Spatial organization and demography of badgers (*Meles meles*) in Bialowieza Primeval Forest, Poland, and the influence of earthworms on badger densities in Europe

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Abstract: From 1996 to 2001 we studied the spatial organization and demography of Eurasian badgers, *Meles meles*, in Białowieża Primeval Forest in eastern Poland, one of the best preserved woodlands in temperate Europe. Badger density estimated on the basis of main sett distribution (0.54 sett/10 km^2) and group size (3.9 individuals per sett, on average) was 2.11 badgers/10 km^2. Average annual productivity of the population was 64% and the mortality rate of badgers >1 year old was 22–38% per annum. The size of territories of badger groups ($n = 7$), estimated by radiotelemetry, varied from 8.4 to 25.5 km^2 (mean 12.8 km^2). Individual home ranges of badgers ($n = 13$) covered, on average, 9.3 km^2, and varied seasonally and among animals of different age and sex classes (from 4.0 to 24.4 km^2). Home ranges of adult badgers were significantly larger than those of subadults. Badgers occupied larger home ranges in summer, when earthworm availability was low. The size of both group territories and individual home ranges was influenced by the distribution of oak–lime–hornbeam (OLH) forests, habitats rich in earthworms. Based on our findings and a review of literature, we propose that the standing crop of biomass of earthworms (*Lumbricus* spp.), the main food of badgers in a large part of their geographic range, and mean annual temperature are crucial factors shaping the densities of badgers in the European temperate and boreal zones. We also suggest that abundance of food resources is the essential factor underlying the great variation in badger sociality (from pairs to large groups).

Résumé : De 1996 à 2001, nous avons étudié l'organisation spatiale et la démographie des blaireaux, *Meles meles*, de la forêt primitive de Białowieża (dans l'est de la Pologne), l'une des régions boisées les mieux préservées de l'Europe tempérée. La densité des blaireaux a été estimée d'après la répartition des terriers principaux (0,54 terrier/10 km^2); les groupes (en moyenne 3,9 individus par terrier) étaient formés de 2,11 blaireaux/10 km^2. La productivité annuelle moyenne de la population est de 64 % et le taux de mortalité des blaireaux de >1 an varie de 22 à 38 % par année. Les territoires occupés par des groupes ($n = 7$, estimés par radiotélémétrie) mesurent de 8,4 à 25,5 km^2 (12,8 km^2 en moyenne). Les domaines individuels ($n = 13$) couvrent en moyenne 9,3 km^2 et cette mesure fluctue avec les saisons et varie aussi chez les divers animaux en fonction de leur âge et de leur sexe (de 4,0 à 24,4 km^2). Les domaines des adultes sont significativement plus grands que ceux des sub-adultes. Les blaireaux occupent des domaines plus grands en été, alors que la disponibilité des vers de terre est faible. La taille des territoires des deux groupes et des domaines individuels est influencée par la répartition des forêts de chênes–tilleuls–hêtres, habitats riches en vers de terre. L'analyse de nos données et une revue de la littérature nous amènent à conclure que la biomasse des vers de terre *Lumbricus*, la principale source de nourriture des blaireaux sur une grande partie de leur répartition géographique, et la température moyenne annuelle sont les facteurs déterminants de la densité des blaireaux dans la zone boréale et tempérée d'Europe. Nous croyons aussi que l'abondance des ressources alimentaires est le facteur essentiel qui régit la grande variation observée dans la socialité des blaireaux (des couples aux grands groupes).

[Traduit par la Rédaction]

Introduction

The Eurasian badger, *Meles meles*, is a species with a very large geographic range and it shows remarkable plasticity in life-history traits. The size of social groups varies from 2 to 23 adults (e.g., Rogers et al. 1997; Goszczyński 1999), their

densities from 3 to 480 individuals per 10 km^2 (review in Kowalczyk et al. 2000; see also Tuyttens et al. 2000*a*), and their territory sizes from 0.14 to nearly 10 km^2 (e.g., Cheeseman et al. 1981; Rodriguez et al. 1996; Brøseth et al. 1997). Among factors affecting group territory size and densities of badgers, food abundance and sett availability have

been most often reported (Kruuk and Parish 1982; Roper 1993). Despite remarkable variation in habitats occupied by badgers, over a large part of their range they feed on earthworms (review in Goszczyński et al. 2000a). Availability of earthworms was reported to shape badger group size, body mass, survival, and reproduction (Kruuk and Parish 1982, 1985; Hofer 1988; Woodroffe 1995; Woodroffe and Macdonald 2000). Setts, which are used for reproduction, for winter sleep, and as daytime shelters throughout the year, are essential components of badger territories and are inherited by successive generations of badgers. Some studies have shown that food availability, sett distribution, and territory use by badgers depend on the spatial distribution of suitable and preferred habitats (Hofer 1988; Feore and Montgomery 1999; Revilla et al. 2000).

Badgers live in groups occupying a common sett and the same territory, but individuals from a group do not cooperate in foraging, caring for young, or defence against predation (Neal 1986; Kruuk 1989). Macdonald (1983) described the social system of badgers as group territoriality, and pointed out that the factor which allows several animals to share the same territory is the availability of food resources that are rapidly renewable and patchily dispersed in space and time. The resource-dispersion hypothesis has been invoked most often to explain badger sociality. It states that the spatial distribution of food patches influences the spatial organization of badgers, while the quality of these patches determines badger group size (Macdonald 1983; Woodroffe and Macdonald 1993; Johnson et al. 2001).

Although badgers are among the most studied species of predators, it is still not clear how flexible spatial organization is in this species, and which factors determine its territoriality and group formation. Most studies on badger ecology have been done in continental Western Europe and the British Isles, where badgers inhabit heavily transformed, man-made habitats. In such habitats, badgers attain very high densities, occupy small territories, and live in large social groups (e.g., Cheeseman et al. 1981; Rogers et al. 1997; Feore and Montgomery 1999). In better preserved forest habitats in Central and Eastern Europe, badgers are forest dwellers. They are often hunted and, in many regions, they coexist with large predators (wolf (*Canis lupus*) and lynx (*Lynx lynx*)). In such regions and habitats, densities of badgers are low and their territories are large and usually occupied by pair of animals (Kowalczyk et al. 2000; Revilla and Palomares 2002). Because the Eurasian badger shows plasticity of social and spatial organization throughout its geographic range, it is considered a model species for studying the evolution of group living.

Białowieża Primeval Forest (BPF) in eastern Poland, where this study was conducted, is one of the best preserved lowland temperate forests in Europe. In BPF, badgers utilize only natural food resources (because of the scarcity of farmlands and orchards), and their diet is dominated by earthworms (Jędrzejewska and Jędrzejewski 1998; Goszczyński et al. 2000a). During a 6-year study based on radiotelemetry of badgers, observations at their breeding setts, and surveys of earthworm abundance, we aimed to describe (*i*) the demography and social structure of the badger population, (*ii*) the size and spatial distribution of group territories in relation to habitat diversity and earthworm abundance, and

(*iii*) the home-range size of individual badgers and factors affecting its variation.

Furthermore, assuming that results obtained in Europe's last pristine lowland forest can be treated as a model for comparison with other regions and habitats in the European temperate and boreal zones, we reviewed the available literature in an attempt to define biogeographical patterns in the habitat- and food-related variation in badgers' spatial organization and densities.

