.9 km).

In BPF, wolf pups were born between 28 April and 6 May (authors’ unpublished observations). DMDs of wolves shrank throughout April and were shortest in May, when small pups required nearly constant care and attendance

**Fig. 4.** (A) Month-to-month variation (mean  $\pm$  SE) in the size of daily ranges of radio-collared wolves from January to December. Daily ranges were calculated as minimum convex polygons embracing wolves' daily routes. For sample sizes see Fig. 1. (B) Daily ranges as a percentage (mean  $\pm$  SE) of annual territories of wolf packs. Annual home ranges are calculated as minimum convex polygons with 100% of locations.



**Table 5.** Daily ranges (km<sup>2</sup>) of wolves in BPF.

	Young nonbreeding females	Adult breeding females	Adult females with litters lost	Old nonbreeding female	Young nonbreeding male	Adult breeding male
January	—	28.4 $\pm$ 7.5	30.7 $\pm$ 13.6	—	31.1 $\pm$ 8.4	—
February	26.7 $\pm$ 20.2	28.2 $\pm$ 4.2	27.7 $\pm$ 17.0	17.4 $\pm$ 9.4	—	44.5 $\pm$ 9.8
March	15.5 $\pm$ 4.0	26.8 $\pm$ 3.8	15.5 $\pm$ 3.2	36.1 $\pm$ 17.9	—	42.9 $\pm$ 10.1
April	—	13.2 $\pm$ 3.1	—	—	—	—
May	4.3 $\pm$ 1.9	5.0 $\pm$ 2.5	—	18.7 $\pm$ 8.7	—	17.8 $\pm$ 7.1
June	8.6 $\pm$ 2.4	15.7 $\pm$ 4.4	17.8 $\pm$ 13.0	—	—	—
July	5.7 $\pm$ 1.2	12.1 $\pm$ 4.7	23.5 $\pm$ 18.3	—	—	—
August	16.8 $\pm$ 4.6	19.8 $\pm$ 5.9	—	—	—	—
September	8.7 $\pm$ 1.8	23.5 $\pm$ 8.1	13.3 $\pm$ 5.9	—	—	—
October	16.4 $\pm$ 7.7	19.8 $\pm$ 6.1	28.0 $\pm$ 6.1	—	7.2 $\pm$ 3.3	—
November	22.9 $\pm$ 13.0	29.3 $\pm$ 6.6	19.0 $\pm$ 4.9	—	22.5 $\pm$ 8.0	—
December	23.7 $\pm$ 5.8	13.4 $\pm$ 2.6	—	—	—	—
Whole year	14.2 $\pm$ 2.0	21.0 $\pm$ 1.6	21.9 $\pm$ 3.0	—	31.0 $\pm$ 4.3	—
Range	0–68.0	0–132.4	1.2–86.4	—	1.6–132.4	—

**Note:** Values are given as the mean  $\pm$  SE. Daily ranges were determined as minimum convex polygons embracing the daily movement routes of wolves. For further details see Table 1.



from the female. Interestingly, though males' movements were also concentrated around the breeding den, they did not shorten much (by only 20%, compared with 65% for those of breeding females). Also, an old female that was no longer breeding moved in May as much as she did in winter. Subadult females not only markedly curtailed their daily movements, but also the period of their restricted mobility lasted much longer (May, June, and July) than for breeding females, demonstrating that subadult females indeed served as helpers at the den and stayed with pups when adults were hunting. As early as June the pack with pups leaves the breeding den and shifts rendezvous sites more often. In autumn, DMDs of wolves increased again and this increase can be explained by the necessity to fulfill the growing food demands of the young. In September–November, DMDs of packs with young were 35% longer than those of unsuccessfully breeding packs (27 versus 19.8 km).

