WOLF PACK TERRITORY MARKING IN THE BIAŁOWIEŻA PRIMEVAL FOREST (POLAND)

by

K. ZUB[1,2], **J. THEUERKAUF**[1,3,4], **W. JĘDRZEJEWSKI**[1], **B. JĘDRZEJEWSKA**[1], **K. SCHMIDT**[1] **and R. KOWALCZYK**[1,5]

([1] Mammal Research Institute, Polish Academy of Sciences, 17-230 Białowieża, Poland; [3] Wildlife Biology and Management Unit, Department of Ecosystem and Landscape Management, Munich University of Technical Sciences, 85354 Freising, Germany; [4] Current address: International Centre of Ecology, Polish Academy of Sciences, ul. Bełzka 24, 38-700 Ustrzyki Dolne, Poland)

(Acc. 3-IV-2003)

Summary

We analysed data on territory marking with urine, scats, and ground scratching by wolves (*Canis lupus*) belonging to four packs in the Białowieża Primeval Forest, Poland. The aims were to determine: (1) seasonal variation in the marking rates, (2) significance of various kinds of marking in territory demarcation, and (3) relationship between spatial distribution of wolves' marking and their use of territory. Continuous radio-tracking and subsequent snow tracking of the collared wolves were the main methods. Deposition rates of scats showed little variation in time and space, whereas rates of urine marking and ground scratching showed large seasonal and spatial variation. Wolf marking rates with urine and ground scratching were highest during the cold season (October-March) and peaked during the mating season, in January and February. Marking intensity did not grow with the number of wolves in a pack, and *per capita* rates of marking were highest in wolves travelling singly or in pairs. Mean marking rates per km of wolf trail were low in the core areas of territories, and increased

[2] Corresponding author's e-mail address: karolzub@bison.zbs.bialowieza.pl

[5] This study was financed by the Polish State Committee for Scientific Research (grant 6 P04F 026 12), the Mammal Research Institute budget, the European Natural Heritage Fund (Euronatur, Germany), the Flaxfield Nature Consultancy (The Netherlands and UK), the German Academic Exchange Service (to JT), and the German Donor's Association for the Promotion of Sciences and Humanities (to JT). We thank M. Chudziński, W. Jastrzębski, R. Kozak, S. Rouys, I. Ruczyński, S. Śnieżko, P. Wasiak, and all the assistants and volunteers, who helped us during the field work. We are grateful to Linus Svensson, Pehr H. Enckell and two anonymous reviewers for helpful comments on the manuscript.

when wolves approached the boundaries. However, densities of marks (number of marks per square km) increased in territory centre (due to intense use of core area by the pack), and in peripheral areas, which bounded other territories (due to increased marking activity by wolves when moving along the territory edge). Our findings did not support the 'olfactory bowl' model of wolf territory marking, as marks were not distributed equally along territory boundaries. Instead, marks were concentrated in 'hot spots' more vulnerable to penetration by intruders (territory edge) or more valuable to owners (vicinities of breeding dens).

Keywords: *Canis lupus*, territory, urine marking, ground scratching, Białowieża Forest, economic constrains, 'hot-spots' model.

Introduction

Scent marking is an important aspect of olfactory communication in mammals. This behaviour probably originated from a response to unfamiliar surroundings or situations, but has gained numerous social functions throughout evolution (Kleiman, 1966). Wolves *Canis lupus* mark to assert dominance, in pair-bonding, to achieve reproductive synchrony, for spatial orientation and territory maintenance, and to mark empty food caches (Peters & Mech, 1975; Rothman & Mech, 1979; Harrington, 1981; Asa *et al.*, 1984; Paquet & Fuller, 1990; Paquet, 1991; Vila *et al.*, 1994). Scent marking in wolves and other canids involves urination, defecation, and anal gland secretions aimed at specific, usually conspicuous objects. Ground scratching is a form of marking, which in addition to olfactory information involves a visible sign. Animals that are marking often adopt special postures that convey visual messages to other individuals. Without information on the stance taken by the animal, it is difficult to determine whether urination and defecation have behavioural or eliminative characters (Bekoff, 1979; Paquet & Fuller, 1990). Moreover, urine-marking rates are controlled by hormones and therefore vary seasonally (Asa *et al.*, 1990). Marking rates are also influenced by the presence of various stimuli such as previous marks, marks of other conspecifics, conspicuous landmarks and novel objects or smells, as well as by suitable ground for scratching (Kleiman, 1966; Peters & Mech, 1975).