Materials and methods

Study area

Białowieża Primeval Forest (52°30′–53°00′N, 23°30′–24°15′E), located on the Poland–Belarus border, is one of the best preserved temperate lowland forests in Europe. The Polish part of the forest covers 595 km^2 and includes Białowieża National Park (105 km^2) and the exploited forests. The area is generally flat (134–176 m asl), with small hills and shallow depressions. Soils are mainly brown and podzol, with a smaller amount of semi-boggy soils. The water table varies from 15 m below ground in dry coniferous forests to 0.2 m in wet habitats (Kwiatkowski 1994). Tree stands dominated by pine (*Pinus silvestris*) and spruce (*Picea abies*) cover 48.5% of the area, alder (*Alnus glutinosa*) and ash (*Fraxinus excelsior*) 18.6%, rich deciduous stands dominated by oak (*Quercus robur*), hornbeam (*Carpinus betulus*), lime (*Tilia cordata*), and maple (*Acer platanoides*) 14.8%, and aspen (*Populus tremula*) and birch (*Betula* sp.) 11.7% (Jędrzejewska and Jędrzejewski 1998). Within BPF, open habitats (glades with meadows, riverside open sedge and reed marshes) cover 6.4% of the area. During the 80 years of forest exploitation in the managed part of BPF (490 km^2), replanting of pine and spruce has resulted in their current over representation compared with natural stands and they are widespread even on rich soils typical of deciduous stands. The actual area of OLH forest habitat is 56.5%, wet ash–alder forest 19.2%, and coniferous and mixed forests 17.9% (calculated from Kwiatkowski 1994). In spring, over 25% of BPF (mainly ash–alder forests and river valleys) is flooded.

The climate of BPF is transitional between Atlantic and continental types, with clearly marked cold and warm seasons. The mean annual temperature in 1997–2001 was 7.9°C (range –22.1 to 28.8°C). The coldest month was January (mean daily temperature –2.3°C) and the warmest was July (mean daily temperature 19.3°C). Snow cover persisted for an average of 80 days per year (range 60–96 days), with a maximum recorded depth of 23 cm. Mean annual precipitation during the study period was 586 mm.

BPF is inhabited by a rich community of predators, with three medium-sized carnivores, the badger, red fox (*Vulpes vulpes*), and raccoon dog (*Nyctereutes procyonoides*) (the last having colonized BPF in the 1950s), and two large predators, the wolf and lynx. Badgers are not hunted in BPF, although they are game species in other parts of Poland. Incidental poaching with snares or by blocking sett entrances occurred.

Surveys of setts and numbers of badgers

Based on our field searches as well as information obtained from game wardens and forestry personnel, we tried to find all setts located in BPF. From 1996 to 2001 we found

143 burrows (including fox and raccoon dog dens). All burrows found were checked at least twice a year. Main setts of badgers ($n = 23$, i.e., 16% of all burrows found) were recognized based on criteria of Thornton (1988). These setts were surveyed more often. For each sett, the type of habitat was recorded and badgers' habitat selection was calculated using Ivlev's electivity index, D (modified by Jacobs 1974): $D = (r - p)/(r + p - 2pr)$, where r is the number of setts located in a given habitat as fraction of the number of all main setts of badgers and p is the fraction of the total area of BPF constituted by a given habitat (from Kwiatkowski 1994). D varies from –1 (strongest negative selection) to 0 (random selection) to +1 (strongest positive selection).

To estimate the number of badgers occupying the main setts, observations at 8 setts (located in the central part of BPF and chosen for radiotelemetry studies) were conducted from late May to early August. In BPF, cubs usually emerge from setts in the second half of May and start to follow adults in late June. Ninety-five sessions of evening observations were conducted and 26 records of group size collected in 1996–2001. Numbers of adults and cubs (including animals wearing radio collars) were recorded. Counting badgers at the sett may not be a very accurate method of determining group size (e.g., Macdonald et al. 1998), but this applies to high-density populations rather than low-density ones (cf. Goszczyński 1999). In BPF, setts are occupied by few individuals, and adult badgers had left the setts shortly after emergence, so it was easy to count them. On some days badgers rested in setts other than the main one (average 29% of days; Kowalczyk et al. 2003), so we conducted 3–5 surveys at each sett every year, and the maximum number of animals seen was accepted as the group size. If the radio-collared animals were not present at a sett during a survey session (e.g., they rested in another sett), they were added to the number of animals seen. Our estimates of group size were additionally validated by trapping and radio-collaring. In 6 setts where both counting and trapping were conducted, the badger groups consisted of 1 or 2 radio-collared individuals at a time (average 1.7) and only 1–4 (average 1.8) non-radio-collared badgers, including cubs. Given the body-size differences among the non-radio-collared badgers, we believe that the error in the group-size estimate was small.

Radiotelemetry of badgers

Badgers were caught in foot-snare traps (see Quinn and Parker 1987) or box traps ($40 \times 40 \times 120$ cm) placed near 8 setts. All traps were equipped with a radio alarm system, which shortened the time the badger spent in a trap to 1–2 h. Trapping was carried out from March to November, mainly in spring. The captured animals were immobilized by an intramuscular injection of a xylazine–ketamine mixture (Kreeger 1997). The sex of the badger was determined, and age (yearling or adult) was estimated on the basis of body mass, date of capture, and tooth wear. Of 14 captured badgers (13 in foot-snare traps and 1 in a box trap), 13 (10 adults and 3 yearlings) were fitted with radio collars (1 cub was not radio-collared) (see Appendix A). We used transmitters produced by Advanced Telemetry Systems (U.S.A.) that weighed 125 g. Their signal range was maximally 800–1000 m.

In 1997–2001, all radio-collared badgers were located from the ground 3–5 times per week. During the night we determined each badger's position by triangulation (Mech 1983). We followed the forest compartment lines (grid 533 × 533 m) and attempted to map the locations of badgers with an accuracy of 25 m. We estimated that location error of moving badgers was no larger than 100–150 m. During the day, animals were located more precisely in their resting sites. Additionally, 67 sessions of 24 h of continuous radio-tracking were conducted. During these sessions, the position of an animal was taken every 15 min. In total, 8370 radio locations were collected (Appendix A). The average time of active collar-wearing for each badger was 459 days (range 37–1101 days).

Based on radiotelemetry data, we mapped and calculated the size of each group territory (defined as the area occupied by all radio-collared badgers of that group) and individual home range of badgers. In each group, 1–3 adult and subadult badgers (mean = 2.0, SD = 0.8) were radio-collared during the whole study period. At any time, 1 or 2 individuals (mean = 1.6, SD = 0.5) were radio-tracked simultaneously, which constituted, on average, 67% of the mean number of adults and subadults per group. We estimated mortality rates for badgers ≥1 year old (juveniles were not radio-collared). For analyzing territories and individual home ranges we used a minimum convex polygon (MCP) method using 100 and 95% of all radio fixes collected. To show the spatial pattern of territory use by badgers, we used an adaptive kernel method using 95 and 75% of radio fixes (Worton 1989; Seaman and Powell 1996). In the kernel analysis we used only those fixes collected during 24-h sessions of continuous radio-tracking and (as recommended by De Solla et al. 1999) we did not reduce the sample size, to avoid autocorrelation of data. Kernel ranges were calculated for four groups with 7–18 (average 14) 24-h sessions. Extra-territorial excursions were not recorded. Data for dispersing badgers are not included in the home-range analysis.

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

Mortality rates were calculated using the method described by Trent and Rongstad (1974) and Heisey and Fuller (1985). Mortality was calculated for two time periods: 1 year and 4 years (the whole study period). We estimated minimum and the maximum annual mortality rates for badgers. For the minimum estimate we used the number of radio-collared badgers actually found dead; for the maximum estimate we assumed that all animals with which radio contact was lost had died.

