

NOTE

Selection of den, rendezvous, and resting sites by wolves in the Białowieża Forest, Poland

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Abstract: We studied wolf (*Canis lupus*) selection of 19 den, 10 rendezvous, and 31 resting sites found between 1986 and 2000 in the Białowieża Forest (Poland). Our objective was to determine whether wolves selected sites far from villages, forest edges, and roads, and whether these sites had dense ground cover for concealment. We also tested whether wolves selected a particular forest type for their den sites. Den and rendezvous sites were located at greater distances from villages, forest edges, and intensively used roads than random points. Locations of resting sites were not affected by these manmade structures. Wolves selected dry coniferous forests for den sites but also used other forest types. We concluded that the suitability of an area for pup raising depended mainly on the spatial distribution of forest, human settlements, and public roads, and to a lesser extent on habitat characteristics.

Résumé : Nous avons étudié la sélection par des loups (*Canis lupus*) de 19 antres, 10 lieux de rendez-vous et 31 points de repos trouvés entre 1986 et 2000 dans la forêt de Białowieża (Pologne). Notre but était de déterminer si les loups sélectionnent des sites éloignés des villages, de l'orée de la forêt et des routes ou des sites où la végétation au sol est dense et leur permet de se dissimuler. Nous avons aussi vérifié si, pour établir leurs antres, les loups sélectionnent un type particulier de forêt. Les antres et les lieux de rendez-vous se situent plus loin des villages, de l'orée de la forêt et des routes à forte circulation que des points aléatoires. L'emplacement des points de repos n'est pas affecté par les structures d'origine humaine. Les loups établissent leurs antres dans les forêts de conifères sèches, mais ils utilisent aussi d'autres types de forêt. Nous avons conclu que les facteurs qui affectent la sélection de l'environnement chez les loups durant l'élevage des jeunes sont principalement la répartition des forêts, celle des habitations et celle des routes publiques, alors que l'habitat joue un rôle secondaire.

Introduction

Wolves (*Canis lupus*) in Europe and North America are recolonizing areas from which they had been extirpated (Mech 1995; Boitani 2000). The success of their recovery depends as much on public acceptance as on habitat suitability, which should provide adequate food resources as well as areas of low human activity where wolves can retire (Boitani 2000). The ability to predict potential den and rendezvous sites is necessary to protect these areas during the breeding season (Wisconsin Wolf Advisory Committee 1999). Although there

are studies on den and rendezvous sites from North America (Murie 1944; Ballard and Dau 1983; Fuller 1988; Ciucci and Mech 1992) and Russia (Tehsin 1987; Ryabov 1988), there is a lack of data on the habitat selection of denning wolves as well as on the potential influence of humans on den, rendezvous, and resting site selection. We tested whether wolves of the Białowieża Forest (Poland) selected den, rendezvous, and resting sites that were farther from villages, forest edges, and roads than random and had a dense ground cover offering concealment. We also assessed which forest type wolves selected for den sites.

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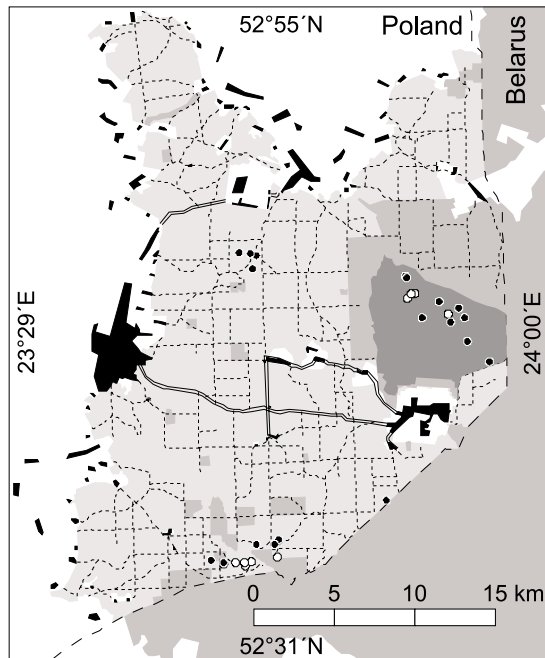
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Fig. 1. Locations of den (black dots circled in white) and rendezvous (white dots) sites of four wolf (*Canis lupus*) packs in the Białowieża Forest with distribution of the commercial forest (light grey), nature reserves and Belarussian National Park (medium grey), the strict reserve of the Polish Białowieża National Park (dark grey), human settlements (black), heavily used public roads (double lines), forest roads (dotted lines), and state border between Poland and Belarus (broken line).