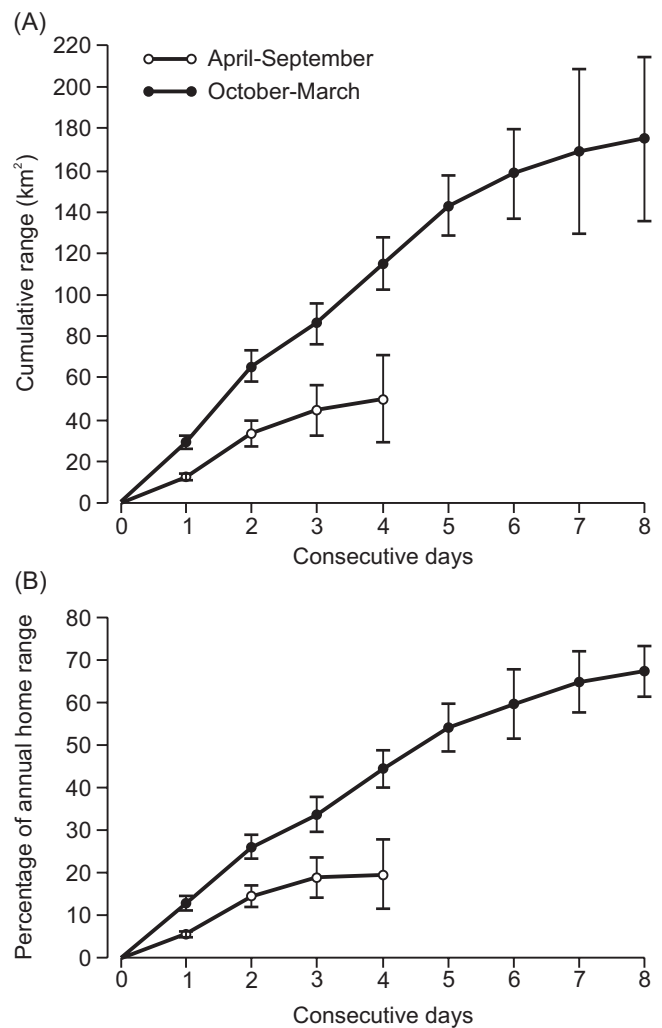
As revealed by our study, prey density was a powerful external factor affecting wolf mobility. As expected, the less abundant red deer were, the longer the daily routes of wolves were. This accords with the well-known fact that food abundance plays an important role in regulating wolf populations (e.g., Keith 1983; Messier 1985b; Fuller 1989), acting via longer DMDs, larger territories, and thus lower densities of wolves in conditions of low prey abundance. In BPF, a pack of wolves kills a new ungulate prey every 2 days and consumes it nearly completely within 1–2 days (Jędrzejewski et al. 2002b). Therefore, wolves quickly shift from consuming one prey item to hunting for another. In effect, the difference in their travel distance on the day before killing a prey and the day after making the kill was fairly small (26%). This stands in contrast to the behavior of another large carnivore inhabiting BPF, the Eurasian lynx (*Lynx lynx*). In BPF, radio-collared lynxes killed an ungulate prey (roe deer or red deer) every 5 days and remained near a kill for 2–4 days, feeding on it and securing it from scavengers (Okarma et al. 1997). On average, the DMD of a lynx was 14 km on a day when it was searching and hunting, and only 2.8 km on the first day after it made a kill (Jędrzejewski et al. 2002a).

Snow, when deep enough, restricts the movements of many species of mammals. Fuller (1991) documented that in north-central Minnesota, mean SLDs of radio-collared wolf packs were 4.6 km when snow depth averaged 22 cm and decreased to 3.2 km when mean snow accumulation was 44 cm. In our dataset, maximum snow depth was only 23 cm, so the hampering effect of snow on wolves' travel was very weak.

Bibikov et al. (1985) mentioned yet another factor affecting wolves' travel: disturbance by hunters. In Russia, hunters usually keep track of wolves and follow them for 1 or more days until they find their diurnal resting site. Over 19 daily routes, wolves disturbed and pursued by hunters covered, on average, 32.6 km/day, whereas the normal mean DMD for wolves during that period was 18.5 km.

Data on the speed of travelling wolves are still scarce. The mean rates of wolf movement (i.e., mean distance walked per hour, including all bouts of resting, stopping, and pausing) calculated from Burkholder (1959), Bibikov et al. (1985), Ciucci et al. (1997), and this paper ranged from 0.8

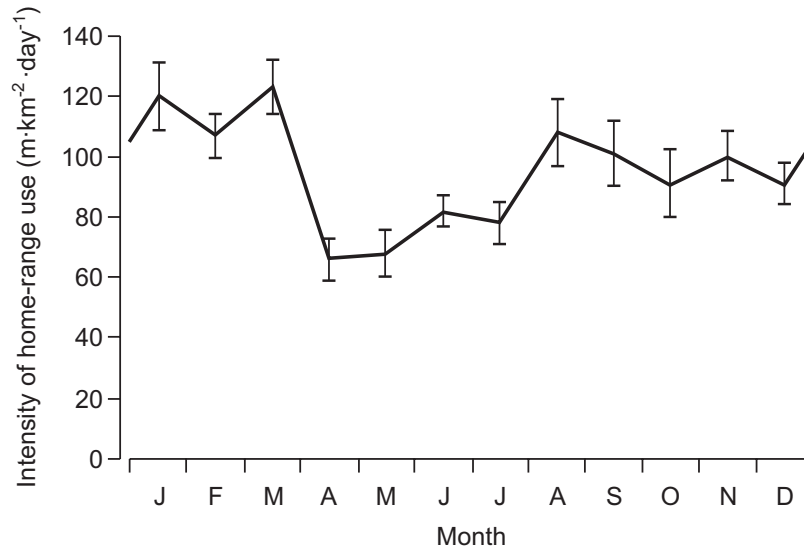
**Fig. 5.** (A) Cumulative ranges (mean  $\pm$  SE) covered by wolves during consecutive days of radio tracking. Ranges are calculated as minimum convex polygons embracing 1–8 daily routes. The sample size for each day ranged from 3 to 67 days of radio-tracking. For April–September, data were too few to show >4 consecutive days. (B) Cumulative ranges on days 1–8 as a percentage (mean  $\pm$  SE) of wolves' annual territories.



