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SPATIOTEMPORAL SEGREGATION OF WOLVES FROM HUMANS IN THE BIALOWIEŻA FOREST (POLAND)

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Abstract: Knowledge about the impact of human activity on the behavior of wolves (*Canis lupus*) is important to predict habitats suitable for wolf recolonization and for planning management zones. We tested the hypothesis that wolves live spatiotemporally segregated from humans. From 1994 to 1999, we radiotracked 11 wolves in 4 packs and monitored human activity in the Białowieża Forest, Poland. Wolves avoided permanent human-made structures (settlements, forest edge to arable land, roads, tourist trails) more in the day than at night. Wolf avoidance increased with increasing human use. Particularly large settlements and intensively used public roads reduced the area used by wolves. Wolves avoided human presence in the forest (traffic, forestry operations) by temporarily selecting areas where people were absent. One of the wolf packs selected a national park zone with restriced access (50 km^2) as the core area of its home range in both day and night. Conversely, wolf packs living in a commercial forest with small nature reserves ($\leq$4 km^2) did not select reserves in the day or night. We concluded that spatiotemporal segregation is an adaptation of wolves to coexist with humans while keeping their activity pattern optimized toward food acquisition. The distribution of areas with restricted human access, forest, settlements, and intensively used public roads are important factors determining the suitability of an area for wolves.

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Key words: *Canis lupus*, disturbance, habitat suitability, human activity, Poland, recolonization, reserves, roads.

Boitani (2000) highlighted the need for knowledge on the capacity of wolves to coexist with human activity, a factor that he regarded as a key element for the conservation of wolves in Europe. Wolves are now recolonizing many areas of Europe and North America where they were extirpated (Mech 1995, Boitani 2000). Because some of the areas that wolves are recolonizing are densely populated by people, wildlife managers need information on the impact of human activity on wolves. However, only a few studies have focused on the influence of human activity on wolf behavior. Thiel et al. (1998) documented that some wolves in Minnesota and Wisconsin even tolerated humans close to their den sites; other studies reported that wolves usually avoided contact with humans. This avoidance can be spatial, as in Alaska, where wolves avoided areas surrounding public roads (Thurber et al. 1994). In contrast, Vilà et al. (1995) and Ciucci et al. (1997) suggested that wolves and humans are temporally segregated, because radiomarked wolves in Italy and Spain mainly were nocturnal. However, in the Białowieża Forest, the daily movement patterns of wolves living with various levels of human activity were not different (Theuerkauf et al. 2001). We therefore hypothesized that humans and wolves are spatiotemporally separated.

We radiotracked wolves and monitored human activity in the Białowieża Forest to test our hypothesis on the spatiotemporal segregation of wolves and humans. Our objectives were to determine whether (1) wolves avoided human-made structures (human settlements, forest edge with arable land, roads) more during the day than at night, (2) the home ranges of wolves were smaller during the day than at night, (3) the size of human settlements or the intensity of road use influenced the level of wolf avoidance, (4) wolves reduced their use of forest areas when humans used these areas intensively compared to periods when people were absent, (5) wolves were more sensitive to human activity when resting than when active, (6) human activity close to a wolf was less than the mean human activity in the wolf's home range, (7) wolves selected nature reserves more during the day than at night, and (8)

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wolves used a forest area more intensively after the area became protected as a reserve.

STUDY AREA

The Białowieża Forest is a forest complex of 1,450 km^2 (52°30′–53°00′N, 23°30′–24°15′E) that straddles the Polish–Belarussian border (Fig. 1). The forest is a mosaic of deciduous, coniferous, and mixed tree stands. The Polish side of the Białowieża Forest consists of the Białowieża National Park and a commercial forest (480 km^2), in which timber harvest, reforestation, and hunting occur. Fifty km^2 of the Białowieża National Park have been protected as a strict reserve since 1921. No hunting, forestry, or motorized traffic is permitted in the strict reserve, and public access is limited. In July 1996, the Białowieża National Park was enlarged to 100 km^2. The extended portion of the national park is open to the public, but vehicle access is restricted, hunting is not allowed and forestry interventions are limited to cutting of sick trees and fencing off regeneration areas. The Białowieża Forest also has 22 small (0.1–3.7 km^2) nature reserves, which are less protected against forestry operations than the national park. The whole Belarussian side of the Białowieża Forest (870 km^2) is a national park, but hunting and limited logging are allowed. On the Belarussian side, a guarded fence was built in 1981 along the state border (in a distance of 0–1.5 km). The zone between the border and the fence is used little by humans.

Human density on the Polish side of the Białowieża Forest is about 7 inhabitants per km^2 and 70 inhabitants per km^2 in the surrounding region (Podlasie Province, capital: Białystok, Poland). The density of forest roads passable by 2-wheel-drive vehicles is about 1.2 km/km^2 in the commercial forest, but only about 50 km of paved roads (0.1 km/km^2) are intensively used by the public.