Censuses of earthworm availability

Earthworm biomass was estimated at randomly selected points in 1997–2000 (Nordström and Rundgren 1972; Brøseth et al. 1997). Soil samples (volume $20 \times 20 \times 25$ cm) were taken in four types of habitat: (1) OLH forest ($n = 120$); (2) mixed and coniferous forests ($n = 51$); (3) alder and ash–alder wet forests ($n = 31$); (4) meadows ($n = 49$). Samples were collected in spring ($n = 77$), summer ($n = 120$), autumn ($n = 20$), and winter ($n = 8$). The samples were hand-sorted for earthworms, which were identified to

species according to the key in Kasprzak (1986), and biomass was estimated as fresh wet mass.

Results

Density and demography of badgers

In the Polish part of BPF, 23 setts were recognised as main badger setts (Fig. 1). OLH forests were strongly preferred by badgers as habitats for establishing setts (18 setts, i.e., 78 versus 57% of the area covered by these forests; $D = 0.47$). Coniferous and mixed forests were used in proportion to their availability in the study area (5 setts, i.e., 22 versus 18% of BPF area; $D = 0.12$). No setts were found in wet forests or open meadows ($D = –1$). Badgers' habitat preferences were statistically significant ($G = 9.12$, df = 3, $P < 0.05$, G test). The nearest neighbour distance between occupied setts varied from 2.1 to 6.2 km (mean = 4.1 km, SD = 1.1 km). Setts separated by OLH, mixed, and coniferous forests were located closer to each other (3.3 ± 1.0 km (mean $\pm$ SD), $n = 8$, range = 2.1–4.7 km) than those separated by ash–alder wet forests and marshy river valleys (4.6 ± 1.0 km, $n = 10$, range 3.2–6.2 km) (Mann–Whitney two-tailed test, $U = 66$, $n_1 = 10$, $n_2 = 8$, $P < 0.05$). In 1996–2001, 23 setts were surveyed for a total of 96 sett-years. Badgers occupied the setts in 88 sett-years (92%). Two setts were abandoned, one because it was overtaken by wolves (for breeding and pup rearing) and the other for an unknown reason.

Badger groups occupying a sett comprised 2–7 individuals (both adults and cubs), the average being 3.9 (Table 1). The number of adults per group varied from 2 to 4 (average 2.4) and the number of cubs from 0 to 4 (average 1.5) per year per sett. In a total of 26 sett-years, the presence of cubs was recorded in 16 (60%). We recorded three litters with 1 cub, five with 2 cubs, six with 3 cubs, and two with 4 cubs (mean = 2.4 cubs per litter, SD = 1.0 cub per litter). Mean annual productivity of the population (number of cubs per adult) varied from 45 to 87% (mean = 64%, SD = 18%, $n = 5$ years).

Of 13 radio-collared badgers, 3 died during the study period and 3 others were lost. Annual mortality rates of badgers older than 1 year varied from 0 to 59%. Average annual mortality was 22% if minimum estimates are considered and 38% if maximal values are considered (Table 2). The cumulative mortality rate over 4 years was 52–77%. Among 8 badgers found dead during the study (3 radio-collared and 5 non-collared), 3 were hit by cars on roads and 5 died from unknown causes (2 during their winter sleep and 3 in spring–autumn).

Based on the number of active setts and mean size of social groups, we calculated the density of badgers in BPF. The minimum estimate (based on 23 setts in the whole Polish part of BPF, i.e., 595 km²) was 0.39 setts and 1.52 badgers per 10 km². The maximum estimates for BPF (based on 7 setts in the 130-km² area covered by radiotelemetry) were 0.54 setts and 2.11 badgers per 10 km².

Spatial organization of badgers

We radio-tracked 13 badgers belonging to seven social groups (Fig. 2). In each group, 1–3 individuals were followed (a maximum of 2 badgers at the same time). Individual home ranges of badgers covered, on average, 9.3 km²

(SD = 5.4 km²) when estimated as MCP with 100% of fixes and 7.3 km² (SD = 4.0 km²) when estimated as MCP with 95% of fixes. Their size varied considerably between animals of different age and sex classes (from 4.0 to 24.4 km²; data for complete radio-tracking periods, MCP 100%) (Table 3, Fig. 2). Home ranges of adult badgers (average 10.3 km²) were significantly larger than those of subadults (average 4.3 km²) (Mann–Whitney test, $U = 20$, $n_1 = 10$, $n_2 = 2$, $P = 0.05$). Adult females tended to have larger home ranges than adult males, but the difference was not significant. Sizes of badgers' home ranges also varied seasonally. In spring, they covered 6.5 km², on average, then increased to 7.7 km² in summer, when earthworm availability was lowest (see below), and decreased again to 4.5 km² in autumn (Table 3). However, these differences were not significant ($U = 44.5$–76.5, $P > 0.05$). In spring and summer, females' home ranges were much larger than those of males, and the difference was significant in spring ($U = 32$, $n_1 = 9$, $n_2 = 4$, $P = 0.05$). In spring, adults occupied larger home ranges than subadults ($U = 20$, $n_1 = 13$, $n_2 = 2$, $P = 0.05$). Individual home ranges covered, on average, 70% of group territory area (both calculated as MCP 100%), and also varied among sex and age classes of badgers. The value was 87% for adult females (range 65–100%), 77% for adult males (range 61–100%), and 36% for subadults (range 17–48%) (Fig. 2). Overlap of home ranges of badgers belonging to the same group varied from 39.5 to 100% (average 71%).

The size of territories of badger groups varied from 8.4 to 25.5 km² (mean = 12.8 km², SD = 5.7 km²) when estimated as MCP comprising 100% of fixes, and from 3.7 to 17.0 km² (mean = 9.2 km², SD = 4.2 km²) when estimated as MCP with 95% of fixes (Table 4). Territories of badger groups were exclusive or overlapped negligibly. Territories covered almost the whole area except for marshy river valleys and open habitats near human settlements (Fig. 1).

We used the kernel method to analyse the intensity of area utilization by badgers. Badgers spend most of their time (95% of locations) in an area of 5.5–10.3 km² (mean 7.1 km², SD = 2.2 km²), i.e., 40–56% (mean 50%) of the whole territory (delineated by MCP 100%). Core areas based on 75% of radio-telemetry fixes covered from 0.2 to 1 km² (mean = 0.7 km², SD = 0.3 km²), which is equivalent to 5% of the whole territory.