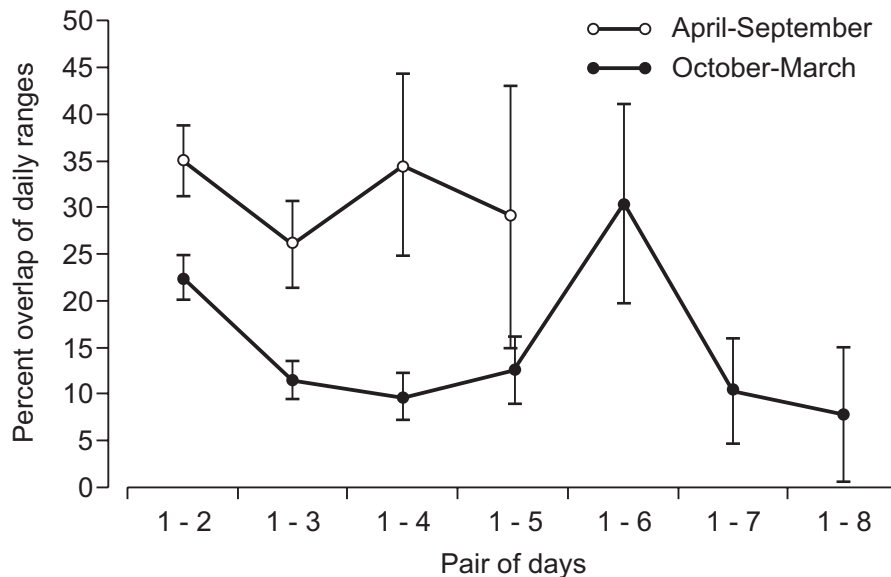
to 1.1 km/h. If only bouts of movements (directional and nondirectional) are considered, but with short stops and pauses included, the mean speeds of wolves would range from 2 to 4 km/h (Musiani et al. 1998; this study). Finally, when rigorously measured during directional travelling with all stops excluded, the speed of travelling wolves reached 6–13 km/h (Mech 1994b).

Wolves are territorial, with packs maintaining exclusive or scarcely overlapping territories (Peterson et al. 1984; Ballard et al. 1987; Okarma et al. 1998). Patrolling of a territory by wolves was a very fast process in our study area, especially in autumn–winter. Wolves covered nearly 70% of the whole territory in 8 days, on average. In spring–summer, the movements of breeding and subadult females were concentrated not far from the breeding den, but those of an adult male were not (compare Fig. 2). Unfortunately, our data on males'

**Fig. 6.** Month-to-month variation in the index of intensity of home-range use by radio-collared wolves (mean  $\pm$  SE) from January to December. The index represents the length of daily routes in metres per 1 km<sup>2</sup> of wolves' annual territory. For the sample size for each month see Fig. 1.



**Fig. 7.** Percent overlap (mean  $\pm$  SE) of wolves' daily ranges on 4–8 consecutive days of radio tracking during two seasons. Pairs of days denote the overlap between the ranges covered on day 1 and day  $n$  (days 2–8). Sample sizes ranged from 3 to 123 pairs of days. In April–September, data were too few to show overlaps for >4 consecutive days.



movements are too few to reveal whether adult males keep control over the whole territory in spring–summer as well.

