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Seasonal and spatial pattern of shelter use by badgers *Meles meles* in Białowieża Primeval Forest (Poland)

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In 1997–2001, we investigated the use of day-time shelters by radio-collared badgers *Meles meles* (Linnaeus, 1758) in the Białowieża Primeval Forest, eastern Poland. Each social group of badgers utilised, on average, 9 different shelters per territory (range: 4–20). The main setts, occupied for breeding and winter sleep, were also most frequently used for day-time rest throughout the year (73% of days). Badgers living in the pristine oldgrowth stands utilised larger number of shelters and spent more days in hollow trees (mainly lime *Tilia cordata*), compared to badgers inhabiting younger secondary tree stands. Number of shelters used by individuals varied between seasons and depended on sex and age of animals. In summer, badgers used more shelters than in spring and autumn. In winter, they stayed in their main setts only. Adult males occupied more shelters and spent fewer days in the main sett than other badgers. In spring, females rearing young used only the main setts. The average underground space used by badgers within the main sett was 128 m^2. It was largest in summer and smallest in winter, and also varied between males and females. We proposed that, in a low-density population, badgers used several setts and other daily shelters to reduce energy expenditure when exploring their large territories and foraging. Furthermore, setts may play a role of marking sites. Analysis of the biogeographical pattern of sett use by European badgers showed that the number of setts used by social groups increased with increasing territory size, whereas the density of setts (*n* setts/km^2) was negatively correlated with territory size. We proposed that different factors could shape the utilisation of setts by badgers in low- and high-density populations.

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Introduction

Eurasian badgers *Meles meles* (Linnaeus, 1758) are semi-fossorial animals. Their burrows called setts are used for breeding, winter sleep, and – year round – as a shelter during day-time resting. The setts are often inherited by generations of badgers. Within their territories, social groups of badgers may construct and use from one to over 25 setts of different type and size (Roper 1993, Ostler and Roper 1998, Revilla *et al.* 2001). Main setts are essential components of badger territories used by all group members, and if complex enough, they secure successful reproduction (Roper 1993). However, in low-density populations, badgers may use large number of setts, with no clear preference to any one (Brøseth *et al.* 1997, Revilla *et al.* 2001). Function of multiple sett use by badgers has been discussed (Roper 1993, Butler and Roper 1996, Brøseth *et al.* 1997, Roper *et al.* 2001), however, the reasons for such behaviour are still not clear. The defence of badgers against ectoparasites was proposed by Butler and Roper (1996) as the explanation for use of many setts or many chambers within a large sett, but so far it has been studied in one high-density population.

The internal use of setts by badgers was investigated in a high-density population in southern England, where badgers are active year round (Roper and Christian 1992, Butler and Roper 1996, Roper *et al.* 2001). However, in the north-eastern, cold-climate regions of Eurasia, badgers spend over 70% of their lifetime either during winter lethargy or sleeping underground during the day in the active season (see Kowalczyk *et al.* 2003a for review).

This study was conducted in Białowieża Primeval Forest (BPF; eastern Poland), where badgers live in very low densities and occupy large territories (8.4–25.5 km^2, Kowalczyk *et al.* 2003b). Social groups are small and usually consist of 2–3 adult badgers and cubs. In BPF, badgers spent over 3 months for winter sleep (Kowalczyk *et al.* 2003a). We propose that, in large territories, badgers use multiple setts to reduce energy expenditure in territory exploring (as suggested by Roper 1992 and Brøseth *et al.* 1997). Moreover, numerous setts may play a role of marking points in territory maintenance (see Revilla and Palomares 2002). To test our hypothesis, we analysed the utilisation pattern of setts and other shelters by badgers, and distribution of daily shelters in their territories. We also studied: (1) influence of forest structure on shelter use, (2) internal use of setts, (3) biogeographical pattern of sett use by badgers in Europe.

