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Daily movement and territory use by badgers *Meles meles* in Białowieża Primeval Forest, Poland

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We used radio-telemetry to study movement and territory use by 13 Eurasian badgers *Meles meles* in a well-preserved continuous woodland of Białowieża Primeval Forest (BPF), Poland. Daily movement distance (DMD) of badgers averaged 7 km, and daily range (DR) covered 2.1 km², i.e. 19% of their total home-range size. DMD and DR varied seasonally, being largest in summer when the availability of food resources was lowest. DMD was positively correlated with home-range size of badgers and the duration of their daily activity. Badgers moved with an average speed of 0.9 km/hour (maximum 7.1 km/hour). Nevertheless, travel speed was more than twice as fast after the emergence and before the return to the sett than during the peak of badger activity. This behaviour suggests that badgers moved directly to well-known and well-defined feeding patches. Indeed, we also found that the lengths of daily foraging routes was positively correlated with the number of patches of oak *Quercus robur*-lime *Tilia cordata*-hornbeam *Carpinus betulus* forests in a territory (ranging within 1-11), habitat which presents the highest earthworm abundance in BPF. Adult badgers of both sexes visited territory boundaries significantly more often than subadult individuals. Consecutive nightly ranges of badgers overlapped by 24%, which may indicate a rotational way of area use in order to defend large territories. Review of available data on mobility of badgers showed that mean daily movement ranged from 1.2 km in England to 7.0 km in our study. DMDs were positively correlated with home-range size. Average speed of badger movement varied from 0.3 km/hour in Spanish badgers to 1.1 km/hour in Swiss badgers. Our local data as well as the review of other European studies suggest that it is the length of the daily foraging routes that links food resources and home-range size. In areas with low abundance of earthworms and/or widely dispersed foraging patches, badgers move longer distances, cover larger daily ranges and defend large territories.

Key words: daily movement distance, daily range, Meles meles, speed, temperate forest

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Badgers *Meles meles* are territorial and social animals. Members of a group often visit and mark boundaries and shelters in their territory (Revilla & Palomares 2002). When foraging, they slowly and systematically search the ground layer. In a large part of their geographic range, badgers feed on earthworms, but in some locations they rely on fruits, insects or cereals (see review in Goszczyński et al. 2000). These resources are patchily distributed, so the typical foraging behaviour of badgers is patch feeding, although long-distance foraging was also observed (Kruuk 1978, Shepherdson et al. 1990).

The spatial and social organisation of badger populations differ among regions. Mean size of group territories varies from 0.14 km² in the open habitats of the British Isles (Cheeseman et al. 1981) to nearly 13 km² in the continuous woodlands of eastern Poland (Kowalczyk et al. 2003b). Additionally, the smallest territories are occupied by large groups of badgers (sometimes > 20 individuals), while the large territories are usually held by a pair of adults and their cubs (Kowalczyk et al. 2003b). Such variation in life habits gives a unique opportunity to study patterns of territory use and movement of badgers under different food supply and habitat conditions. One of the interesting questions is: are large territories used in the same way as small territories? So far studies on movement and territory use by badgers have been scarce and have been conducted in open or sparsely-wooded areas (Cresswell & Harris 1988, Revilla & Palomares 2002).

Our objective was 1) to investigate the mobility and territory use by badgers in a low-density population (2.1 individuals/10 km²; Kowalczyk et al. 2003b) inhabiting well-preserved temperate woodlands, and 2) to compare our result with result obtained for other European populations.

Study area

Our study was conducted in Białowieża Primeval Forest (BPF), located in eastern Poland on the border with Belarus (52°30'-53°N, 23°30'-24°15'E). The Polish part of BPF covers 595 km², of which 94% are forests and 6% are open areas (meadows and marshes in river valleys and glades with human settlements). The well-preserved, continuous woodlands are a mosaic of coniferous, mixed and deciduous tree stands dominated by spruce *Picea abies*, pine *Pinus silvestris*, oak *Quercus robur*, black alder *Alnus glutinosa*, and hornbeam *Carpinus betulus* (see Jędrzejewska & Jędrzejewski 1998 for details). The Polish part of the BPF includes the protected forests of Białowieża National Park (BNP; 100 km²), and

exploited forests (495 km²). The strictly protected section of the national park (47 km²) contains large amounts of fallen dead wood (101-133 m³/ha) compared to exploited forests (0-1 m³/ha; Kirby et al. 1991, Bobiec 2002, Nilson et al. 2002). The terrain is generally flat (elevations ranging within 134-197 m a.s.l.) and climate is transitional between Atlantic and continental types with clearly marked cold and warm seasons. Mean annual temperature in 1997-2001 was 7.9°C. The coldest month was January (mean daily temperature: -2.3°C), and the warmest was July (19.3°C). Snow cover persisted for an average of 80 days per year (range: 60-96 days) with a maximum recorded snow depth of 23 cm. Mean annual precipitation during the study period was 586 mm.