In many species of mammals marking is linked to territory defence (Macdonald, 1980; Gosling, 1982; Hutchings *et al.*, 2001). Because the establishment and maintenance of marks involves a cost, animals are not able to mark the whole territory. Instead, a limited number of marks must be placed in a way to maximise the chance of being detected by conspecifics (Gosling &

Roberts, 2001a). The distribution pattern of marks within territories varies in relation to economic constrains and have been well described for many mammalian species (review: Gosling & Roberts, 2001b). In wolves, the primary function of marking is territory maintenance (Peters & Mech, 1975; Paquet & Fuller, 1990; Paquet, 1991), and various distribution patterns of marking sites were suggested for this species. Peters & Mech (1975) proposed an 'olfactory bowl' model, where marks were more numerous along peripheries than in the centre of the territory. Bowen & Cowan (1980) suggested a similar model for coyotes *Canis latrans* but studies by Barrette & Messier (1980) did not provide support. Also Paquet & Fuller (1990) questioned, whether such a model is appropriate for wolves, because they did not find differences in the frequency of marks between peripheries and centres of wolf territories in the Riding Mountain National Park, USA.

In this paper, we report the results of a radio- and snow-tracking studies on wolves, conducted in a large woodland in eastern Poland (see Okarma *et al.*, 1998; Jędrzejewski *et al.*, 2001, for details). We present data on marking by wolves, and relate them to known home ranges and other information on wolf ecology in the study area. The main objectives of the study were to: (1) determine the factors that affect marking rates in various seasons, (2) estimate the significance of various kinds of marking for territory demarcation, and (3) detect any relationship between the spatial distribution of wolves' marking and the intensity of territory use.

Material and methods

Study area

Białowieża Primeval Forest (BPF, 52°30′-53°N, 23°30′-24°15′E) covers 1450 km^2 and is located on the Poland-Belarus border. It is the best preserved woodland of its size in temperate Europe. The study was conducted in the Polish part of BPF (595 km^2), which consists of managed (harvested and replanted) stands and a protected part (Białowieża National Park, covering 100 km^2). Tree stands are composed of Norway spruce *Picea abies*, Scots 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 a.s.l. (see Jędrzejewska & Jędrzejewski, 1998, for details). The Polish part of BPF has a dense network of forest roads and paths (approximately 1 km/km^2), and five paved roads. During the study period (1996-1999), the mean temperature was −3.6 °C in January and 18.7 °C in July. Annual precipitation averaged 567 mm and snow cover persisted for an average of 86 days. Maximal snow depths in winter seasons varied between 13 and 63 cm. Five ungulate species occur in the BPF: red deer *Cervus elaphus*, wild boar *Sus scrofa*, roe deer *Capreolus capreolus*, European bison *Bison bonasus*, and moose *Alces alces* (Jędrzejewska *et al.*, 1997). In the 1990s, typical home ranges of wolf packs covered 100-300 km^2, wolf densities were 2-2.6 individuals/100 km^2, and mean pack size was four to five wolves (Okarma *et al.*, 1998).

General methods

In 1996-1999, we radio-tracked 11 wolves belonging to 4 packs, referred in the text as the Białowieża National Park (BNP), Ladzka, Leśna I, and Leśna II packs, formed by 2 to 7 individuals in various years. The Leśna II pack was founded in 1997/98 by a pair of wolves, which left Leśna I pack; their ranges largely overlapped during the following year (see Jędrzejewski *et al.*, 2001, 2002, for details). Radio-tracked packs neighboured with other wolf groups except for the north-western edges of the Białowieża Forest. Radio-locations were taken at 15-min intervals, usually during sessions of continuous radio-tracking that lasted from 2 to 9 days and were run by a team of observers working in 8-h shifts. The mean distance between the observer and the wolves was 940 m, and the presence of an observer had no effect on activity or movements of the tracked wolf (Theuerkauf & Jędrzejewski, 2002). During radio-tracking, when following forest roads, as well as during any field work in the forest we mapped all visible scent marks, and recorded the type of marking (urine, scats, scratching), number of marks, location of marking (road, road junction, forest) and, whenever possible, the estimated number of wolves. During periods with snow cover (November-April), we snow-tracked radio-collared wolves and recorded all marks visible in snow. Number of tracked animals, habitat, type and place of marking, number of marks, occasionally also a target of marking (trunk, log, wooden or concrete post, side of the road *etc.*) were noted. The length of wolf trail was measured by pacing or GPS. We did not attempt to discriminate between raised-leg urination (RLU) and squat urination (SQU). In many cases, however, urine marks were accompanied by scratching, what indicates behavioural rather than eliminative character of urination.