Factors affecting size of badgers' home ranges and group territories

Earthworm abundance in various habitats and seasons and the availability of different forest habitats were related to the observed variation in badgers' home ranges and group territories. Nine species of earthworm were found in BPF. Three of them (*Allobophora caliginosa*, *Lumbricus rubellus*, and *Dendrobaena octaedra*) constituted 90% of earthworm numbers and biomass. Other species were *Octolasium lacteum*, *Allobophora rosea*, *Dendrodrilus rubidus*, *Lumbricus terrestris*, *Eiseniella tetraedra*, and *Helodrillus* sp. The mean body mass of an earthworm was 0.44 g (range 0.01–3.28 g). Earthworm biomass varied strongly among habitats and seasons. Mean biomass of earthworm was 422 kg/ha (SE = 151 kg/ha) in OLH forests, 338 kg/ha (SE = 98 kg/ha) in meadows, 310 kg/ha (SE = 94 kg/ha) in ash–alder wet forests, and 52 kg/ha (SE = 13 kg/ha) in drier mixed and coniferous forests. In all habitats, earthworm biomass was highest

Fig. 1. Distribution of main setts (●) and group territories (solid lines) of radio-tracked badgers (*Meles meles*) in Białowieża Primeval Forest (BPF) in 1996–2001. The shaded area denotes forest.
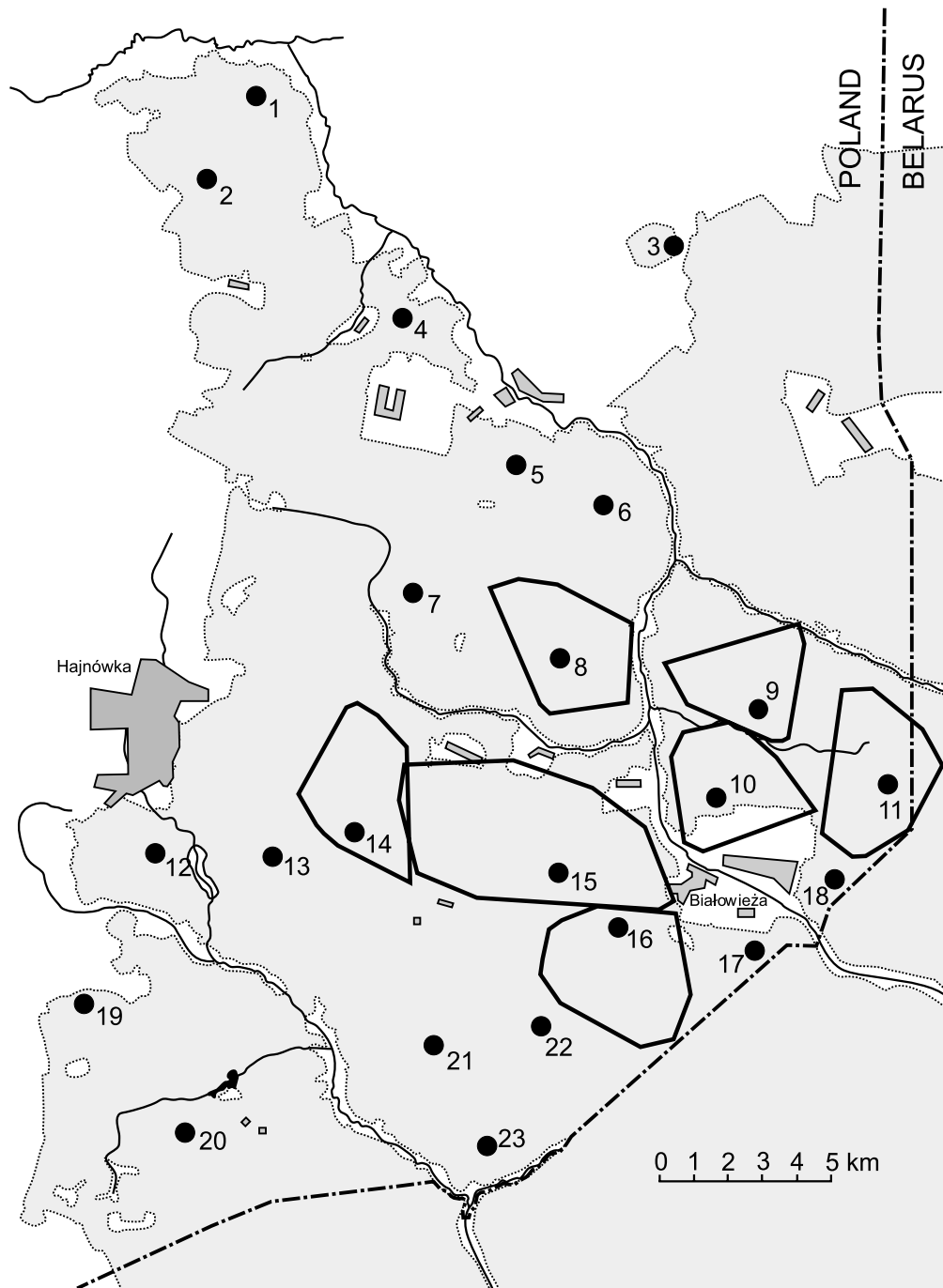
in spring (mean = 486 kg/ha, SE = 84 kg/ha), decreased in summer (mean = 106 kg/ha, SE = 30 kg/ha), and increased again in autumn (mean = 204 kg/ha, SE = 89 kg/ha). In winter, earthworms were not available. The differences in standing crop of earthworm biomass among seasons and habitats were statistically significant (Kruskal–Wallis ANOVA, seasons: $H = 14.65$, df = 2, $P = 0.001$; habitats: $H = 33.15$, df = 3, $P < 0.005$).

We analysed the roles of (*i*) the percentage area of OLH, (*ii*) badger body mass (BM), and (*iii*) number of fixes used

to calculate home ranges (*F*) in shaping the variation in size of badgers' home ranges. The three factors explained 74% of the observed variation: $Y = 1.424 - 0.067\text{OLH} + 0.773\text{BM} + 0.002F$, $R^2 = 0.74$, $n = 10$, $P = 0.03$). Semi-partial correlations squared (sr^2, showing the contribution of each independent variable to the total variation explained; see Tabachnick and Fidell 1983) were highest for the percentage area of OLH forests ($sr^2 = 0.087$) and lower for the number of fixes (0.072) and badger body mass (0.052). The size of individual home ranges decreased with increasing

Table 1. Composition and size of social groups of badgers in Białowieża Primeval Forest (BPF).

Sett No.	Adults and subadults		Cubs		All badgers	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
8	2.5±0.7	2–3	1.5±0.7	1–2	4.0±1.4	3–5
9	2.5±0.7	2–3	0.5±0.7	0–1	3.0±0.0	3–3
10	2.5±0.6	2–3	1.3±1.5	0–3	3.7±1.7	2–6
14	2.0	—	0	—	2.0	—
15	2.7±0.8	2–4	2.2±1.5	0–4	4.8±1.5	3–7
16	2.3±0.5	2–3	1.5±1.9	0–4	3.7±1.7	2–6
17	2.3±0.5	2–3	0.7±1.5	0–3	3.0±1.4	2–5
20	2.0±0.0	2	2.7±0.6	2–3	4.7±0.6	4–5
All setts	2.4±0.6	2–4	1.5±1.4	0–4	3.9±1.5	2–7

Note: Data are from observations at 8 main setts from 1996 to 2001. Sett numbers are as in Fig. 1. For each sett, data covered 1–6 years (n = 26 sett-years in total).

Table 2. Annual mortality rates of badgers >1 year old in BPF, calculated from radiotelemetry data using Trent and Rongstad's (1974) method.

	No. of badger-days	No. of badger deaths		Mortality rate	
		Min.[a]	Max.[b]	Min.[a]	Max.[b]
1 Mar. 1997 – 28 Feb. 1998	775	1	2	0.376	0.611
1 Mar. 1998 – 28 Feb. 1999	2060	1	1	0.162	0.162
1 Mar. 1999 – 29 Feb. 2000	2298	0	1	0	0.147
1 Mar. 2000 – 28 Feb. 2001	823	1	2	0.358	0.589
Average ± SD	1489±803	0.75±0.50	1.5±0.58	0.224±0.178	0.377±0.257
Cumulative mortality rate for 4 years	5956	3	6	0.521	0.771

Note: Between 5 and 10 individuals were radio-tracked each year.
[a]Estimate based on the number of badgers actually found dead.
[b]Estimate based on the assumption that all animals with which radio contact had been lost had died.

area of OLH forests in badger ranges, and larger badgers held bigger home ranges. To estimate the influence of the most important biological factor (OLH forest), we calculated the regression equation with the two other independent variables held constant at their mean values: body mass at 10.2 kg and number of fixes at 662 (Fig. 3).