Forestry is the main source of human activity in the commercial forest. Other groups of people use the forest seasonally. From July to October, 27% of forest visitors are mushroom collectors; from September to January 15% are hunters; and from May to September 40% are tourists, whereas from October to April only 4% of humans in the commercial forest are tourists. From May to September, around 100 tourists per day visit the strict reserve of the Białowieża National Park, but the number of tourists decreases to about 20 per day from October to April (estimate based on data of B. Jaroszewicz, Białowieża National Park, personal communication). The area visited by tourists is restricted to a 4-km tourist trail near the park's entrance. The rest of the strict reserve is open for permit holders to conduct research or education. Humans traveling in the commercial forest use mostly cars (80%), but also lorries and tractors (10%), as well as bicycles (10%). Tourists mainly go on foot or bicycle and usually stay on roads or trails.

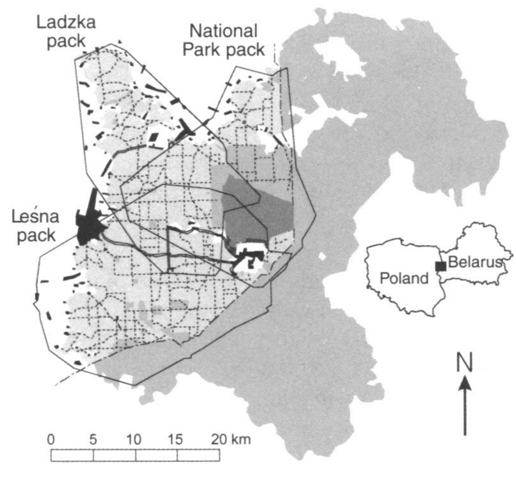

Fig. 1. Białowieża Forest, Poland, with distribution of the commercial forest (light gray), nature reserves (mean gray), the strict reserve of the Polish Białowieża National Park (dark gray), human settlements (black area), heavily used public roads (double lines), forest roads (dashed lines), state border (dashed and pointed line), and the cumulative home ranges (continuous lines) of wolf packs.

At the beginning of our study, 3 wolf packs inhabited the Polish side of the Białowieża Forest (Okarma et al. 1998). The core area of 1 pack (National Park pack) was within the strict reserve of the Białowieża National Park (Fig. 1). The number of wolves in this pack varied during our study between 4 and 7 wolves (in midwinter). Another pack (Ladzka pack, 3–6 wolves) lived in the northwestern part of the Białowieża Forest, an area with few small nature reserves. The third pack (Leśna pack, 4–7 wolves) lived in the southern part of our study area, which includes most small nature reserves and a large part of the border zone. This pack split in December 1997 into 2 packs (Leśna I and II packs), but because their home ranges overlapped largely after the separation, we pooled data of the 2 packs when comparing them with the other 2 packs. Forest road density was 0.8 km/km^2 in the home range of the National Park pack and 1.0 km/km^2 in the home ranges of the Ladzka and Leśna packs.

Wolves have been protected since 1989 in the Polish side of the Białowieża Forest, but humans are still the main mortality factor. During our study, 6 of 12 radiomarked wolves died in poachers' snares set for wild boar (*Sus scrofa*) or were shot. In the Belarussian side, hunters on average killed 80% of the wolf population each year between 1975 and 1994 (Jędrzejewska et al. 1996). Immigration of wolves from the northeast compensated for the high human-caused mortality.

The main prey of wolves in the Białowieża Forest (Jędrzejewski et al. 2000, 2002) is red deer (*Cervus elaphus*), followed by wild boar and roe deer (*Capreolus capreolus*). During our research, the mean densities of prey species for the entire study area were about 3–7 red deer, 1–6 wild boar, and 1–5 roe deer per km^2 (Kossak 1997, Jędrzejewski et al. 2000). Wolves occasionally fed on carrion at garbage dumps (Ladzka pack) or killed cattle (Leśna I pack).

METHODS

Wolves

From 1994 to 1999, we captured 12 wolves in 4 packs either with Aldrich foot snares equipped with radioalarm systems or by the fladry and net method (Okarma and Jędrzejewski 1997) and fitted them with radiocollars (Okarma et al. 1998). We relocated wolves in 24-hr radiotracking sessions of usually 6 days (range 1–9 days; described in detail in Theuerkauf and Jędrzejewski 2002). Data samples for 11 radiomarked wolves (5 breeding females, 1 breeding male, 4 young females, 1 young male) were large enough for analysis (557–8,336 relocations/wolf; 3–42 months of radiotracking).

Radio locations gathered by 24-hr radiotracking can be autocorrelated (Salvatori et al. 1999). However, time intervals that ensure temporal independence often are large, which can lead to an important underestimate of home-range size of radiomarked 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. We instead eliminated autocorrelation among consecutive radio locations by calculating 1 value for each wolf. Accordingly, we used the variation among wolves and not among radio location data for statistical testing of selection (Otis and White 1999).