Seasonal changes in territory utilization by wolves are largely driven by their reproductive biology. In May–June, when small pups stayed in the den, daily ranges of wolves were smallest, with a high degree of overlap from one day to another, and DMDs were shortest. Confinement of wolves' hunting and searching for prey to such a small area was facilitated by the fact that the denning period of wolves coincides with peak seasonal abundance of young of their two main prey species, the red deer and the wild boar. Wolves' DMDs and their rates of territory utilization increase towards autumn, along with the development of pups. Interest-

ingly, while DMDs covered by wolves grow fast (in September they are already as long as in late winter), daily ranges utilized by wolves in autumn remain about half the size of those utilized in late winter. Therefore, in autumn, daily movements are more concentrated than in winter, which most probably results from the fact that pups still cannot keep pace with adults and have to spend much time at rendezvous sites. Moreover, in the mating season in late winter, wolves seem to be engrossed in patrolling, defending, and marking the whole territory, especially near the boundaries (Peters and Mech 1975), so their movements are more directional and daily ranges are very large. The fast patrolling of a territory is often associated with intense marking by

scratching and scent signals (authors' unpublished data) and visiting old prey remains (Jędrzejewski et al. 2002b). The main reason for patrolling the territory may be to defend it against alien wolf intruders, as is suggested by the high incidence of intraspecific strife along territorial boundaries reported for North American wolves (Mech 1994a).

Yet another reason for the rotational use of territory may be the indirect effect of predators, termed behavioral depression of prey availability (Charnov et al. 1976), which supposedly lowers the hunting success of a predator. Jędrzejewska and Jędrzejewski (1989) proposed that rotational use of territory by a predator, i.e., visiting new parts of the territory every day and returning to previously utilized areas after several days, would minimize the evasive response of prey. Ungulates do recognize the odor of large predators (Müller-Schwarze 1972) and become more alert when they perceive risk from their enemy. Therefore, wolves' utilization of various parts of their territory on consecutive days may help them cope with the antipredator adaptations of ungulates.

## Acknowledgements

This study was financed by the Polish National Committee for Scientific Research (grant 6 P04F 026 12), the Mammal Research Institute, the European Natural Heritage Fund (Euronatur), the Flaxfield Nature Consultancy (the Netherlands and U.K.), the German Academic Exchange Service, and the German Donors' Association for the Promotion of Sciences and Humanities. Permits to capture and radio-collar wolves were issued by the Ministry of Forestry and Nature Protection, and Dr. C. Okołów, Director of Białowieża National Park. We thank S. Śnieżko, I. Ruczyński, P. Wasiak, M. Chudziński, W. Jastrzębski, R. Kozak, and all the assistants and volunteers who helped us during the fieldwork. We are grateful to L. Szymura for managing computer database, K. Zub, who helped with the analysis of data and drew the figures, and two anonymous reviewers whose comments helped us improve the manuscript.