Material and methods

During 1997-2000, badgers were captured, immobilised and fitted with radio-collars (Advanced Telemetry System Inc, Isanti, Minnesota, USA). Age (yearling or adult) of captured badgers was estimated on the basis of tooth wear (Hancox 1988), body mass and date of capture. We radio-tracked 13 badgers: seven adult males, three adult females, and three subadult individuals belonging to seven groups (1-3 badgers per group). For detailed information on radio-tracking methods see Kowalczyk et al. (2003b).

We monitored the movement of radio-collared badgers during 59 sessions of continuous radio-tracking (each session lasting 12-24 hours). Badgers were followed from the emergence from their sett to the return to their sett at the end of their activity period. Radio-tracking during day-time was reduced, when it became evident that badgers are nocturnal (Kowalczyk et al. 2003a). During continuous sessions of radio-tracking, badgers were localised at 15-minute intervals by triangulation (Mech 1983). We followed the forest compartment lines (grids of 533 × 533 m) and attempted to map the locations of badgers with a maximal error radius of 25 m. We estimated that location error of moving badgers was ≤ 100-150 m. Additionally, we conducted 24 sessions of continuous radio-tracking that lasted for 2-8 hours. These sessions were added to the analysis of the speed at which badgers moved.

From the continuous sessions of radio-tracking, we estimated: 1) daily movement distance (DMD) as the sum of straight-line distances between consecutive locations during badger activity; 2) daily range (DR) as the area encompassing the daily movement route (calculated by 100% Minimum Convex Polygon; MCP); 3) dai-

Table 1. Movement characteristics of badgers in Białowieża Primeval Forest during 1997-2000. The results are expressed as mean \pm SD with minimum and maximum values given in parentheses. DMD is daily movement distance, DR the daily movement range, DR% the daily range as a percentage of a total home range, Speed the speed of travel, and N gives the number of continuous radio-tracking sessions. The statistical results were obtained using ANOVA.

Movement parameter	Sex/age groups of badger				Statistical significance	
	All badgers (N = 59)	Adult males (N = 29)	Adult females (N = 22)	Subadults (N = 8)	F	P
DMD (km)	7.0 \pm 3.1 (0.1-17.5)	6.9 \pm 2.9 (0.8-14.1)	7.3 \pm 3.7 (0.1-17.5)	6.1 \pm 1.6 (3.3-7.8)	0.369	NS
DR (km ²)	2.1 \pm 2.2 (0.1-12.0)	1.8 \pm 1.8 (0.11-7.41)	2.9 \pm 2.8 (0.34-12.02)	0.9 \pm 0.8 (0.3-2.4)	3.826	0.028
DR%	19 \pm 18 (1-94)	18 \pm 18 (1-61)	18 \pm 20 (2-94)	20 \pm 18 (6-54)	0.064	NS
Speed (km/hour)	0.9 \pm 0.4 (0.3-2.0)	1.0 \pm 0.3 (0.4-1.8)	0.9 \pm 0.4 (0.3-2.0)	0.7 \pm 0.2 (0.4-1.2)	1.550	NS

ly range as a percentage of total home range (DR%); and 4) speed of travel, calculated as km/hour.

Throughout the text we use the term 'territory' for the area used by a social group of badgers, and the term 'home range' to refer to areas used by individual badgers.

Data were analysed for the three seasons: spring (1 March-31 May), summer (1 June-31 August) and autumn (1 September-30 November). In BPF, badgers are not very active in winter. From 1 December to 28/29 February, they were active on 17% of days only (usually short-time and short-distance emergences; see Kowalczyk et al. 2003a for details).