We created 10,000 random points with a Geographic Information System (GIS) inside our study area, which we defined as the cumulative area of all the wolves' home ranges (100% minimum convex polygons). We calculated selection by comparing radio locations of a wolf with the locations of random points inside the home range of the given wolf. We used Ivlev's electivity index (Jacobs 1974) to indicate selection:

$$\text{Selection index} = (p_w - p_r)/(p_w + p_r - 2\,p_w\,p_r),$$

where p_w is the proportion of wolf locations in a given category, and p_r is the proportion of random points in a given category. Selection indices can vary from +1 (total selection) to −1 (total avoidance). We categorized wolf or random point locations in 500-m-wide classes according to the distance to human-made structures (settlements, forest edges, roads, tourist trails; 250-m-wide classes for distances of 0–1 km to roads or tourist trails) or parts of our study area under different protection (commercial forest, nature reserves, strict reserve, border zone). We calculated selection indices for all categories first for each wolf, and then mean selection indices and 95% confidence intervals (CI) for the variation among wolves. We considered that wolves selected (avoided) a given category if the lower (upper) limit of the 95% CI was higher (lower) than zero. To map the spatiotemporal home-range use of wolves, we calculated selection indices for squares of 250 × 250 m. Because our location error was 194–291 m (Theuerkauf and Jędrzejewski 2002), we used a 500-m radius around the center of the square to compensate for the radio location error.

We defined summer as the period from May to September when wolves are concentrated around dens or rendezvous sites and when many tourists are in the forest. Winter was the period from October to April when wolves use their entire home ranges (Jędrzejewski et al. 2001) and human activity in the forest is mainly limited to forestry operations and hunting ungulates. Breeding females in our study area stayed mostly at the den (denning period) from about 2 weeks before a birth until 6 weeks after the birth (Theuerkauf et al. 2003*a*). We defined the forest edge as the peripheral borders of the Białowieża Forest as well as all borders to human settlements within the forest.

Human Activity

We documented human activity from 1997 to 1999 either visually or with a magnetic traffic counter card (NC-30, Nu-Metrics, Uniontown, Pennsylvania, USA) at 39 counting points on roads in the Białowieża Forest. During visual counts, which lasted 2–24 hr (total 569 hr), we counted people and vehicles that passed a given point. The traffic counter card dug in forest roads recorded hourly the numbers of passing vehicles for continuous periods of 1 week (total 5,712 hr). We checked the reliability of the card under our field conditions during 150 hr of direct observations. 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 its data with those gathered visually.

We classified roads inside the forest as primary roads (public paved roads with 1,000–10,000 vehicles per week), secondary roads (regularly used forest roads with 48–500 vehicles per week), and tertiary roads (rarely used forest roads with <40 vehicles per week). We calculated the average human activity on roads in the home range of a wolf by multiplying the proportion (by length) of each road class in the home range of a wolf by the average human activity on the given road class, and then adding the values for the 3 road classes.

In addition, we recorded human activity during radiotracking by noting the number of people and vehicles that passed the person tracking wolves. In 95% of cases, trackers were between 200 and 2,200 m from the wolf, so the count of human activity represents human activity within a radius of about 2 km around the radiomarked wolves. We found no detectable influence of the radiotracker on the behavior of the tracked wolf (Theuerkauf and Jędrzejewski 2002). To test whether wolves selected areas of low human activity, we compared the average human activity on roads around wolves with the average human activity on roads used for radiotracking.

The forestry administration provided us with information about daily locations of forestry operations in an area where we had radiotracked wolves continuously (3 weeks in Jan, Feb, and May 1999). To evaluate the reaction of wolves to forestry operations, we compared wolf use of areas around forestry operations during working hours (day during the working week) and during nonworking hours (nights and weekends).

RESULTS

Permanent Human-made Structures

Wolves in the Białowieża Forest selected areas in the center of their home ranges that were far from the forest edge, especially in summer (Fig. 2). The daytime home ranges of the 11 wolves ($\bar{x}$ = 205 km^2, SE = 23 km^2) were reduced compared to nightly home ranges ($\bar{x}$ = 257 km^2, SE = 29 km^2; *t*-test for pairs: P = 0.001). Wolves used only 74% (SE = 2%) of their home ranges in the day compared to 93% (SE = 2%) at night.

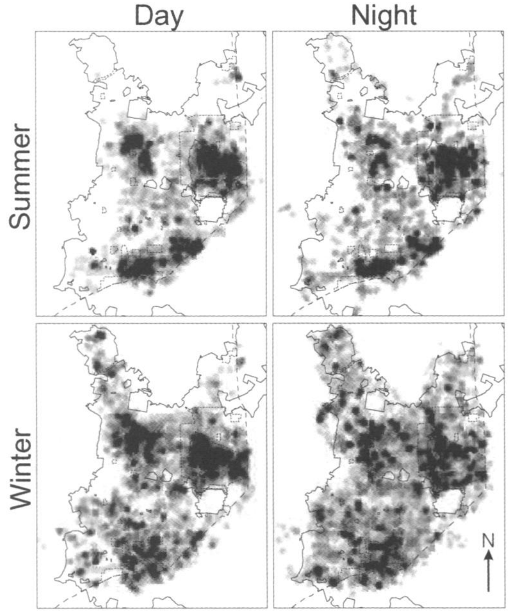

Fig. 2. Selection of 250 × 250-m squares inside the home ranges of 11 wolves of 4 packs in the Białowieża Forest, Poland, from 1994 to 1999 (black squares: selection index >0.75; dark gray: selection index between 0 and 0.75; medium gray: selection index between –0.75 and 0; light gray: selection index <–0.75; white area: not used; continuous lines: forest edge to agriculture land with villages; dotted lines: nature reserves; dashed and pointed line: state border).