We obtained 34,181 radio-locations of wolves (241 in 1996, 11,543 in 1997, 15,907 in 1998 and 6,490 in 1999). For the BNP pack, we collected 10,820 locations, for the Ladzka 10,967, for Leśna I pack 7,569, and for Leśna II pack 4,825 locations. We recorded 418 marks (285 scratches, 95 urine and 38 scats) during radio-tracking and other field work in the forest. In 1996-1999, we snow tracked wolves on 109 occasions (10 in the winter season of 1996/97, 52 in 1997/98, 44 in 1998/99 and 3 in December 1999), which amounted to 475 km of wolves' trails. Mean distance of continuous snow tracking was 4.35 km (SD 2.83). During all snow-tracking sessions, we recorded 1035 markings by wolves (413 scratches, 521 urine markings, and 101 scats). These data were used to estimate the mean number of marks per 1 km of trail.

All radio-locations and all marks were analysed with the program Tracker (Radio Locations Systems). Spatial distribution of marks was analysed using the Kernel method. Territories were expressed as Minimum Convex Polygons with 100% of localisations (MCP 100%) and MCP comprising 75, 50, and 25% of locations. The resulting 4 zones (each comprising 25% of locations) within the MCP 100% were numbered from 1 (central zone) to 4 (outermost zone). In each zone, we analysed marking density (expressed as numbers of marks per 1 km^2), as well as marking rates (number of marks in relation to the time wolves spent in each zone). We additionally split all snow tracking samples into two groups: the first including routes in the main part of the territory (MCP 90%) and the second, including routes along the edge of territory (beyond MCP 90%). We analysed marking rates in these two zones, expressed as the number of marks per 1 km of wolf trail. Snow-tracking samples that crossed both zones were excluded from the analysis. The relation between the size of wolf pack and marking rates recorded during snow tracking were analysed using two measurements: mean number of marks per pack and *per capita*.

Results

Wolf marking rates were high in the cold season, and peaked during the mating season, in January-February (Fig. 1). The number of scratchings increased gradually from October, reached a peak in January (1.9 scratches/km of wolf trail) and declined rapidly in February and March. Between April and September the intensity of ground scratching, expressed as number of scratches per 1,000 radio-locations, was low and rather stable. Urine marking followed a similar seasonal pattern, with number of marks per 1 km of wolf trail being highest in February (3.0 marks/km) (Fig. 1). The number of scats (mean ± SE) found during snow-tracking did not show any distinct variation from November till April (0.30 ± 0.06 scats/km, $N = 109$).

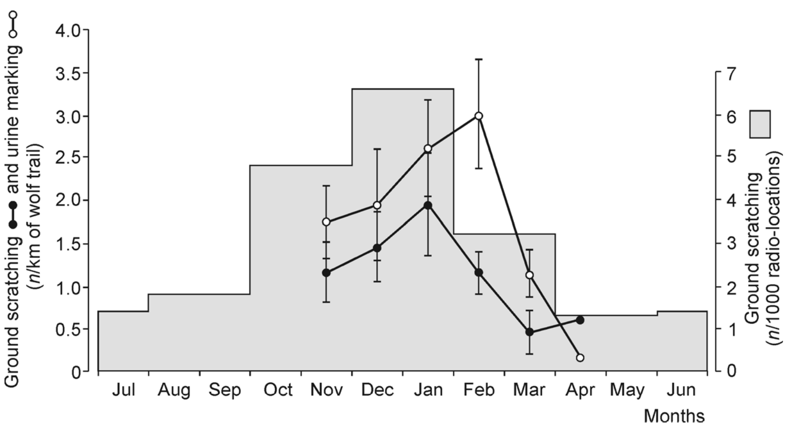

Fig. 1. Seasonal variation in the marking rates by radio-collared wolves *Canis lupus* in Białowieża Primeval Forest (E Poland). Data were collected during radio-tracking of 4 packs in 1996-1999 ($N = 1453$ records of marking covering whole year) and by snow tracking of wolves (1996-1999, November-April, totally 475 km). The latter data are shown as mean values ± SE. Ground scratching is presented as the numbers per 1000 radio-locations (whole year) and as the numbers/1 km of wolf trail (cold season). Urine marking is expressed only as numbers/1 km of wolf trail (cold season).