Study area and methods

The study area was the Polish part of the Białowieża Forest (580 km²), which is situated on the border with Belarus. A 100 km² section of the forest is protected as the Białowieża National Park (Fig. 1) with a strictly protected core area of 50 km² in which harvesting of plants or animals is prohibited, entry is limited to permit holders, and no motorized traffic is allowed. There are 22 additional small (0.1–3.7 km²) nature reserves in the Białowieża Forest. Human activity in the strict reserve of the National Park is low except for a small area close to the park's entrance where tourists are given guided tours. Human activity is more intense in the rest of the forest, which is exploited commercially. Human density is about 7 inhabitants/km² in the Białowieża Forest and 70 inhabitants/km² in the Białystok administration district surrounding the study area. The density of forest roads suitable for two-wheel-drive vehicles is about 1.2 km/km² in the commercial forest, but only about 50 km of paved roads (0.1 km/km²) is intensively used by the public. The Belarussian part of the Białowieża Forest (870 km²), which is adjacent to the study area, is a national park, but limited logging is allowed and wolves are hunted (Jędrzejewska et al. 1996). Wolves have been protected since 1989 in the Polish part of the Białowieża Forest, but some wolves from the commercial forest and national park died in snares set by poachers for wild boar (*Sus scrofa*) or were shot. In the study area, the core area of one wolf pack was the strict reserve of the Białowieża National Park. Three other packs lived in the com-

mercial part of the Białowieża Forest. For a detailed description of the study area, see Jędrzejewska and Jędrzejewski (1998).

We grouped the 19 vegetation types occurring in the Białowieża Forest (Kwiatkowski 1994) into four forest types according to species composition and ground humidity. We classified habitats as dry or wet forests (groundwater level lower or higher than 2 m below the surface) and coniferous or deciduous forests depending on the dominating tree species. Accordingly, the category dry coniferous forests included fresh pine (*Pinus sylvestris*) forests, pine – spruce (*Picea abies*) mixed forests, and thermophilous pine–spruce forests described by Kwiatkowski (1994). Dry deciduous forests included fresh oak (*Quercus robur*) – linden (*Tilia cordata*) – hornbeam (*Carpinus betulus*) forests, pine–oak mixed forests, thermophilous oak forests, thermophilous oak–hornbeam forests, and eutrophic oak–linden–hornbeam forests. We considered alder (*Alnus glutinosa*) – spruce forests, bog spruce forests, bog pine forests, humid pine forests, and humid oak – spruce forests as wet coniferous forests. Wet deciduous forests included humid oak–linden–hornbeam forests, ash (*Fraxinus excelsior*) – elm (*Ulmus campestris*) flood-plain forests, ash–alder flood-plain forests, bog oak forests, bog alder forests, and bog birch (*Betula pubescens*) forests.

We found most den, rendezvous, and resting sites of wolves during a radio-tracking study of wolves from 1994 to 1999 (Jędrzejewski et al. 2001) but included other den sites found between 1986 and 2000 in the analyses. We defined den sites as places where a breeding female raised pups up to weaning. We only used den sites for which we found indications that wolves used them to raise their young. We considered a place as den site with burrows when we found burrows with signs of long wolf use. However, we observed that wolves also use surface beds for raising pups in the Białowieża Forest. We therefore considered a place as a den site with surface beds when we did not find burrows but lairs with signs of long wolf use (beds with many wolf hairs) at a location where a radio-collared female had stayed stationary during the first weeks of May. We considered a place as a den site by radio-tracking when we did not find a burrow or surface beds but a radio-collared female had stayed stationary during the first weeks of May. When wolves were not active, our mean radio-tracking error, which we estimated by comparing radiolocations with confirmed locations of den, rendezvous, and resting sites, was 110 m (Theuerkauf and Jędrzejewski 2002). We considered the location of a radiolocated den site sufficiently accurate for estimating distances to roads, villages, and forest edges and the general forest type using the vegetation map of Kwiatkowski (1994).