Wolves not only avoided coming out of the forest into arable land, but also rarely made incursions into the 2-km-wide forest zone that borders the forest edge (Fig. 3). Daytime avoidance of arable land by wolves was almost total and more pronounced than at night for the 2-km edge zone. Wolves increased both their avoidance level and the width of the avoided forest zone with increasing size of human settlements. The avoidance zone for the largest town in our study area (24,000 inhabitants) was 2 km at night and 3.5 km during the day. Wolves avoided a zone of 0.5 km at night and 1 km in the day around forest settlements with few houses.

Mean distances between wolves and edges of the forest bordering human settlements were larger in the day than at night (Table 1). The difference between day and night became more

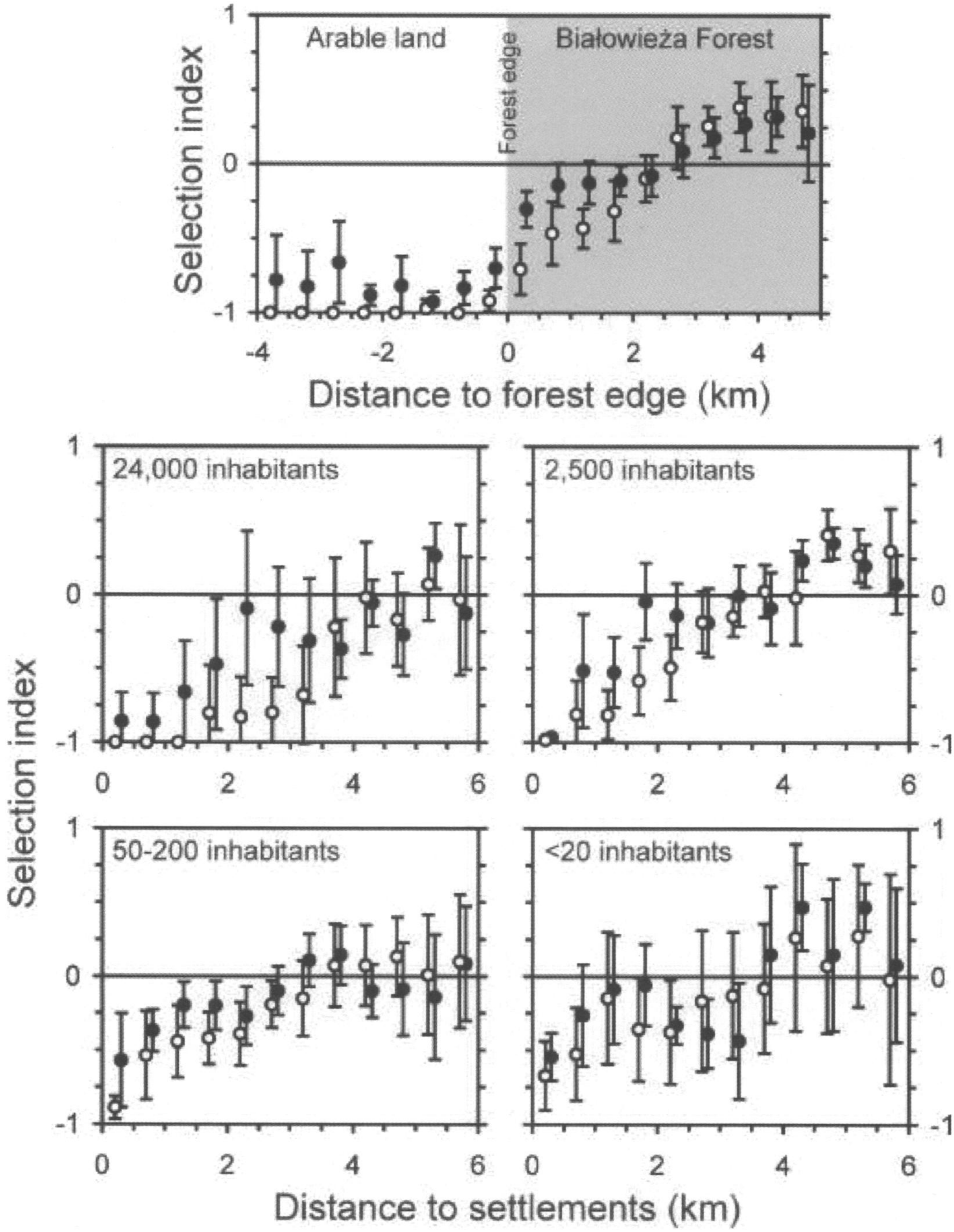

Fig. 3. Mean wolf selection indices (with 95% CI of the variation among wolves) in relation to distance to forest edge and settlements of different sizes (based on number of human inhabitants) during the day (white dots) and night (black dots) for 11 wolves of the Białowieża Forest, Poland, from 1994 to 1999.

pronounced with low levels of human activity, and was most significant for the National Park pack in winter when human activity in the home range of this pack was lowest. Breeding females ($n = 5$) were farther from edges of the forest bordering human settlements during the denning

Table 1. Comparison (*t*-test for pairs) between day and night of distances (km) of wolf radio locations to edges of the forest bordering human settlements in the Białowieża Forest, Poland, 1994–1999 (4 wolves of the National Park pack, 3 wolves of the Ladzka pack, and 4 wolves of the Leśna packs). Seasonal human activity in the wolves' home ranges: low (<10 people per day on roads/trails on average), moderate (30–60), high (150–200).