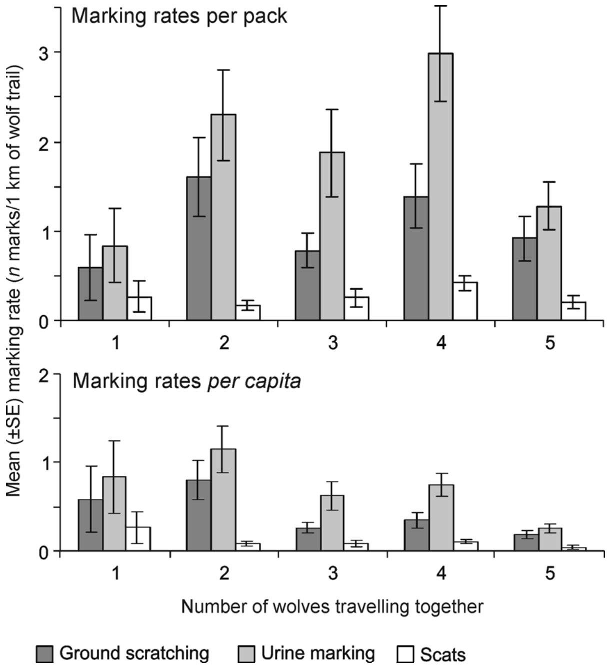

Fig. 2. Marking rates (mean ± SE) calculated per wolf pack and *per capita*. Data collected by snow tracking, total lengths of wolf trails ranged from 24 km in a single wolf to 176 km in a pack of 4 wolves.

Marking rates per pack did not depend on the number of wolves in a pack (Kruskall-Wallis test, $N = 102$, $H = 5.65$, $p = 0.2$) (Fig. 2). However, *per capita* numbers of all three kinds of marks were significantly higher in a single wolf and/or pairs travelling together than in packs of 3-5 wolves (Kruskall-Wallis test, $N = 102$, $H = 12.7$, $p = 0.01$) (Fig. 2).

We analysed how the marks were distributed in the four zones of packs' territories, each including 25% of localisations, from the central core area, to the outermost, peripheral belt. Mean area (±SE) of the central core zones was 7.5 ± 3.7 km^2 (3% of the home range area), the second zones 26.0 ± 5.9 km^2 (11%), the third ones 60.7 ± 10.9 km^2 (26%), and the fourth outermost zones 144.0 ± 18.8 km^2 (60%). Number of marks generally increased from the inner parts of territories towards the edges (Fig. 3). However, the density of markings (number of marks per km^2) either declined towards peripheries (scats) or did not differ among the four zones (scratching, urine marking) (Fig. 3). The density of urine marks was highest in the second zone (0.87 ±

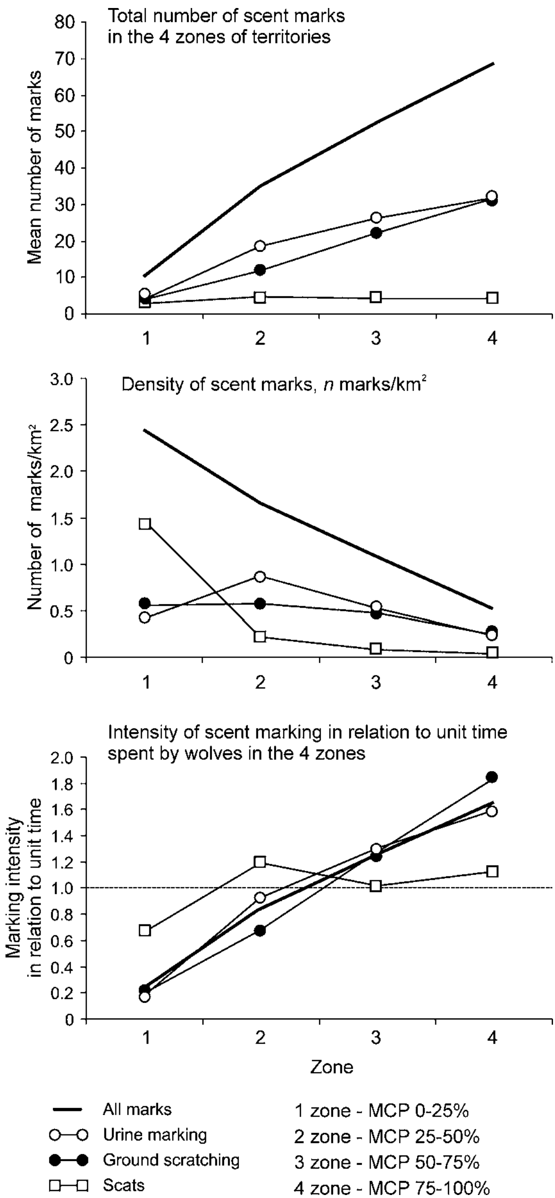

Fig. 3. Number of scent marks in four zones of wolf territories (mean values for all packs). Each zone comprises 25% of radio-locations. Upper panel presents the mean number of marks in the four zones. Middle panel shows the density of scent marks in each zone. Lower panel presents the intensity of scent marking in relation to the time spent by wolves in the zones (1 = marking rates proportional to 25% time spent by wolves in each zone).