Results

Badgers travelled, on average, 7.0 km per 24-hour period (Table 1). Daily movement distance (DMD) was similar between sex/age groups of badgers but varied seasonally (Tables 1 and 2). The longest distances occurred in summer (8.2 km) and the shortest in autumn (4.8 km). Mean DMD during the nights when badgers returned to

the same sett at the end of their activity period, did not differ when compared to nights when badgers changed setts (6.9 and 7.1 km, respectively; ANOVA: $F_{1,57} = 0.037$, $P = 0.85$). DMD was positively correlated with home-range size (MCP 95%; $r = 0.34$, $N = 59$ daily routes, $P = 0.01$), and with the duration of the badger's daily activity period ($r = 0.55$, $P < 0.0005$). The larger the home range was, the longer was the duration of their activity period, and the greater were the distances travelled per night. Furthermore, the number of patches of oak-lime *Tilia cordata*-hornbeam forests (i.e. habitats rich in earthworms; 1-11 per territory) was positively correlated with the length of daily foraging routes of badgers and explained 81% of between-territory variation in mean DMDs (Fig. 1).

On their daily routes adult badgers of both sexes visited territory boundaries (i.e. were recorded within 0-200 m from their territory borders as delimited by MCP 100%) more often than subadult individuals (58-69 and 37%, respectively; G-test for homogeneity of percentages, females-subadults: $G = 4.40$, $df = 1$, $P < 0.05$, males-subadults: $G = 9.46$, $df = 1$, $P < 0.01$).

Table 2. Seasonal changes in movement parameters of badgers in Białowieża Primeval Forest in relation to food (earthworms) availability. Earthworm abundance is expressed as mean \pm SE after Kowalczyk et al. (2003b). For the other parameters the results are expressed as mean \pm SD with minimum and maximum values given in parentheses. The statistical results were obtained using ANOVA. For explanations of the parameter abbreviations see Table 1.

Parameter	Season			Statistical significance (ANOVA)	
	Spring N = 21	Summer N = 30	Autumn N = 8	F	P
Earthworm abundance (kg/ha)	486 \pm 84	106 \pm 30	204 \pm 89		
DMD (km)	6.0 \pm 2.7 (0.1-10.6)	8.2 \pm 3.1 (3.9-17.5)	4.8 \pm 1.9 (1.9-7.8)	6.110	0.004
DR (km ²)	1.7 \pm 1.6 (0.3-6.8)	2.8 \pm 2.7 (0.4-12.0)	0.7 \pm 0.6 (0.1-1.8)	6.171	0.004
DR%	17 \pm 20 (5-94)	22 \pm 18 (2-61)	9 \pm 13 (1-40)	1.646	NS
Speed (km/hour)	1.0 \pm 0.4 (0.3-1.7)	0.9 \pm 0.3 (0.4-2.0)	0.7 \pm 0.3 (0.4-1.7)	2.541	NS

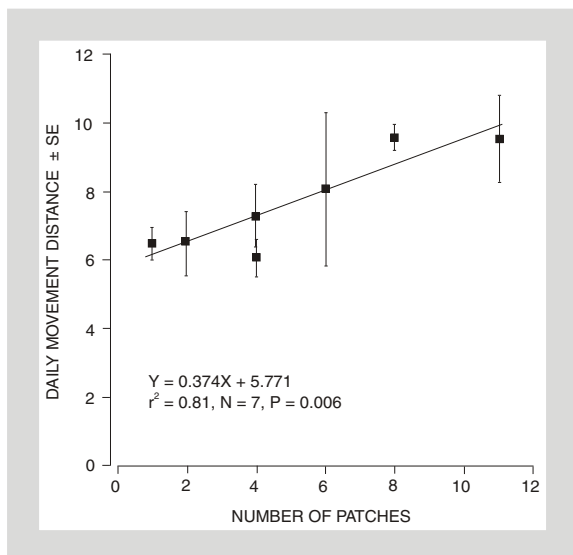


Figure 1. Daily movement distance (DMD; in km) of badgers (mean for each territory) in relation to the number of patches (0-11) of oak-lime-hornbeam forests in territories.

Daily ranges (DR) of badgers included, on average, 2.1 ± 2.2 km², i.e. 19% of their total home range size (see Table 1). Daily ranges differed significantly among age/sex groups of badgers (see Table 1) and among seasons (see Table 2). The largest DRs were recorded in adult reproducing females (N = 3 lactating individuals), and the smallest in subadult individuals. In summer, when the abundance of earthworms reached its seasonal lowest level (see Kowalczyk et al. 2003b), badgers every night