	National Park pack						Leśna packs						Ladzka pack					
	Day		Night			Human	Day		Night			Human	Day		Night			Human
	$\bar{x}$	SE	$\bar{x}$	SE	P	activity	$\bar{x}$	SE	$\bar{x}$	SE	P	activity	$\bar{x}$	SE	$\bar{x}$	SE	P	activity
Summer	4.1	0.1	3.7	0.2	0.018	moderate	3.4	0.2	3.4	0.1	0.987	high	2.9	0.1	2.5	0.1	0.185	high
Winter	3.6	0.2	2.7	0.1	0.005	low	3.0	0.3	2.6	0.3	0.092	moderate	2.6	0.2	2.2	0.2	0.044	moderate

period ($\bar{x}$ = 3.8 km, SE = 0.4 km) than during the rest of the year ($\bar{x}$ = 3.0 km, SE = 0.2 km; *t*-test for pairs: $P = 0.047$). Other wolves that we tracked in all seasons ($n = 3$) were not farther from the forest edge during the denning period than during the rest of the year (*t*-test for pairs: $P = 0.662$).

In the commercial forest, radiomarked wolves ($n = 11$) avoided a band of 0.75 km around primary roads at night and 2 km during the day (Fig. 4). Wolf avoidance of secondary roads was 0.25 km at night and 1 km during the day. Wolves avoided tertiary roads the least, leaving a 0.25-km-wide buffer during the day but none at night. Wolves in the strict reserve ($n = 4$) avoided tourist trails in the day as much as primary roads. In contrast to primary roads, wolves did not avoid tourist trails at night. We did not detect avoidance by wolves of other, less used tracks in the strict reserve (all 95% CIs included the value 0). Wolves were not further in the day from the forest edge (*t*-test: $P = 0.919$), human settlements ($P = 0.919$), primary roads ($P = 0.863$), secondary roads ($P = 0.896$), tertiary roads ($P = 0.544$), or tourist trails ($P = 0.381$) when resting than when active.

Temporary Human Presence

Although the average human activity on roads within wolf home ranges was higher in summer than in winter (Fig. 5), the mean daily number of humans or vehicles on roads in a 2-km radius around wolves was not higher (*t*-test: $P = 0.596$ for humans, $P = 0.533$ for vehicles) in summer ($\bar{x}$ = 7.1, SE = 2.1 for humans; $\bar{x}$ = 4.7, SE = 1.4 for vehicles) than in winter ($\bar{x}$ = 9.2, SE = 3.0 for humans; $\bar{x}$ = 6.0, SE = 1.5 for vehicles). In both seasons, the hourly mean numbers of humans or vehicles on roads in the 2-km radius around wolves were lower than those on all roads used for radio-tracking or on all roads in wolf home ranges (Wilcoxon-test: all $P < 0.001$). Wolves used the area up to 1.5 km around forestry operations less during working hours than during nonworking hours (Fisher's exact test: $P = 0.043$).

Reserves

The daily patterns of reserve selection differed greatly among packs. The National Park pack strongly selected the strict reserve but avoided other reserves and the border zone (Table 2). Wolves of the National Park pack also avoided the new part of the national park except on winter nights. During the winter, the Leśna packs used nature reserves and the border zone in the day more than randomly, but they did not clearly select these protected areas. The Ladzka pack neither selected reserves nor showed a particular daily pattern in reserve selection. Wolves of the National Park pack ($n = 4$) used the area of the new national park less before its creation (8% of time, SE = 2%) than after (17%, SE = 3%; *t*-test: $P = 0.004$). Wolf use of this area increased at a rate of 0.5% monthly (linear regression: $P = 0.048$) during the 3 years after protection was established. Before the creation of the new national park, the monthly use did not increase ($P = 0.818$).