0.26 marks/km^2) and the density of scratches was similar in the first and the second zones (0.56±0.3 and 0.58±0.28 scratches/km^2). The density of scats was 8-times higher (1.46 ± 0.86 scats/km^2) in the first zone than in the other zones. Total marking density was highest in the central zone (2.45 ± 0.82 marks/km^2), and decreased gradually to the edges. When comparing the area of each zone, density of marks were higher than expected in zones 1-3 and lower than expected in zone 4 (G-test, $G = 55.80$, df = 3, $p < 0.0001$). This difference was statistically significant for each of the three kinds of marks (G from 11.4 to 49.8, $p < 0.01$).

Although the proportion of time wolves spent in each zone was the same (25%), the relative marking rate compared to unit time was lower than expected in the inner parts of home range, and higher at the edges ($G = 34.5$, df = 3, $p < 0.0001$ for urine marks; $G = 42.4$, $p < 0.0001$ for scratching), except for scats, which were distributed equally in all zones ($G = 4.4$, $p = 0.8$) (Fig. 3). Therefore, wolves deposited urine marks and scratched most frequently, when they were visiting the peripheral zones of territories.

The average length (±SE) of snow tracking done in the main parts of territories, comprising 90% of radio-locations (3.95 ± 0.33 km, $N = 57$ sections, total length 224.9 km) was comparable to that in the peripheral areas (4.15 ± 0.49 km, $N = 24$, total length 99.5 km). The rates of marking with urine and scratching were higher in the peripheries than in the main parts, though the difference was not statistically significant (Table 1). Number of scats deposited per 1 km of trail was similar in the two areas (Table 1). Based

TABLE 1. *Rates of marking*

Part of territory	Ground scratching	Urine marks	Scats	Sum of all marks
Snow tracking — pooled data				
MCP 90%	0.92 (±0.18)	1.58 (±0.19)	0.27 (±0.06)	2.74 (±0.34)
Peripheries	1.31 (±0.49)	2.04 (±0.58)	0.28 (±0.08)	3.63 (±1.07)
Continuous radio-tracking sessions and snow tracking				
MCP 90%	0.33 (±0.08)	1.27 (±0.22)	0.39 (±0.08)	1.61 (±0.23)
Peripheries	1.80 (±0.37)	4.09 (±0.87)	0.35 (±0.12)	5.89 (±0.97)

Rates of marking by wolves (in mean number of marks per 1 km of trail, ±SE) in two parts of their territories: the main part (MCP 90% — minimum convex polygon with 90% of locations) and the peripheral part (including the outermost 10% of locations).

on data from continuous radio-tracking sessions (followed by snow tracking), we were able to directly record the change in wolves' behaviour when they moved from the main part of their territory toward its boundary. For 6 radio-tracking sessions (lasting from 3 to 8 days), we calculated the mean values of marking on days when wolves were near the territory edge and on days preceding and following these periods (Table 1). In all cases peripheral areas penetrated by wolves adjoined the territories of other packs. Rates of ground scratching and urine marking increased significantly (Mann-Whitney U test, $U = 141$ and 103, respectively, $p < 0.001$). Number of scats left per 1 km of trail did not change ($U = 309$, $p = 0.8$). When wolves approached the territory boundary, their rate of marking (all marks summed) increased 3.5-fold (Table 1).

Areas comprising 75% of mark locations (plotted using the Kernel method) were compared with the distribution of radio-locations and overlaps of home ranges of the 4 wolf packs (Fig. 4). Densities of marks were highest in the centres of wolf territories as well as in some of the areas, where neighbouring territories overlapped. The latter situation was especially manifest in packs Ladzka and BNP, which overlapped more than the other packs. Also, the border zone of these two packs was located in the contiguous forest with no manifest terrain features. There was markedly less territorial marking recorded between Ladzka and Leśna packs, and between BNP and Leśna packs. In both cases, the border zones between packs included visible spatial barriers avoided by wolves: a 20-km bituminous road with fairly heavy traffic, a parallel railway (not active since the early 1900s) and the large glade with Białowieża village (Fig. 4).