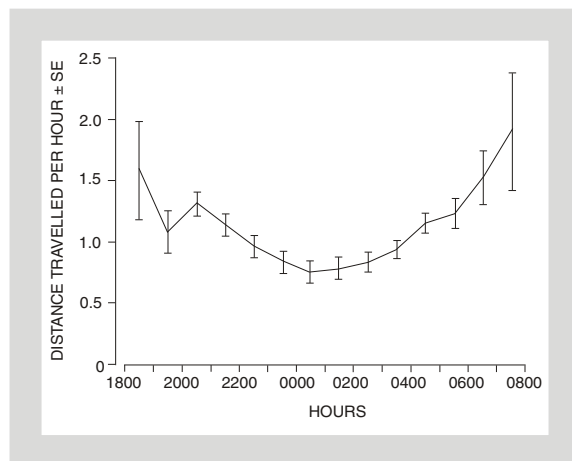


Figure 3. Variation of speed of movement expressed as distance travelled per hour \pm SE throughout a circadian rhythm of badger activity in BPF. For the hourly periods, the sample size varied from 3 to 73.

searched an area nearly two-fold larger than in spring, and over three times larger than in autumn (see Table 2). However, the percentage of total home range area covered during one night (DR%) did not vary between seasons and age/sex groups of badgers.

To find out if badgers avoided using the same area on consecutive nights, the percentage of DR overlap was calculated on the basis of 2-4 day sessions of radio-tracking. We found that night by night, badgers usually foraged in different parts of their home ranges. On consecutive nights DRs overlapped by 0-71%, on average 24% (N = 12 dyads compared; Fig. 2).

Badgers moved with an average speed of 0.9 km/hour. We did not find any significant differences between age/sex groups of badgers or seasons, though in autumn badgers tended to move slower than in spring and summer (see Table 2). The speed of movement varied throughout a circadian rhythm of activity (Fig. 3). Badgers moved more than twice as fast after the emergence and before the return to their sett than during the peak of their activity period (ANOVA: $F = 4.11$, $P < 0.0005$). When watching badgers at setts, we observed that badgers spent very short time around the sett, and then, as recorded by radio-tracking, they moved away fast for as long as 1-2 km. They slowed down when they reached a feeding patch. During the first and last hours of their activity period (i.e. 25% of total daily

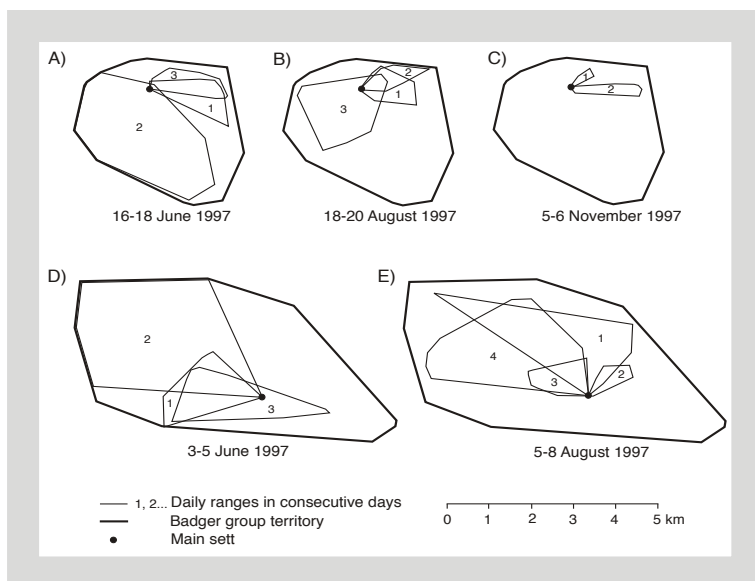


Figure 2. Examples of the daily ranges of an adult male (A-C) and an adult female (D-E) badger in their territories on consecutive days (marked with numbers according to date). Daily ranges are minimum convex polygons embracing the daily movement routes of badgers.

activity time), they covered on average 2.8 km, which corresponds to 40% of their DMD. The maximal speed of movement recorded for individual badgers varied from 2.5 to 7.1 km/hour, on average 4.7 ± 1.6 km/hour. We found differences in the mean and maximal speed between badgers inhabiting pristine woodland of BNP (six individuals) and those in the exploited stands of BPF (seven individuals). Badgers in BNP moved more slowly (mean 0.8 vs 1.1 km/hour; Mann-Whitney test: $U = 3$, $P = 0.028$) than badgers in the exploited stands in BPF. The difference was also significant for their maximal speed (mean 3.5 km/hour in BNP vs 6.0 m/hour in exploited stands; Mann-Whitney test: $U = 0$, $P = 0.006$).