## References

- Ballard, W.B., Whitman, J.S., and Gardner, C.L. 1987. Ecology of an exploited wolf population in south-central Alaska. *Wildl. Monogr.* No. 98. pp. 1–54.
- Ballard, W.B., Reed, D.J., Fancy, S.G., and Krausman, P.R. 1995. Accuracy, precision, and performance of satellite telemetry for monitoring wolf movements. *In Ecology and conservation of wolves in a changing world. Edited by L.N. Carbyn, S.H. Fritts, and D.R. Seip.* Canadian Circumpolar Institute, University of Alberta, Edmonton. pp. 461–467.
- Bibikov, D.I., Kudaktin, A.N., and Filimonov, A.N. 1985. Territoriality, movements. *In The wolf: history, systematics, morphology, ecology.* [In Russian.] *Edited by D.I. Bibikov.* Nauka, Moscow. pp. 415–431.
- Burkholder, B.L. 1959. Movements and behavior of a wolf pack in Alaska. *J. Wildl. Manag.* **23**: 1–11.
- Carbyn, L.N., Fritts, S.H., and Seip, D.R. (Editors). 1995. Ecology and conservation of wolves in a changing world. Canadian Circumpolar Institute, University of Alberta, Edmonton.
- Charnov, E.L., Orians, G.H., and Hyatt, K. 1976. Ecological implications of resource depression. *Am. Nat.* **110**: 247–259.
- Ciucci, P., Boitani, L., Francisci, F., and Andreoli, G. 1997. Home range, activity and movements of a wolf pack in central Italy. *J. Zool. (Lond.)*, **243**: 803–819.
- Cleveland, W.S. 1979. Robust locally weighted regression and smoothing scatterplots. *J. Am. Stat. Assoc.* **74**: 829–836.
- Fritts, S.H., and Mech, L.D. 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in north-western Minnesota. *Wildl. Monogr.* No. 80. pp. 5–79.
- Fuller, T.K. 1989. Population dynamics of wolves in north-central Minnesota. *Wildl. Monogr.* No. 105. pp. 1–41.
- Fuller, T.K. 1991. Effect of snow depth on wolf activity and prey selection in north-central Minnesota. *Can. J. Zool.* **69**: 283–287.
- Goszczyński, J. 1986. Locomotor activity of terrestrial predators and its consequences. *Acta Theriol.* **31**: 79–95.
- Harrington, F.H., and Paquet, P.C. (Editors). 1982. Wolves of the world: perspectives of behavior, ecology, and conservation. Noyes Publications, Park Ridge, N.J.
- Jędrzejewska, B., and Jędrzejewski, W. 1989. Evasive response of prey and its effect on predator–prey relationship. [In Polish with English summary.] *Wiad. Ekol.* **35**: 3–21.
- Jędrzejewska, B., and Jędrzejewski, W. 1998. Predation in vertebrate communities: the Białowieża Primeval Forest as a case study. Springer-Verlag, Berlin and New York.
- Jędrzejewska, B., Jędrzejewski, W., Bunevich, A.N., Miłkowski, L., and Okarma, H. 1996. Population dynamics of wolves *Canis lupus* in Białowieża Primeval Forest (Poland and Belarus) in relation to hunting by humans, 1847–1993. *Mammal Rev.* **26**: 103–126.
- Jędrzejewska, B., Jędrzejewski, W., Bunevich, A.N., Miłkowski, L., and Krasinski, Z.A. 1997. Factors shaping population densities and increase rates of ungulates in Białowieża Primeval Forest (Poland and Belarus) in the 19th and 20th centuries. *Acta Theriol.* **42**: 399–451.
- Jędrzejewski, W., Schmidt, K., Okarma, H., and Kowalczyk, R. 2002a. Movement pattern and home range use by the Eurasian lynx in Białowieża Primeval Forest (Poland). *Ann. Zool. Fenn.* **39**. In press.
- Jędrzejewska, W., Theuerkauf, J., Jędrzejewska, B., Selva, N., Zub, K., and Szymura. 2002b. Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). *Ecology*. In press.
- Keith, L.B. 1983. Population dynamics in wolves. *Can. Wildl. Serv. Rep. Ser. No. 45*. pp. 66–77.
- Mech, L.D. 1970. The wolf: the ecology and behavior of an endangered species. The Natural History Press, Garden City, N.Y.
- Mech, L.D. 1994a. Buffer zones of territories of gray wolves as regions of intraspecific strife. *J. Mammal.* **75**: 199–202.
- Mech, L.D. 1994b. Regular and homeward travel speed of arctic wolves. *J. Mammal.* **75**: 741–742.
- Mech, L.D., Frenzel, L.D., Jr., Ream, R.R., and Winship, J.W. 1971. Movements, behavior, and ecology of timber wolves in northeastern Minnesota. *U.S. For. Serv. Res. Pap. NC-52*. pp. 1–35.
- Messier, F. 1985a. Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. *Can. J. Zool.* **63**: 239–245.
- Messier, F. 1985b. Social organization, spatial distribution, and population density of wolves in relation to moose density. *Can. J. Zool.* **63**: 1068–1077.
- Müller-Schwarze, D. 1972. Responses of young black-tailed deer to predator odours. *J. Mammal.* **53**: 393–394.
- Musiani, M., Okarma, H., and Jędrzejewski, W. 1998. Speed and actual distances travelled by radiocollared wolves in Białowieża Primeval Forest (Poland). *Acta Theriol.* **43**: 409–416.

- Okarma, H., and Jędrzejewski, W. 1997. Livetrapping wolves with nets. *Wildl. Soc. Bull.* **25**: 78–82.
- Okarma, H., Jędrzejewski, W., Schmidt, K., Kowalczyk, R., and Jędrzejewska, B. 1997. Predation of Eurasian lynx on roe deer and red deer in the Białowieża Primeval Forest, Poland. *Acta Theriol.* **42**: 203–224.
- Okarma, H., Jędrzejewski, W., Schmidt, K., Śnieżko, S., Bunevich, A.N., and Jędrzejewska, B. 1998. Home ranges of wolves in Białowieża Primeval Forest, Poland, compared with other Eurasian populations. *J. Mammal.* **79**: 842–852.
- Peters, R.P., and Mech, L.D. 1975. Scent marking in wolves: a field study. *Am. Sci.* **63**: 628–637.
- Peterson, R.O., Woolington, J.D., and Bailey, T.N. 1984. Wolves of the Kenai Peninsula, Alaska. *Wildl. Monogr.* No. 88. pp. 1–52.
- Potvin, F. 1987. Wolf movements and population dynamics in Papineau-Labelle Reserve. *Can. J. Zool.* **66**: 1266–1273.