Similarly, we attempted to explain the observed variation in the size of badger group territories. OLH forests covered from 1.3 to 5.6 km^2 (mean = 3 km^2, SD = 1.5 km^2) of various territories, which was equivalent to 12–81% of their area (estimated as MCP 95%) (mean = 39%, SD = 25%) (Table 4). Mixed and coniferous forests covered, on average, 42% (SD = 25%), wet forests 17% (SD = 12%), and meadows 2% (SD = 3%) of each territory. Estimated biomass of earthworms in territories (based on availability of a given habitat and mean biomass of earthworms in that habitat) varied from 11 100 to 36 400 kg/km^2 (mean = 24 300 kg/km^2, SD = 8900 kg/km^2) (Table 4). OLH forests provided, on average, 63% (SD = 20%) of earthworm abundance in territories. Wet forests supplied 23% (SD = 17%) of earthworm biomass, but these forests were flooded during spring and sometimes also in summer and autumn. The contributions of mixed and coniferous forests and meadows to the total worm supply in territories were low (mean = 12% (SD = 12%) and 2% (SD = 3%), respectively).

In the multiple regression analysis, we checked whether (i) the percentage of the area of OLH forests in territories and (ii) the size of badger groups holding a territory (GS) influenced the size of badger-group territories. These two independent variables explained 70% of the observed variation in territory size (T): $T = 6.197 − 0.098\text{OLH} + 2.040\text{GS}$, $R^2 = 0.70$, $n = 6$); however, the relationship was not statistically significant, owing to the small sample size ($P > 0.1$; social-group size was estimated for six out of seven studied territories of badger groups). The size of badger territories decreased as the percent area of OLH forests grew (Fig. 3). As expected, larger groups (pooled numbers of adults and young) held bigger territories. Semipartial correlations squared showed that the percent area of OLH forests was more important ($sr^2 = 0.354$) than group size ($sr^2 = 0.181$). The number of fixes used to calculate the size of group territories did not have a significant effect on estimated territory size ($P = 0.2$); furthermore, it was mutually correlated with group size, as more badgers from larger groups were livetrapped and radio-tracked.

OLH forests were patchily dispersed in the study area. We recorded 36 patches of OLH forest in the area covered by badger territories, the average size of the patch being 84.1 ha (range 28–603 ha). Group territories embraced from 1 to 11 patches (average = 5.1, SD = 3.5). Territory size was related to the number of patches (NP) of OLH forest it contained ($T = 6.262 + 1.268\text{NP}$, $R^2 = 0.59$, $n = 7$, $P = 0.04$). In other words, territories located in areas with large patches of OLH forest were smaller than those located in areas where

Fig. 2. Individual home ranges and group territories of badgers radio-tracked in BPF in 1997–2001. Badger ID Nos. and sett numbers are listed in Appendix A and shown in Fig. 1. M1* denotes male 1 that dispersed from sett 15 to sett 14.
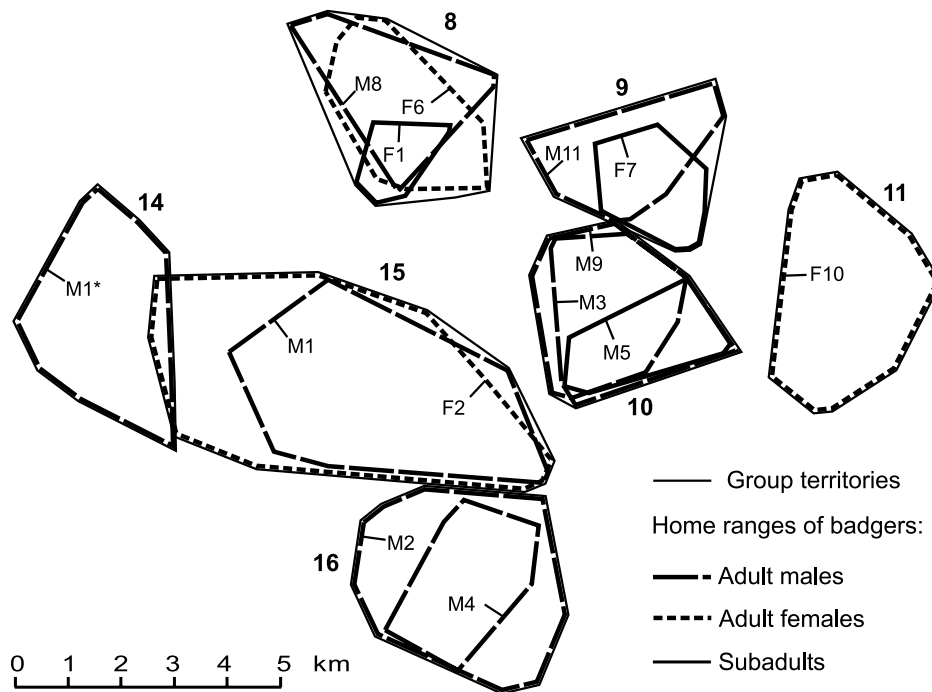
patches of OLH forest were small and interspersed with less suitable habitats.

Discussion

Demography and spatial organization of badgers in BPF compared with other Eurasian populations

In BPF, badger groups occupying a sett and territory consisted usually of a pair of adults with young. Individuals from the same group utilized overlapping home ranges, the size of which varied among individuals and seasons. The number of adults per group in BPF was similar to numbers in other low-density populations (e.g., 2.1 in Central Poland, Goszczyński and Skoczyńska 1996; 2.3 in Kazakhstan, Lobachev 1976; 2.2 in Switzerland, Ferrari 1997; 3.2 in Spain, Revilla and Palomares 2002) but lower than numbers in high-density populations (4.2–13.3 in the British Isles, Cheeseman et al. 1981; Kruuk and Parish 1982; O'Corry-Crowe et al. 1993; Rogers et al. 1997; Macdonald and Newman 2002). In the British Isles, up to 4 breeding females per group were observed (Rogers et al. 1997; Woodroffe and Macdonald 2000). The number of cubs seen emerging from a sett was low in BPF compared with other regions (2.4–3.0 cubs per litter, Stubbe 1970; Goszczyński and Skoczyńska 1996; Neal and Cheeseman 1996; Gorshkov 1997; Hofmann 1999), while population productivity (0.65) was among the highest reported in the literature (0.29–0.68, da Silva et al. 1993; Goszczyński and Skoczyńska 1996; Rogers et al. 1997; Hofmann 1999; Tuyttens et al. 2000a). Mortality rates of adults and subadults were lower than those reported in other populations (Anderson and Trewhella 1985; Bevanger et al. 1996; Rogers et al. 1997; Revilla et al. 2001). In Western Europe, mortality rates of badgers are often higher because they become road casualties (Gallagher

and Nelson 1979; Aaris-Sørensen 1995). Wolves, lynxes, and brown bears (*Ursus arctos*) have been reported to prey on badgers (Shaparev 1977; Olsson et al. 1997). In BPF, badger remains were found in wolf scats (Jędrzejewska and Jędrzejewski 1998). We also recorded that wolves and lynxes inspected badger setts (data from snow-tracking), and a pack of wolves utilized one of the badger setts as its breeding den. Additionally, severe winters may cause mortality of cubs and adults (Lindström 1989).