Most of marking by the two packs Leśna I and Leśna II that originated from one maternal pack and were closely related genetically (W. Jędrzejewski and co-workers, unpubl. data) concentrated in the core areas of their territories, which greatly overlapped. Packs BNP, Leśna I and II were neighbours to other wolf packs in the Belarussian part of BPF, but the Poland-Belarus state border has been a wide belt of cleared, ploughed soil and a tall, barbed-wire fence. In a few places only, did we record our wolves trespassing the border.

Because wolves often used roads for travelling, the mean distance (±SE) of snow tracking on the roads (4.98 ± 0.44 km; total distance snow-tracked 220.7 km) was longer than in the forest (3.02 ± 0.34 km, total 84.7 km). The type of route influenced the proportion of marks left by wolves when

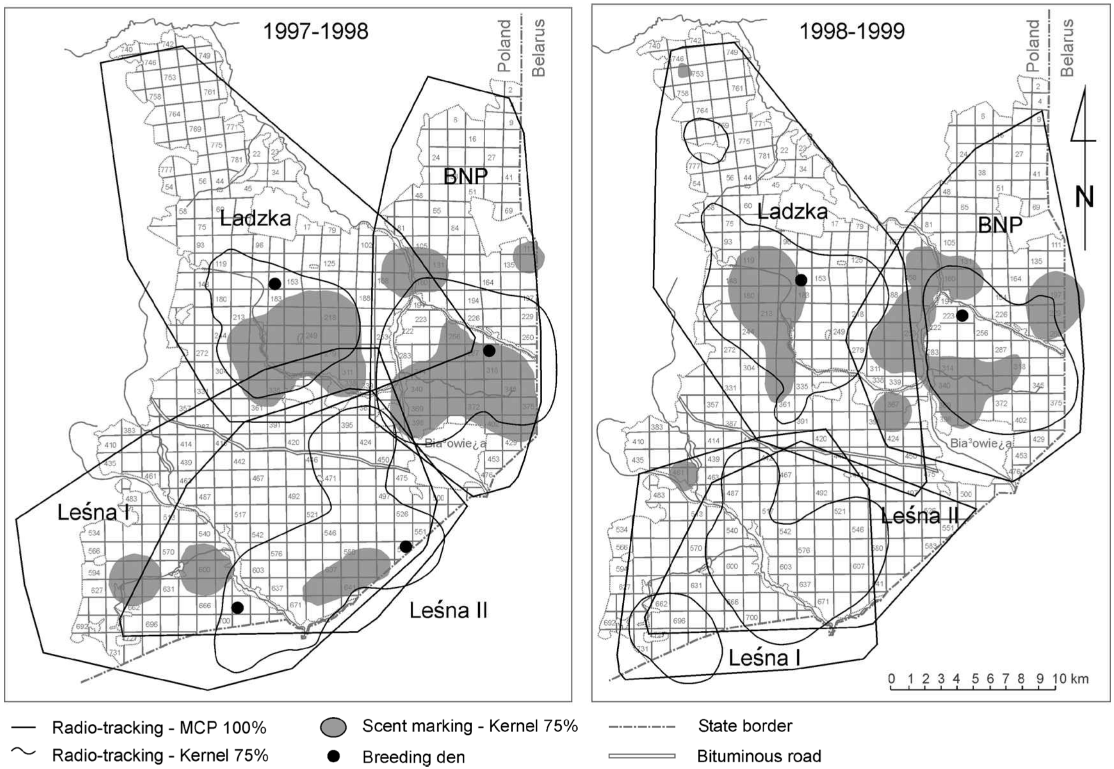

Fig. 4. Areas with high density of marks (urine marking and ground scratching) in wolf territories. Territories: MCP 100% and Kernel 75% based on radio-locations obtained in 1 Nov. 1997 - 31 Oct. 1998, and 1 Nov. 1998 - 31 Oct. 1999. Marks: Kernel 75% plotted using data collected in the cold seasons (1 Nov. - 30 Apr., records pooled for all packs).

TABLE 2. *Intensity of marking by wolves in BPF in relation to type of travel route*

Travel route	Ground scratching	Urine marks	Scats	Sum of all marks
Forest	0.60 (±0.23)	2.54 (±0.61)	0.40 (±0.10)	3.54 (±0.73)
Roads and paths	1.43 (±0.24)	2.08 (±0.33)	0.15 (±0.04)	3.65 (±0.53)

All types of scent marks are presented as number of signs per 1 km of wolf trail (±SE).

travelling (Table 2). Wolves scratched more often on roads than in the forest ($U = 336$, $p = 0.001$). In contrast, they left more scats in the forest ($U = 459$, $p = 0.07$). When travelling on forest roads, wolves left a higher proportion of all kinds of marks at junctions (62% of ground scratching, 57% of urine marking, and 56% of scats recorded on roads).