Study area

Białowieża Primeval Forest (BPF), located on the Polish-Belarussian border (52°30'–53°N, 23°30'–24°15'E), is one of the best preserved temperate lowland forests in Europe. The Polish part of the Forest covers 595 km^2 and includes strictly protected Białowieża National Park (BNP, 105 km^2), and the exploited forests (490 km^2). The latter are exploited by small clear-cuts and replantation. The relief of the area is generally flat (134–197 m a.s.l.). 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. stands 11.7% (Kwiatkowski 1994, Jędrzejewska and Jędrzejewski 1998). Open habitats cover 6.4% of the area. During the 80-year long exploitation of the forest in the managed part of BPF, replanting of pine and spruce has resulted in their current over-representation (54% of the area) compared to natural stands of BNP (27% of the area). The average age of trees in BNP is 131 years, and in exploited part of the forest 72 years. The BNP contains 101–133 m^3 of dead wood per hectare, while in exploited forests fallen trees and dead wood are very scarce (0–1 m^3/ha; Bobiec 2002). The densities of large trees are higher in natural forests of BNP than in other old-growth forests of Europe (Nilsson *et al.* 2002).

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 of mean daily temperatures: –22.1 to +28.8°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 with a maximum recorded depth of 23 cm. Mean annual precipitation during the study period was 586 mm. In BPF, three species of other denning predators occur: wolf *Canis lupus*, red fox *Vulpes vulpes*, and raccoon dog *Nyctereutes procyonoides*, the last one having colonized BPF in the 1950s.

Material and methods

Thirteen badgers (7 adult males, 3 adult reproducing females, and 3 yearlings) belonging to seven social groups were radio-tracked in 1997–2001. Badgers were caught in foot-snare traps or box traps placed near setts and equipped with radio alarms, which shortened the time the badger spent in a trap to 1–2 hours. The captured animals were immobilized by an intramuscular injection of xylazine--ketamine mixture (Kreeger 1997), sexed, aged (yearling or adult – on the basis of body size, date of capture, and tooth wear), and fitted with radio-collars (Advanced Telemetry System, USA). The average time of active collar wearing by all badgers was 459 days (range 37–1101). For details about radio-collared badgers see Kowalczyk *et al.* (2003b).

Two to seven days a week, badgers were located precisely in their resting sites during the day, usually between 08:00 and 15:00 hrs. The type of daily resting site was described and mapped. In total, we collected 1812 daily locations of badgers (1471 in spring–autumn and 341 in winter) during 2015 badger-days of radio-tracking. Additionally, 67 sessions of continuous radio-tracking were conducted during which badgers were located at 15-min intervals. Those sessions were used to determine, if badgers utilised several shelters to avoid long-distance travels back to the sett at the end of their nocturnal foraging. Spring sessions of continuous radio-tracking of adult females were excluded from the analysis, because during the nursing period, reproducing females returned to the main sett every morning.

We divided the shelters used by badgers into two categories: (1) main setts – burrows occupied continuously for reproduction, winter sleep, and used as a main shelter for day-time rest by all members of a social group, and (2) secondary shelters – setts, hollow trees, and above-ground places used infrequently as day-time resting sites from spring to autumn. If badgers were found in the main setts during the day, we precisely recorded their underground position, as described by Roper and Christian (1992). We measured azimuth and distance to the nearest sett entrance and to the nearest tree. Each location was mapped. We prescribed underground locations of badgers to different chambers, if they differed more than 1 m. On the basis of underground locations (in total 1316 localizations), we calculated within-sett ranges for individual badgers and social groups using Minimum Convex Polygons with 100% of locations.

The spatial pattern of shelter distribution was analysed by the nearest neighbour distance, as described by Clark and Evans (1954). Additionally, for each territory we compared: (1) the mean distance from the main sett to secondary shelters used in territories and the mean distance from the main sett to 25 random points (generated by Microsoft Excel 2003 programme) in a territory; (2) the nearest distance from secondary shelters and random points to territory boundaries; (3) the distance from the main sett to secondary shelters and the distance from the main sett to 24 points located on territory boundaries; the points were radially dispersed every 15 degrees outwards from the main sett. Furthermore, we calculated the parts of each territory covered by all shelters as MCP ranges determined by shelter locations.