DISCUSSION

Vilà et al. (1995) and Ciucci et al. (1997) assumed that wolves and humans may be temporally segregated in Italy and Spain, where radiomarked wolves mainly were nocturnal. In contrast, wolves in Canada (Kolenosky and Johnston 1967), in Alaska (Peterson et al. 1984, Fancy and Ballard 1995), in forests of Minnesota (Mech 1992), and in the Białowieża Forest (Theuerkauf et al. 2003*a*) were active at night and in the day. In Alaska, Thurber et al. (1994) reported that wolves avoided areas surrounding public roads. This might lead to the conclusion that wolves avoid humans spatially in areas with low human density (e.g., Alaska), and temporally in regions with high human activity (e.g., southern Europe). However, in the Białowieża Forest, we found no difference among the daily movement patterns of wolves living with various levels of human activity (Theuerkauf et al. 2001). Further, wolves in the Bialowieża Forest were active throughout the day,

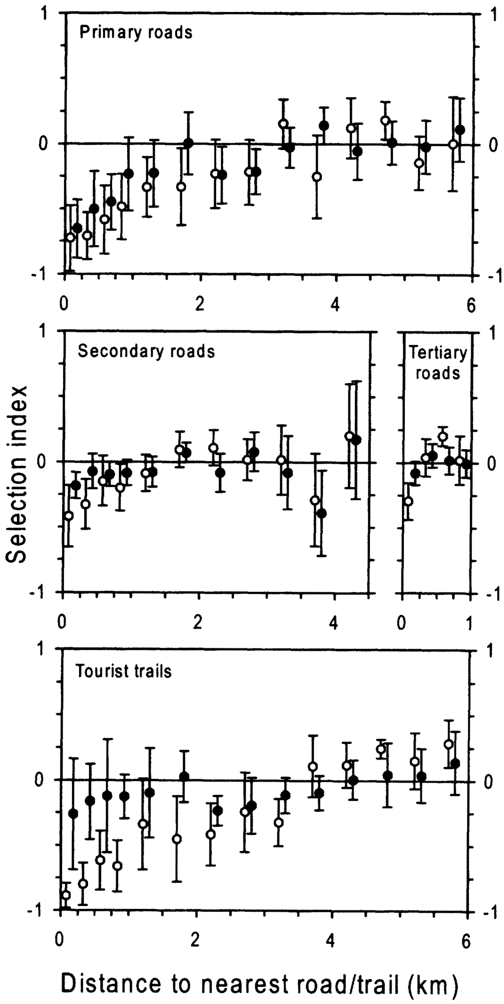

Fig. 4. Mean wolf selection indices (with 95% CI of the variation among wolves) in relation to distance to roads in the commercial forest (11 wolves) and tourist trails inside the strict reserve of the Białowieża National Park, Poland, (4 wolves) during the day (white dots) and night (black dots) from 1994 to 1999 (250-m-wide distance classes up to 1 km from the road/trail and 500-m-wide distance classes when further away).

although human activity in some parts of the forest was high (Theuerkauf et al. 2003*a*). During periods when many people were in the Białowieża Forest, wolves used areas where human activity was low. We conclude that the segregation between wolves and humans is spatiotemporal as wolves react to human activity by temporarily avoiding areas being used by humans.

Reasons other than avoidance of humans may account for the nocturnal behavior of wolves in Italy (Ciucci et al. 1997) and Spain (Vilà et al. 1995). In Ciucci et al.'s (1997) study, wolves took regular advantage of anthropogenic food sources, such as garbage dumps. Because these dumps were near human settlements, wolves used the dumps at night (Ciucci et al. 1997). In the Białowieża Forest, wolves almost completely met their food requirements by hunting red deer, wild boar, and roe deer in the forest (Jędrzejewski et al. 2000). Wolves were active and hunted throughout the day, but both the number of prey killed and activity peaked at dawn and dusk, which appeared to coincide with peaks in the activity patterns of their prey (Theuerkauf et al. 2003*a*). Activity patterns of wolves feeding on wild prey should therefore be adjusted to the activity rhythms of their main prey species. Bimodal activity patterns are common in many prey species such as red deer (Georgii 1981, Georgii and Schröder 1983), roe deer (Cederlund 1981, Jeppesen 1989), white-tailed deer (*Odocoileus virginianus*; Montgomery 1963, Kammermeyer and Marchinton 1977), and moose (*Alces alces*; Geist 1963), whereas wild boar often are more nocturnal (Briedermann 1971, Russo et al. 1997). Besides feeding on carrion and domestic animals, Spanish wolves also prey on wild ungulates, which may be the reason why the activity patterns of wolves were nocturnal but with activity peaks at dawn and just after dusk (Vilà et al. 1995). In Ciucci et al.'s (1997) study, the only potential prey for wolves were wild boar, which are mainly nocturnal in Italy even in regions where they are not hunted (Russo et al. 1997).

A possibililty exists, however, that wolves under heavy persecution by man would become more nocturnal. Kitchen et al. (2000) showed a temporary shift in the behavior of coyotes (*Canis latrans*), which moved less in the day during a period of persecution by humans compared to coyotes that had not been persecuted for >8 years. During the period of persecution, coyotes adjusted their activity patterns presumably to reduce the chance of encounters with human hunters, but increased their diurnal activity quickly after the persecution had stopped. Ciucci et al. (1997) and Vilà et al. (1995) did not report a heavy persecution in their study areas of Italy and Spain. We therefore expect the activity patterns of wolves that are not heavily persecuted to be affected more by their mode of food acquisition than by the influence of humans.