We defined rendezvous sites as places where young wolves stayed for several days and to which the adults returned regularly and resting sites as places where wolves had been detected by radio-tracking to be inactive for more than 1 h but that wolves did not reuse. We only included rendezvous and resting sites in the analysis when we found signs of wolf use at these sites (beds with wolf hairs, scats, wolf tracks, gnawed bones) or when we confirmed a resting site by snow-tracking.

We calculated distances between the location of sites used by wolves and the nearest manmade structure (villages, edges between the Białowieża Forest and arable land, roads) and determined the forest type for den, rendezvous, and resting

Table 1. Means (with 95% confidence intervals (CI)) of habitat characteristics and distances to manmade structures of den, rendezvous, and resting sites compared with a *U* test with random sites in the Białowieża Forest.

Habitat structure or distance	Den		Rendezvous		Resting		Random
	Mean ± CI	<i>P</i>	Mean ± CI	<i>P</i>	Mean ± CI	<i>P</i>	Mean ± CI
Vegetation cover at knee height (%)	11±8	0.808	24±6	0.270	17±10	0.489	25±9
Canopy cover (%)	43±43	0.746	44±37	0.523	25±20	0.074	49±14
Vision distance (m)	18±11	0.435	11±5	0.082	20±14	0.450	21±6
Distance to villages (km)	4.3±0.7	<0.001	4.5±0.8	<0.001	2.8±0.5	0.168	2.4±0.3
Distance to forest edges (km)	3.9±0.6	<0.001	4.2±0.6	<0.001	2.5±0.5	0.154	2.1±0.3
Distance to primary roads (km)	5.8±0.7	<0.001	7.1±0.9	<0.001	3.3±0.8	0.948	3.4±0.5
Distance to secondary roads (km)	2.2±0.6	0.005	3.2±0.4	<0.001	1.6±0.4	0.296	1.4±0.2
Distance to tertiary roads (km)	1.1±0.5	0.041	0.9±0.7	0.678	0.8±0.3	0.300	0.5±0.1

Table 2. Numbers of den sites with burrows, den sites with surface beds, and radiolocated den sites occurring in different forest types compared with 100 random sites in the Białowieża Forest using a Fisher's exact test.

Forest type	Burrows	Surface		Radiolocated	All dens	Random points	<i>P</i>
		beds					
Dry coniferous	4	2		1	7 (37)	14 (14)	0.004
Dry deciduous	2	0		1	3 (16)	34 (34)	0.176
Wet coniferous	2	0		2	4 (21)	15 (15)	0.503
Wet deciduous	1	3		1	5 (26)	37 (37)	0.441

Note: Values in parentheses are percentages.

sites using a Geographic Information System (GIS). We assessed selection by comparing distances and forest type of sites used by wolves with those of 100 random points generated by GIS within the study area. As data on distances were not normally distributed, we compared means of distances between wolf and random sites by a Mann–Whitney *U* test. We compared the numbers of wolf and random sites in a forest type with a Fisher's exact probability test for 2×2 tables. We identified for analysis three types of forest roads in the study area (J. Theuerkauf, W. Jędrzejewski, K. Schmidt, and R. Gula, unpublished data): primary roads intensively used by the public (1000 – 10 000 vehicles/week), secondary roads (48–500 vehicles/week), and tertiary roads (<40 vehicles/week).

We described habitat characteristics for 6 den, 7 rendezvous, and 10 resting sites found during the summer of 1997 within a 50-m radius of the site's centre. For each of these 23 sites, we also described the habitat at a site randomly chosen within the home range of the given wolf and compared means of wolf and random sites with a *U* test. The habitat characteristics described were (i) the sight distance at wolf eye level (about 50 cm) in the four compass directions, (ii) the estimated percentage of sight-blocking structures on the ground (young trees, shrubs, fallen trees), and (iii) the estimated percentage of open canopy in the 50-m circle.