Food availability has been regarded as the main factor affecting the size of territories of many animals (e.g., Simon 1975; Newton et al. 1977; Mills and Knowlton 1991; Meia and Weber 1995). In BPF, badgers fed mainly on earthworms (30–80% of biomass consumed in various seasons and years, Jędrzejewska and Jędrzejewski 1998; Goszczyński et al. 2000a; Kowalczyk 2001), the abundance of which depended on habitat and season. Our sample of earthworm biomass was not large enough for analysing the correlation between food abundance and individual home-range sizes of the badgers studied. Nonetheless, we found that the standing crop of earthworm biomass was highest in OLH forests and that the area and distribution of this type of habitat were correlated with the size of badger group territories and individual home ranges. Also, in other studies the share of habitats rich in the main food resource determined territory size (Stenström 1991; Rodriguez et al. 1996; Ferrari 1997). In Norway and Scotland, the size of badger territories was affected by the dispersion of habitat patches rich in earthworms (Kruuk and Parish 1982; Brøseth et al. 1997).

In BPF, adult badgers occupied larger home ranges than yearlings, and home-range size increased with body mass. This pattern is common among animals, and results from both higher energetic needs and reproductive activity of adults (e.g., Turner et al. 1969; Gittleman and Harvey 1982;

Table 3. Home-range size (km²; minimum convex polygon (MCP) with 100% of locations) of badgers radio-tracked in BPF in 1997–2001.

Season or period	Adult males (n = 7)		Adult females (n = 3)		Adults (n = 10)		Subadults (n = 3)		All badgers (n = 13)	
	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Spring	6.3±1.9	3.8–10.1	8.9±1.5	7.2–10.8	7.1±2.2	3.8–10.8	2.9±1.5	1.9–4.0	6.5±2.5	1.9–10.8
Summer	6.6±2.3	4.8–10.8	14.6±10.9	6.9–22.3	8.6±5.9	4.8–22.3	3.9±0.5	3.6–4.3	7.7±5.5	3.6–22.3
Autumn	5.5±1.4	3.9–6.4	4.5±0.8	4.0–5.1	5.1±1.2	3.9–6.4	1.6	—	4.5±1.8	1.6–6.4
Whole year	8.1±1.5	6.5–11.3	12.4±7.8	7.2–24.1	9.5±4.8	6.5–24.1	4.3±0.3	4.0–4.5	8.9±5.0	4.0–24.1
Whole radio-tracking period	8.7±2.2	6.5–12.5	14.1±9.1	7.2–24.4	10.3±5.3	6.5–24.4	4.3±0.3	4.0–4.5	9.3±5.4	4.0–24.4

Note: Seasonal ranges were calculated if at least 50 locations of an animal were collected during a given season (except for badgers F1 and M4, which were radio-tracked for a short period only, for which seasonal ranges were calculated on the basis of 27 and 14 locations, respectively); n is the number of radio-tracked badgers.

Holzman et al. 1992; Schmidt et al. 1997; Krasińska et al. 2000). In the suburbs of Bristol, England, adult badgers occupied home ranges twice the size of those of subadults (Cresswell and Harris 1988). However, no such differences were found in badgers in farmland in North Nibley (Tuyttens et al. 2000b). For American badgers (*Taxidea taxus*), home-range size increased with the age of animals, and home ranges of reproducing adults were larger than those of non-reproducing individuals (Minta 1993).

The size of home ranges of adult males did not vary among seasons. Males engage in territory defence by visiting and marking border latrines more often than other individuals do (Pigozzi 1990; Brown et al. 1992; Roper et al. 1993). Thus, the more stable home ranges of males can be explained by their defence of both territories and females against males from neighbouring territories. A similar pattern of territory use by males was found in a low-density population of badgers in Spain (Revilla and Palomares 2002). It has also been found in male coyotes (*Canis latrans*) and red foxes (*Vulpes vulpes*) (Andelt and Gipson 1979; Holzman et al. 1992, Cavallini 1996; White et al. 1996).

Badger cubs suckle for almost 4 months (Neal 1986), and lactating females have higher energetic needs than other individuals (Robbins 1993). This affects their body condition (Cresswell et al. 1992; Woodroffe and Macdonald 1995). In BPF, home-range sizes of adult females showed clear seasonal variation. A similar pattern was observed in females of other social carnivores such as fennec foxes (*Vulpes zerda*) and coyotes (Mackie and Nel 1989; Holzman et al. 1992). In badgers, such differences were found in a low-density population in Spain (Revilla and Palomares 2002), but were not observed in high-density populations (Kruuk and Parish 1987; Cresswell and Harris 1988; Brøseth et al. 1997; Hofmann et al. 2000; Tuyttens et al. 2000b). The pattern of space use by males and females observed in BPF and Doñana National Park, Spain, may be typical for a low-density population. Tuyttens et al. (2000b) and Revilla and Palomares (2002) suggested that different factors affected space use by dominant males (mate-guarding) and females (food availability and energetic needs).

In BPF, individual home ranges were largest in summer, when earthworm availability was lowest. Earlier studies from England showed that earthworm availability affected the foraging behaviour of badgers. Kruuk (1978) found that during nights with high earthworm availability, badgers' foraging was restricted to small habitat patches, while during nights with low availability of worms, long-distance feeding predominated. In central Poland and Germany, badgers also extended their home ranges in summer to gain access to voles (*Microtus* spp.) or fruit in orchards (Goszczyński et al. 2000b; Hofmann et al. 2000). However, in regions where earthworm biomass did not vary significantly between seasons, or alternative food resources were easily available, seasonal changes in badger home-range size were not observed (Cresswell and Harris 1988; Ferrari 1997). In autumn, badgers in BPF occupied the smallest ranges. Earthworms were more abundant in that season than in summer, and badgers could collect enough food from a smaller area. A lack of reproductive activity and building of fat reserves (Kowalczyk 2001) could also contribute to the decline in badger home-range size in autumn. A similar decline was observed in Sweden and Germany

Table 4. Territory sizes of badger groups (estimated as MCP 100 and 95%) and percent area of oak–lime–hornbeam (OLH) forests, and estimated biomass of earthworms in badger territories in BPF in 1997–2001 (calculated for MCP 95% territories).

Sett No.[a]	No. of fixes	Territory size (km^2)		Percent area of OLH forest in territory	Estimated mean earthworm biomass (tonnes/km^2 of territory)
		MCP 100%	MCP 95%		
8	543	11.0	7.6	30	21.7
9	451	8.4	3.7	81	36.4
10	2168	10.6	8.5	67	35.1
11	848	10.8	6.9	38	21.4
14	580	10.7	9.2	27	25.2
15	1693	25.5	17.0	20	19.1
16	2230	12.5	11.3	11	11.1
Mean ± SD	1216±790	12.8±5.7	9.2±4.2	39±25	24.3±8.9

Note: For a list of radio-tracked individuals in each group see Fig. 2 and Appendix A.

[a]See Fig. 1.

(Johansen 1993; Hofmann et al. 2000) and Great Britain (Tuyttens et al. 2000b). In BPF, the most dramatic seasonal effect was the cessation of badger activity in winter, when earthworms were not available (see Kowalczyk et al. 2003).

Factors affecting badger densities in the temperate and boreal zones of Europe

The density of badgers in BPF was lower than other population densities observed (review in Kowalczyk et al. 2000), and their territories were among the largest reported in the literature. In the British Isles, badger group territories varied from 0.1 to 2.1 km^2, while in continental Europe they ranged from 1.4 km^2 in Germany to 4.2–5.4 km^2 in central Poland and Norway (review in Woodroffe and Macdonald 1993; Hofmann et al. 2000), 7.8 km^2 in Spain (Revilla and Palomares 2002), to 12.8 km^2 in BPF (this study). What factors can explain such a huge variation in badger density and territory size?