In mammalian predator–prey systems, fear of predators plays an important role in shaping the behavior of the prey (Brown et al. 1999). Under high levels of predation, prey species are very vigi-

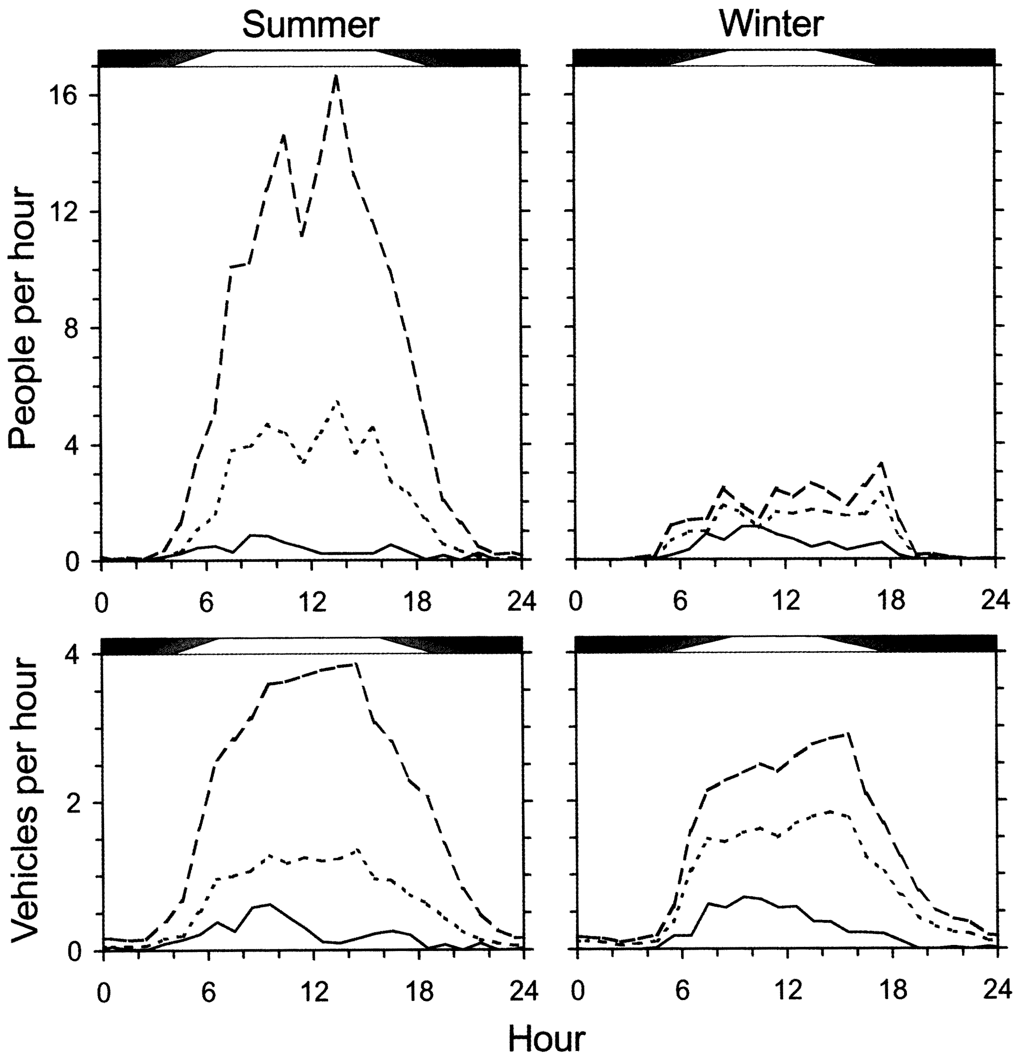

Fig. 5. Daily patterns of average human activity (mean number of people or vehicles per hour) on roads in the wolves' home ranges (dashed lines), mean human activity on roads used for radiotracking during absence of wolves (dotted lines), and average human activity on roads used for radiotracking during the presence of wolves (continuous lines) in the Białowieża Forest, Poland, in 1998 and 1999.

lant. After a reduction of predators, the prey rapidly becomes less wary. Human–wolf relationships likely follow the same principle. Wolves under persecution would thus be more alert and therefore less visible to humans. This does not necessarily mean that wolves would become exclusively nocturnal, because they can spatiotemporally avoid contact with humans. Forest habitat appeared of particular importance in spatiotemporal segregation since wolves rarely left forest cover in daylight in the Białowieża Forest and in Italy (Ciucci et al. 1997). In areas frequented by people, wolves seem able to maintain their activity during the day by taking advantage of available forest cover.

Spatial avoidance of humans by wolves appeared to occur alongside spatiotemporal segregation. Human settlements, public roads, and edges to agricultural land reduced the area used by wolves even at night. Human settlements and roads both produce noise and light, which may explain why the wolf avoidance found in our study increased with the size of settlements and the intensity of road use. Thurber et al. (1994) noted a similar behavior in Alaska where wolves avoided a public

Table 2. Mean reserve selection indices (± difference to the 95% CI limits) for 4 wolves of the National Park pack (protected forest reserve), 3 wolves of the Ladzka pack (commercial forest), and 4 wolves of the Leśna packs (commercial forest) in the Białowieża Forest, Poland, 1994–1999.