Discussion

Marking rates by wolves living in the BPF were similar to those reported from North America (Peters & Mech, 1975; Paquet & Fuller, 1990). However, ground scratching rates were much higher in our study. The size and structure of wolf packs were similar in the BPF and in the North American studies, so the visual component of this behaviour, emphasised by Bekoff (1979), cannot alone explain the difference. One of the functions of scratching is to leave a long-lasting signal, which requires a solid surface to ensure the durability of marks. The nature of the surface may also stimulate wolves to scratch. Barrette & Messier's (1980) observations that reported a positive influence of the presence of hard-packed snow on the frequency of coyote scratching support this assumption. The BPF, with its dense network of forest roads, offers good conditions for long-lasting markings. However, we are not able to explain why wolves inhabiting BPF left more scratches compared to North American wolves.

With the exception of scats, marking rates did not depend on the size of wolf packs. This contrasts with studies on wolf marking in North America (Peters & Mech, 1975; Paquet, 1991), in which the number of marks and the number of wolves were highly correlated. In our study, the numbers *per capita* were highest for single wolves and pairs. The number of urination *per capita,* reported by Peters & Mech (1975), was also highest in wolf pairs travelling together (marks done by single wolves were not recorded). Research on wild wolves (Peters & Mech, 1975) and observations of captive ones (Woolpy, 1968) suggest that scratching and raised leg urinations are primarily associated with dominant wolves.

Our observations on the spatial distribution of signs are not consistent with the 'olfactory bowl' model proposed by Peters & Mech (1975), in which the density of marks was highest and equally distributed along territory edges. In our study, the highest density of marks was observed in the centre and in some places along the edges of the wolves' territories. The model presented by Peters & Mech (1975) was based mainly on observations of two packs, surrounded by other territories. Our investigations indicate that wolves minimised the costs of scent-marking by placing marks only along borders shared with other packs (Fig. 4). Our results support the idea introduced by Gosling & Roberts (2001a) that animals mark the most valuable parts of their territory. We assume that marking is associated with an energy trade off, so wolves usually cannot mark their whole territory. Wolves lower the costs of marking by travelling on traditional trails and roads and concentrating their signs on territory boundaries and at road junctions. We suggest that marking rates vary with the risk of penetration by other packs, because in our study area, wolves intensively marked only home range boundaries that neighboured with another pack. Wolves may also be stimulated to mark more intensively at boundaries because of markings by other packs. Similar pattern of mark distribution was observed in some male ungulates, which more often marked borders shared with conspecifics (Roberts & Lowen, 1997; Brashares & Arcese, 1999).

The influence of the travel route type on the proportion of various kinds of wolf signs was different from results reported by Peters & Mech (1975). In their study, wolves left more urine marks on roads than in the forest, but the densities of scats and scratches were similar in both habitats. We did not find differences between urine deposition rates along roads and in the forest. The slightly higher urination rate in the forest may be explained by the higher availability of targets (trees). As discussed above, scratching rates may depend on the nature of the surface, which would explain higher scratching rates on the forest roads. Our results confirm Peters & Mech's (1975) observations that a high proportion of signs left along roads was placed at junctions. Presumably, road junctions not only offer better conditions for markings, but also increase their chance to be discovered by conspecifics.

While moving in their home ranges, wolves must make strategic decisions on where to mark to find an optimal compromise between the effect and cost. Therefore, a model explaining marking patterns has to take into consideration economic constraints. In our study, marking rates per unit of time that wolves spent in a given part of their home range increased towards the home range edges. The 'olfactory bowl' model (Peters & Mech, 1975) proposed that marking would deter potential intruders and, therefore, wolves should deliberately mark along territory borders. Instead we propose a 'hot spots' model emphasising the informative role of territory marking. According to our model wolves increase marking rates on their usual trails in those parts of territory, which are most valuable for them or most vulnerable to intruders. Such spatial pattern of marks lowers the costs associated with marking but enables intruders to identify the residents and avoid antagonistic encounters (comp. Gosling, 1982; Gosling & Roberts, 2001b). In our study area, most valuable for territory owners were the surroundings of dens, whereas most vulnerable for intruders' penetration were the edges of territories that neighboured other wolf packs.