In their review of the composition of the diet of badgers in Europe, Goszczyński et al. (2000a) revealed a geographic gradient in feeding habits of badgers. The contribution of earthworms to their diet grew from zero at 37–40°N to 40–70% at 55–63°N. The opposite trend was observed for plants in the diet. Thus, in deciduous, mixed, and coniferous forests of the European temperate and boreal zones, earthworms are the staple food resource for badgers. Furthermore, Kowalczyk et al. (2000) documented that badger densities in Europe did not depend on latitude but were negatively correlated with forest cover: the highest densities were recorded in areas with 0–30% forest cover. In the temperate zone, earthworm fauna and biomass differ greatly between forest and nonforest habitats. Woodlands harbour mostly small species from the genera *Allobophora* and *Dendrobaena* with average body mass <1 g. These species forage in humus and shallow soil layers, and the standing crop of earthworm biomass is relatively low (Satchell 1967; Nordström and Rundgren 1974; Nakamura 1981). Open landscapes (pastures, meadows, arable land) are dominated by large species (mainly from the genus *Lumbricus*) with individual body mass >4 g, and the total biomass of earthworms is generally higher than in the forests (Kruuk 1978; Brown 1983; Hofer 1988). Of all European earthworms *Lumbricus* spp. seem to be the most important and preferred prey of badgers. *Lumbricus* spp. were most often found in badger stomachs
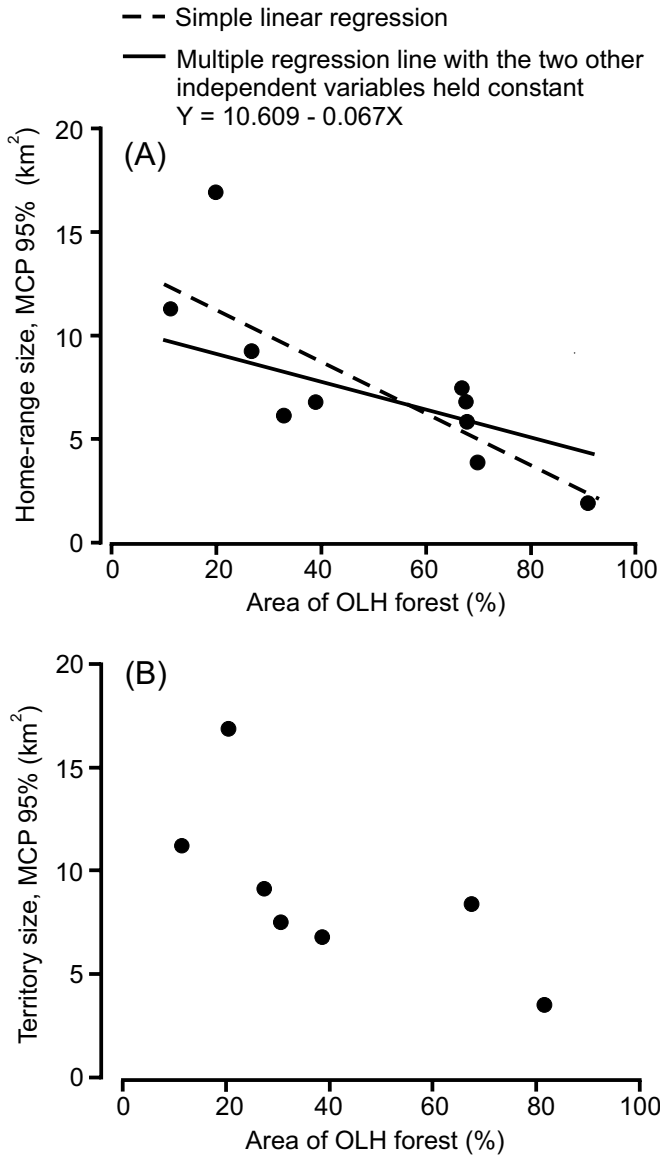
(Kruuk and Parish 1981; Henry 1984; Lüps et al. 1987; Neal 1988; H. Brøseth, unpublished data), and their behaviour (foraging on the soil surface at night) makes them especially accessible for foraging badgers. *Lumbricus* spp. predominate in earthworm communities in open habitats but are rare in forests (Nordström and Rundgren 1973).

Furthermore, earthworm availability to badgers is also affected by temperature. In regions with severe winters (when earthworms are not available), badgers spend up to 5 months inactive (Likhachev 1956; Gorshkov 1997; Kowalczyk 2001). Based on this information, and assuming that data on badgers from the pristine habitats of BPF provide a model for comparison with badgers from other regions, we propose that in the temperate and boreal zones of Europe, where badgers feed predominantly on earthworms, their densities are shaped by the biomass of *Lumbricus* spp. and climate (mean annual temperature).

We reviewed the available literature from Europe and found 8 localities for which data on badger densities, earthworm biomass, and mean annual temperature were available (Appendix B). In these localities, ranging from eastern Poland to Scotland, badger densities (B) were positively related to both mean biomass of the standing crop of *Lumbricus* spp. (L) and average annual temperature (T): $B = -0.283 + 0.00344L + 0.125T$, $R^2 = 0.81$, $n = 8$, $P = 0.017$, where B is log badger density (number of animals per square kilometre; $\ln(n + 1)$) and L is earthworm biomass in kilograms per hectare. These two factors explained 81% of the observed variation in badger densities. Semipartial correlations squared showed that earthworm abundance was far more important ($sr^2 = 0.458$) than temperature ($sr^2 = 0.115$). Though the sample size is small (8 localities), based on the multiple regression analysis we propose a simple graphic model explaining the variation in badger densities in the temperate and boreal zones of Europe (Fig. 4). It indicates that in the forests of central and eastern Europe badgers live at low densities, while the man-made open landscapes of Western Europe and the British Isles can harbour much higher densities.

The positive relationship between density and group size of badgers and biomass of earthworms (*Lumbricus* spp.) was found earlier at the local scale in the British Isles (Kruuk and Parish 1982). Furthermore, Woodroffe and Macdonald