Discussion

Badgers in Białowieża Forest showed a clear seasonal pattern of movement and territory use. As in the cases of activity and home-range size, the longest daily movement and largest daily ranges were recorded in summer, when the availability of earthworms (the main food of badgers in BPF) was lowest (Kowalczyk et al. 2003a,b). The fact that DRs are larger in spring than in autumn, although earthworm abundance in spring is more than two-fold larger than in autumn, can be explained by mating behaviour and increased activity in territory marking after the winter sleep. Similar seasonal variation was recorded in England, Switzerland and Spain (Harris 1982, Ferrari 1997, Revilla & Palomares 2002, Zabala et al. 2002). Prey availability influences the searching behaviour of animals. Kruuk (1978) found that during nights with low earthworm availability the typical behaviour of badgers was long-distance feeding, whereas during nights with high earthworm availability, their feeding was restricted to small habitat patches. Another factor affecting foraging efficiency is vegetation cover (Kruuk et al. 1979). In Białowieża Forest, fully-developed dense plant cover on the forest floor in summer may

decrease foraging efficiency and force badgers to frequently change foraging patches in order to fulfil their energetic demands.

In BPF, the most important factor shaping the territory size of badgers was the area of the oak-lime-hornbeam forests, which are rich in earthworms (see Kowalczyk et al. 2003b). The more fragmented the best foraging habitat was, the longer was the daily movement of the badgers.

Adult badgers involved in territory defence and reproduction displayed different patterns of space use than did non-reproducing subadults. Although the DMDs of subadults were similar to those of adults, they occupied smaller ranges and their routes left impressions of densely packed and rather chaotic zig-zags. This might also result from their lower foraging experience. Adult breeding females covered larger daily ranges than other individuals, which may be explained by their energetic needs during lactation (Robbins 1993). In BPF, adult badgers used their territories in a rotational way. Badgers are known to mark their territories intensively (Pigozzi 1990, Roper et al. 1993, Stewart et al. 2002). In BPF, where territories are large (13 km² on average; Kowalczyk et al. 2003b), badgers were probably unable to patrol the entire territory during one night, so they visited different parts of their territories on consecutive nights.

The differences in the badgers' speed of movement between protected and exploited forests might be related to the large amounts of dead wood in the national park (Kirby et al. 1991, Bobiec 2002, Nilson et al. 2002). A similar pattern was observed in wolves *Canis lupus* inhabiting BPF. They moved faster when travelling on roads or frozen rivers than when travelling in the forest (Musiani et al. 1998).

Including our study, the mobility of badgers has been studied in eight populations. Mean daily movement of badgers in these studies ranged from 1.2 km in Bristol, England, to 7.0 km in our study area in eastern Poland (Table 3). DMDs were positively correlated with home-

Table 3. Comparison of mobility and home-range use (HR) results obtained for badgers in eight populations in Europe. For explanations of the abbreviations see Table 1.

Location	HR (km ²)	DMD (km)	Speed (km/hour)	DR (km ²)	DR%	Source
Spain, Urdaibai	-	1.6	0.37	-	-	Zabala et al. (2002)
England, Bristol	0.25	1.2	0.6	-	-	Cresswell & Harris (1988)
Switzerland, Broye	1.15	3.3	0.5	-	-	Do Linh San (2004)
Switzerland, St.-Blaise-Cressier-Thielle	1.69	3.2	0.9	-	-	Ferrari (1997)
Switzerland, Chaux d'Abel	3.21	5.2	1.1	-	-	Ferrari (1997)
Spain, Donana NP	4.12	4.6	0.3	0.87	21	Revilla & Palomares (2002)
Norway, Trondheim	7.6	4.4	0.4	1.13	15	Johansen (1993)
Poland, BPF	9.30	7.0	0.9	2.06	22	Kowalczyk et al. (2003b), this study

range size ($r = 0.84$, $N = 7$, $P < 0.05$). The longer the daily distances travelled by badgers are, the larger are their home ranges. In previous studies, average speed of movement varied from 0.3 km/hour to 1.1 km/hour (see Table 3). There is a tendency (although not statistically significant) for a positive relationship between the length of daily route and the speed of travelling badgers ($r = 0.48$, $N = 8$, $P = 0.2$). Data on daily ranges are scarce and were collected in populations characterised by relatively large home ranges and long DMDs (see Table 3).

Kowalczyk et al. (2003b) have shown that badger densities and territory sizes are shaped predominantly by food abundance and availability. Data from our study in the Białowieża Forest and other European studies suggest that it is the length of the daily foraging routes that links food resources and badger home-range size. In areas with low abundance of earthworms and/or widely dispersed foraging patches, badgers move longer distances, cover larger daily ranges, and defend large territories.

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