References

Asa, C.S., Mech, D.L. & Ulysses, S.S. (1984). The use of urine, faeces, and anal-gland secretions in scent-marking by a captive wolf (*Canis lupus*) pack. — Anim. Behav. 33, p. 1034-1036.

— —, — —, — — & Plotka, E.D. (1990). The influence of social and endocrine factors on urine-marking by captive wolves (*Canis lupus*). — Horm. Behav. 24, p. 497-509.

Barrette, C. & Messier, F. (1980). Scent-marking in free-ranging coyotes, *Canis latrans*. — Anim. Behav. 28, p. 814-819.

Bekoff, M. (1979). Scent-marking by free-ranging domestic dogs: olfactory and visual components. — Biol. Behav. 4, p. 123-139.

Bowen, W.D. & Cowan, I.M. (1980). Scent marking in coyotes. — Can. J. Zool. 58, p. 473-480.

Brashares, J.S. & Arcese, P. (1999). Scent marking in a territorial African antelope: I. The maintenance of borders between male oribi. — Anim. Behav. 57, p. 1-10.

Gosling, L.M. (1982). A reassessment of the function of scent marking in territories. — Z. Tierpsychol. 60, p. 89-118.

— — & Roberts, S.C. (2001a). Testing ideas about the function of scent marks in territories from spatial patterns. — Anim. Behav. 62, p. F7-F10.

— — & — — (2001b). Scent-marking by male mammals: cheat-proof signals to competitors and mates. — Adv. Study Anim. Behav. 30, p. 169-217.

Harrington, F.H. (1981). Urine-marking and caching behaviour in the wolf. — Behaviour 76, p. 280-288.

Hutchings, M.R., Service, K.M. & Harris, S. (2001). Defecation and urination patterns of badgers *Meles meles* at low density in south west England. — Acta Theriol. 46, p. 87-96.
Jędrzejewska, B. & Jędrzejewski, W. (1998). Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. — Springer, Berlin, Germany.
— —, — —, Bunevich, A.N., Miłkowski, L. & Krasiński, 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, p. 399-451.
Jędrzejewski, W., Schmidt, K., Theuerkauf, J., Jędrzejewska, B. & Okarma H. (2001). Daily movements and territory use by radio-collared wolves (*Canis lupus*) in Białowieża Primeval Forest in Poland. — Can. J. Zool. 79, p. 1993-2004.
— —, — —, — —, — —, Selva, N., Zub, K. & Szymura, L. (2002). Kill rates and predation by wolves on ungulate populations in Białowieża Primeval Forest (Poland). — Ecology 83, p. 1341-1356.
Kleiman, D. (1966). Scent marking in the Canidae. — Symp. Zool. Soc. Lond. 18, p. 167-177.
Macdonald, D.W. (1980). Patterns of scent marking with urine and faeces amongst Carnivore communities. — Symp. Zool. Soc. Lond. 45, p. 107-139.
Okarma, H., Jędrzejewski, W., Schmidt, K., Śnieżko, S., Bunevich, A.N. & Jędrzejewska, B. (1998). Home ranges of wolves in Białowieża Primeval Forest, Poland, compared with other Eurasian populations. — J. Mammal. 79, p. 842-852.
Peters, R.P. & Mech, L.D. (1975). Scent-marking in wolves. — Am. Sci. 63, p. 628-637.
Paquet, P.C. (1991). Scent-marking behaviour of sympatric wolves (*Canis lupus*) and coyotes (*C. latrans*) in Riding Mountain National Park. — Can. J. Zool. 69, p. 1721-1727.
— —, Fuller, W. (1990). Scent marking and territoriality in wolves of Riding Mountain National Park. — In: Chemical signals in vertebrates 5 (D.W. Macdonald, D. Muller-Schwarze & S.E. Natynczuk, eds). Oxford University Press, New York, p. 394-400.
Roberts S.C. & Lowen C. (1997). Optimal patterns of scent marks in klipspringer (*Oreotragus oreotragus*) territories. — J. Zool. Lond. 43, p. 565-578.
Rothman, R.J. & Mech, D.L. (1979). Scent-marking in lone wolves and newly formed pairs. — Anim. Behav. 27, p. 750-760.
Theuerkauf, J. & Jędrzejewski, W. (2002). Accuracy of radiotelemetry to estimate wolf activity and locations. — J. Wildl. Manage. 66, p. 859-864.
Vilá, C., Urios, V. & Castroviejo, J. (1994). Use of faeces for scent marking in Iberian wolves (*Canis lupus*). — Can. J. Zool. 72, p. 374-377.
Woolpy, J.H. (1968). The social organisation of wolves. — Nat. Hist. 77, p. 46.