Fig. 3. (A) Size of individual home ranges ($n = 10$) in relation to percent area of oak–lime–hornbeam (OLH) forest. The broken line shows a simple linear regression. The solid line and equation show the influence of OLH forest with the covarying impacts of badger body mass and number of fixes held constant at their mean values (10.2 kg and 662, respectively). (B) Size of group territories of badgers in relation to percent area of OLH forest ($Y = 13.639 - 0.114$OLH, $R^2 = 0.48$, $n = 7$, $P = 0.08$).
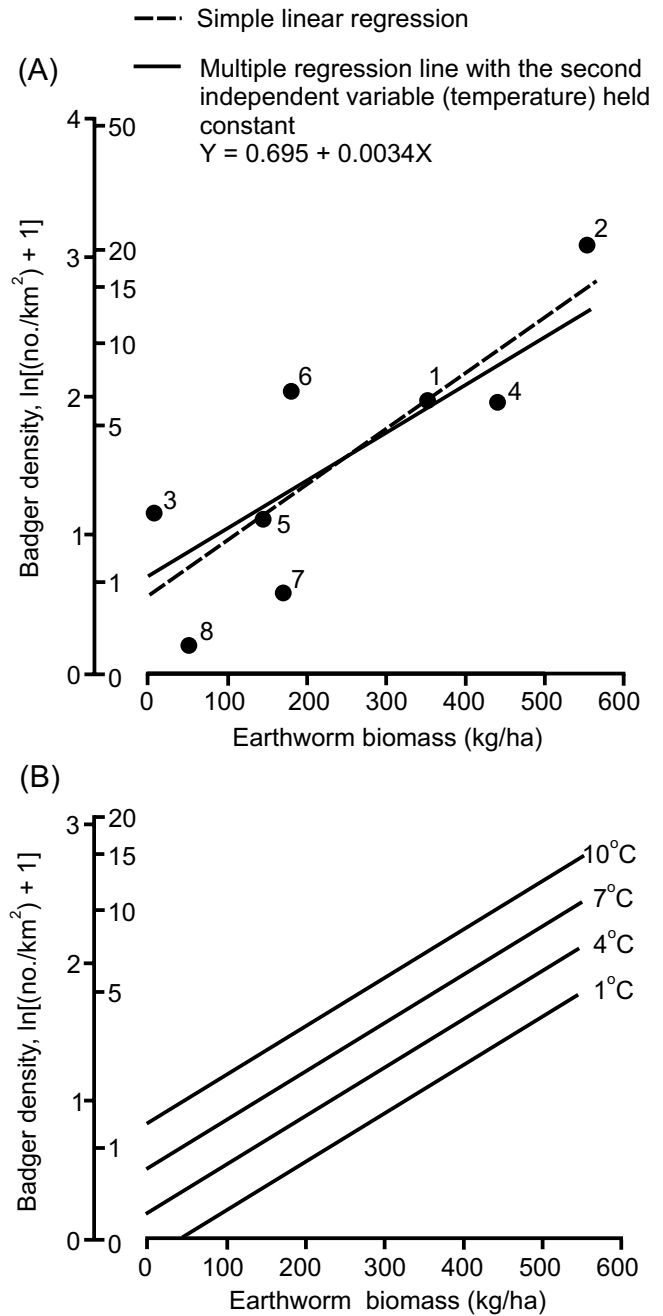

Fig. 4. (A) Densities of badgers in relation to biomass of earthworms (*Lumbricus* spp.) and mean annual temperature in the European temperate and boreal zones. The broken line shows a simple linear regression. The solid line and regression equation show the influence of earthworm biomass with the covarying impact of temperature held constant at its mean value (7.85°C). For details on data points 1–8 see Appendix B. (B) Model explaining the relationship between badger densities and earthworm biomass in the range of mean annual temperatures from 1 to 10°C. Based on empirical data from A and Appendix B.

(1993) reported that the size of badger territories in Great Britain increased with latitude and decreased with rainfall. Also Macdonald and Newman (2002) proposed that the growth in badger numbers in southern England is an effect of improving climatic conditions. These results, although limited to a small part of the badger's geographic range, support the idea that availability of food is the main factor influencing badger densities.

Group living in badgers in relation to food availability

As is shown in this paper, higher densities of badgers were positively related to the increased supply of food resources. In

an earlier paper, Kowalczyk et al. (2000) documented an increase in densities resulting from (*i*) the growing density of social groups and (*ii*) the increasing size of groups. In regions where abundance of food is relatively low and strongly seasonal, badger territories are large and the social unit is

a pair of adults with cubs (e.g., Goszczyński et al. 2000b; Revilla and Palomares 2002; this study). We propose that in such conditions, food supply — and not sett availability — is a limiting resource for badgers. In regions with high food abundance, densities of badger social groups would increase to the level allowed by sett availability. Provided that food resources are still plentiful and sett number is limited, a further increase in badger density may only be achieved by larger social groups. Indeed, this is observed in many high-density populations in Great Britain. For instance, in Woodchester Park, the composition of social groups increased from 2.7 to 8.8 adults over a 16-year period, and no change in territory size was observed (Rogers et al. 1997, 2000). In Wytham Woods, the number of badger groups changed because new setts were excavated, and the size and shape of territories depended on sett location (da Silva et al. 1993; Doncaster and Woodroffe 1993). Thus, we think that the resource-dispersion hypothesis, most often used to explain badger sociality (Macdonald 1983; Woodroffe and Macdonald 1993), may explain why groups of non-cooperating individuals occupy the same territory, but it does not explain the mechanisms that lead to group living. In our opinion, the essential factor underlying the great variation in badger sociality (from pairs to large groups) is the abundance of food resources.

Acknowledgements

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Appendix A

Table A1. Badgers (*Meles meles*) radio-tracked in Białowieża Primeval Forest (BPF) in 1997–2001.

Badger ID No.[a]	Sett No.[b]	Age class	Body mass (kg)	Radio-tracking period	No. of fixes	No. of 24-h radio-tracking sessions	Fate
F1	8	Subadult	9.3	8 Mar. – 25 Apr. 1997	27	—	Contact lost
F2	15	Adult	11.5–16.0	21 Apr. – 17 Aug. 1997			Transmitter failure
				8 Sept. 1998 – 26 Nov. 1999	1526	14	Transmitter failure
F6	8	Adult	9.0	1 Mar. 1998 – 5 June 1999	386	3	Transmitter failure
F7	9	Subadult	8.8	28 May 1998 – 6 Apr. 1999	249	2	Contact lost
F10	11	Adult	10.1	24 Apr. 1999 – 6 June 2001	848	7	Transmitter failure
M1	15, 14	Adult	11.0–20.0	14 Nov. 1997 – 30 Nov. 1999	582	3	Contact lost
M2	16	Adult	9.2–11.2	9 Mar. 1997 – 17 Jan. 1999			Transmitter failure
				14 Mar. 1999 – 9 May 2000	2216	18	Died
M3	10	Adult	11.5–18.0	15 Nov. 1997 – 28 June 2000	859	6	Transmitter failure
M4	16	Adult	9.8	20 Mar. – 25 Apr. 1997	14	—	Died (road kill)
M5	10	Subadult	7.2	1 Mar. 1997 – 7 Sept. 1998	532	6	Died
M8	8	Adult	10.5	31 Mar. – 1 June 1999	136	1	Dispersal
M9	10	Adult	9.2	10 Apr. 1999 – 1 July 2000	793	6	Dispersal (to Belarus)
M11	9	Adult	11.6	15 July 1999 – 21 Apr. 2000	202	1	Probable dispersal
Total					8370	67	

Note: For badgers captured more than once, the body-mass range is given.

[a]M, male; F, female.

[b]See Fig. 1.

Appendix B

Table B1. Badger densities, biomass of earthworms (*Lumbricus* spp.), and mean annual temperatures in eight study areas in Europe.

Area No.	Location	Badger density (no./km^2)	Mean biomass of *Lumbricus* spp. (kg/ha)	Mean annual temp. (°C)	Source
1	Chiltern Hills, England	8.3	353.5	9.8	Nolet and Killingley 1987
2	Wytham Wood, England	21.0	556.2	9.8	Hofer 1988
3	Ardnish, Scotland	2.2	8.7	8.3	Kruuk and Parish 1982
4	New Deer, Scotland	6.1	441.5	8.4	Kruuk and Parish 1982
5	Speyside, Scotland	2.1	147.0	8.4	Kruuk and Parish 1982
6	Hakel Forest, Germany	6.5	180.0	8.7	Hofmann 1999
7	Malvik, Norway	0.8	175.0	1.5	Brøseth et al. 1997
8	Białowieża Primeval Forest, Poland	0.2	50.3	7.9	This study