	National Park pack		Leśna packs		Ladzka pack	
	Day	Night	Day	Night	Day	Night
Summer						
Nature reserves	–0.94 ± 0.06	–0.86 ± 0.15	–0.08 ± 0.78	–0.27 ± 1.01	–0.30 ± 0.29	–0.68 ± 0.44
Strict reserve	0.91 ± 0.07	0.82 ± 0.08				
New National Park	–0.53 ± 0.37	–0.20 ± 0.19				
Border zone	–0.70 ± 0.19	–0.76 ± 0.36	0.06 ± 0.71	0.07 ± 0.56		
Winter						
Nature reserves	–0.81 ± 0.23	–0.83 ± 0.25	0.31 ± 0.48	0.32 ± 0.41	–0.18 ± 0.54	0.12 ± 0.36
Strict reserve	0.87 ± 0.06	0.61 ± 0.17				
New National Park	–0.25 ± 0.07	0.16 ± 0.17				
Border zone	–0.71 ± 0.23	–0.52 ± 0.27	0.19 ± 0.23	–0.12 ± 0.11		

road but selected little used roads for ease of travel. In a Canadian area with little human activity on linear corridors (mostly pipeline or seismic lines), wolves were even closer to these corridors than expected (James and Stuart-Smith 2000). Wolves were most affected by human activity (e.g., avoided human-made structures) in areas where human activity was lowest, indicating that wolves are more sensitive to human activity when they have the least contact with humans. This means that wolves may habituate to some degree to human activity also in areas where they are not completely free of human persecution.

Spatial avoidance is especially important for wolves during the denning period because breeding females are unable to spatiotemporally avoid human contact. Breeding females can either choose particularly quiet places or they have to tolerate human activity. In Minnesota and Wisconsin, some wolf packs tolerated forestry operations close to their den sites (Thiel et al. 1998). In the Bialowieża Forest, breeding females were farther from forest edges that bordered with human settlements during the denning period than during the rest of the year. Den and rendezvous sites were farther than expected from human settlements, the forest edge, and intensively used public roads, but wolves did not abandon the den when foresters worked near the den sites (Theuerkauf et al. 2003*b*).

Distribution of prey may have interfered with the influence of humans on wolf habitat use. Prey abundance in the Białowieża Forest is not affected by roads, however (J. Theuerkauf et al., unpublished data), thus wolf avoidance of roads was not biased by prey. Prey abundance is higher within the strict reserve than in the commercial forest (J. Theuerkauf et al., unpublished data). However, wolves in the National Park regularly leave the strict reserve from dusk to dawn to hunt, but usually return to the reserve during the day. Because wolves in the Białowieża Forest hunt mainly from dusk to dawn (Theuerkauf et al. 2003*a*), we conclude that wolves select the strict reserve during the day to avoid humans, rather than because of higher prey density.

MANAGEMENT IMPLICATIONS

Wolves are protected by law in many European countries and in the United States with the exception of Alaska. As a result, wolves are slowly expanding their ranges in both Europe (Boitani 2000) and the United States (Mech 1995). However, legal protection is not the only factor that determines the speed and extent of wolf recolonization, since the first wolves to recolonize are often killed illegally (Mech 1977).

In the United States, Thiel (1985), Jensen et al. (1986), Mech et al. (1988), and Mech (1989) estimated a road density of about 0.6–0.7 km/km^2 as a threshold for wolf occurrence. Road density was, therefore, a major factor used to predict suitable habitats for wolves in the United States and Italy (Mladenoff et al. 1995, 1999; Mladenoff and Sickley 1998; Corsi et al. 1999). However, in the Białowieża Forest, wolves survived in a commercial forest with a road density of about 1.2 km/km^2, although humans caused many wolf deaths (Jędrzejewska et al. 1996). Similarly, Merrill (2000) reported that a wolf pack in Minnesota survived in a military area with a road density of 1.4 km/km^2. Therefore, wolves likely will recolonize areas of increasingly high road density.

Fritts and Carbyn (1995) outlined the necessity for nature reserves of up to several thousand square kilometers to maintain an isolated wolf population. However, medium-sized nature reserves (e.g., strict reserve of the Bialowieża National

Park: 50 km^2) can serve as core areas for wolves. Wolves are able to disperse over distances of up to 800 km (Fritts 1983), and wolves have crossed highways over 200 times without being killed (Merrill and Mech 2000). Therefore, the exchange of individuals should be high enough to ensure the survival of a wolf population even when packs are patchily distributed in fragmented landscapes. Nature reserves or similar areas with limited human access (e.g., military training areas, state border zones, mountains) can improve the suitability of populated areas where wolf recovery is desired. In addition, nature reserves often have higher densities of potential prey species for wolves, which should improve the nutritional situation for wolves and may reduce depredation on livestock (Meriggi and Lovari 1996).

We conclude that spatiotemporal segregation is an adaptation that enables wolves to coexist with humans while keeping their activity pattern optimized toward food acquisition. The distribution of areas with restricted human access, forest, human settlements, and intensively used public roads are the main factors determining the areas that wolves select. Nature reserves or similarly protected areas of at least 50 km^2 should be especially suitable as core areas for wolf home ranges and function as stepping stones for recolonizing wolves in Europe and North America.

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