Results

We analysed wolf selection of 19 den, 10 rendezvous, and 31 resting sites (11 in summer, 20 in winter) found between 1986 and 2000. Den and rendezvous sites were farther from edges of the forest, settlements, and intensively used roads than random sites (Table 1). All den and rendezvous sites of wolves occupying the Białowieża National Park were in the

strict reserve (50 km²), whereas all den and rendezvous sites of wolves living in the commercial forest with small nature reserves (<4 km²) were outside these reserves (Fig. 1). Wolves did not avoid manmade features for their resting sites (Table 1). The ground vegetation around den, rendezvous, or resting sites was not different from that of random sites and the vision distance at sites used by wolves did not differ from that at random sites. Although small glades were present within the 50-m circles around all den or rendezvous sites, the canopy cover of these sites was no more open than random.

Four den sites were in thermophilous pine – spruce forests, four in humid oak–linden–hornbeam forests, three in fresh oak–linden–hornbeam forests, two in humid pine forests, two in fresh pine forests, one in an ash–alder floodplain forest, one in an alder–spruce forest, one in a bog spruce forest, and one in a pine–spruce mixed forest. The only forest type that wolves selected for den (Table 2) and rendezvous sites (Fisher's exact test, $P = 0.013$) was dry coniferous forests. Wolves did not select a particular type of forest for their resting sites (all $P > 0.35$). Burrows at den sites were often ($n = 6$) enlarged entrances (one or two) of former badger setts or fox dens and always dug in sandy soils ($n = 9$). Surface beds at den sites ($n = 5$) were either under roots of fallen trees or between the roots of large standing spruces. We did not observe females to reuse a den in the following years.

Discussion

Ballard and Dau (1983) described the tree cover at den and rendezvous sites in Alaska as homogenous or mixed stands with semi-open canopies interspersed with glades, and Fuller (1988) noted that dens in Minnesota tended to be

in coniferous forest with a semi-open to closed canopy. Although we found glades to be present at all rendezvous or den sites, we found no preference for a particular forest structure. We suggest that selection of dry coniferous forest for den sites is mainly due to the soil type, as sandy soil seems to be the only substrate in which burrows occur (Murie 1944; Mech 1970; Ballard and Dau 1983; Fuller 1988; Ryabov 1988; this study). However, as wolves may forego excavating dens and use other features such as surface beds, hollow logs, or the base of fallen trees to give birth and raise their young (Joslin 1967; Mech 1970; Fuller 1988; Ryabov 1988; this study), the protection of particular habitat types as potential wolf den sites may not be required.

In the Superior National Forest (Minnesota), where human activity compared with our study area is lower, wolves locate dens randomly throughout their territory and only avoid a 1-km strip at the edge of their territory, probably to minimize confrontation between packs (Ciucci and Mech 1992). In the Northwest Territories (Canada), wolves avoid denning in forests (Heard and Williams 1992). Wolf den and rendezvous sites in the Białowieża Forest, however, were only in forest and farther than random sites from forest edges, villages, and intensively used roads. Wolves probably located den and rendezvous sites in areas where encounters with humans were the least likely but did not select forest with dense ground cover where they may have been more concealed. Wolves living in the Białowieża National Park located their dens and rendezvous sites in the strict reserve (50 km²), but the packs living in the commercial forest did not use small nature reserves (<4 km²), although dens were close to these reserves. Our results suggest that small nature reserves are not sufficient to improve the suitability of an area for wolf breeding. This does not exclude the possibility that small nature reserves may improve the habitat suitability for wolves in general (e.g., prey density).

The reason why wolves in our study did not reuse dens and avoided locating den sites close to villages and roads may be a behavioural adaptation to human persecution. Between 1975 and 1994 in the Białowieża Forest, people took about 30% of pups from the dens for pets or for a bounty payment (Jędrzejewska et al. 1996). However, we observed during radio-tracking that breeding females did not abandon their den sites when occasional forestry work with chainsaws and tractors occurred within 200 m of the den sites, suggesting that wolves did not react strongly to human activity in the forest. Wolves in our study area live at close quarters with humans, which probably explains why they tolerated forestry work within a close distance of their den. Examples from North America also suggest that wolves can adapt to human activity even at the den (Mech et al. 1998; Thiel et al. 1998), whereas wolves in wilderness areas seem to be intolerant of humans (Chapman 1979). We conclude that, in areas where wolves coexist with humans, the distribution of forest, settlements, and public roads is the main factor determining selection of den or rendezvous sites by wolves, whereas habitat characteristics play a secondary role.

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