For each standing and fallen hollow tree used by badgers for day-time rest, we recorded the species of the tree and distance of a resting badger from the basal part of the tree. We calculated badgers' selection of tree species using Ivlev's electivity index, D (modified by Jacobs 1974): $D = (r - p)/(r + p - 2pr)$, where: r is the number of the given tree species that were used by badgers as fraction of all hollow trees used and p is the fraction of a given tree species in the total number of trees with diameter at breast height > 40 cm (suitable for badgers) in the pristine stands of BNP, measured in 1989 on 45 sampling plots 0.5–1 ha each (data from Protection and Management Plan of Białowieża National Park). D ranges from –1 (the strongest negative selection) to +1 (the strongest positive selection), with 0 being random utilisation.

Data on badger sett use were analysed in four seasons: spring (1 March – 31 May), summer (1 June – 31 August), autumn (1 September – 30 November), and winter (1 December – 28 February). In BPF, badgers are not active in winter (Kowalczyk *et al*. 2003a), therefore some analyses were done for the warm seasons only.

Results

Distribution and use of the main setts and other shelters in badger territories

During day-time, badgers rested in various types of shelters (Fig. 1). From spring to autumn, they were found resting in main setts on 73.2% of days, in secondary setts on 11.6%, in hollow trees on 2.9%, and above-ground in dense vegetation on 0.1% of days. On 12.1% of days, day-time shelters were not found. Badgers usually spent a whole day in one shelter. We recorded only 2 cases (of 1471) of moving from one shelter to another during the day; in both cases the two shelters were located < 250 m from each other. The number of shelters utilised by each group of badgers varied from 4 to 20, on average 9.0 ± 5.6 (SD) (Fig. 2, Table 1). Each group used one main sett, plus 1–9 secondary setts, 0–14 hollow trees, and 0–1 other shelters on the ground. The density of all shelters per 1 km^2 of group territory varied from 0.3 to 1.9, on average 0.8 ± 0.6. Day-time shelters were dispersed over the area covering from 8 to 73% of the whole territory, on average 32 ± 26% (Fig. 2). In territories, 1–3 burrows never utilised by radio-collared badgers were also located.

Three badger groups (numbers 2, 4, 6, see Fig. 2) possessed 1–2 shelters that were used more often than other secondary shelters. In two of those territories (numbers 2 and 6), the shelters were former main setts. The mean number of entrances in all setts (main + secondary) was 2.7 ± 2.4 (range: 1–10, n = 35). Main

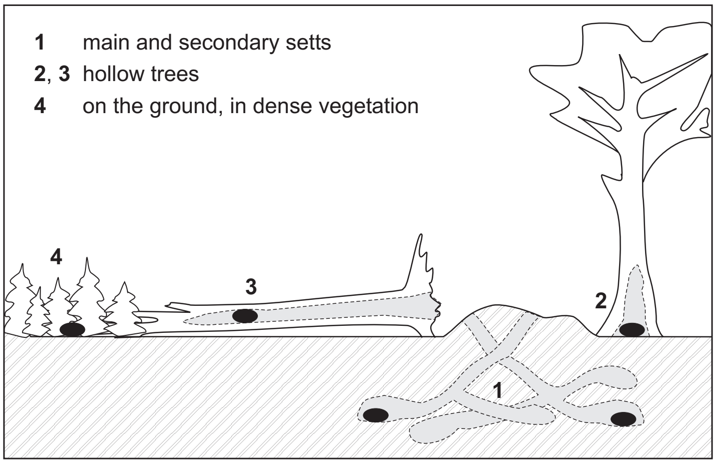

Fig. 1. Types of shelters used by radio-tracked badgers *Meles meles* in Białowieża Primeval Forest. Black dots indicate locations of resting badgers.

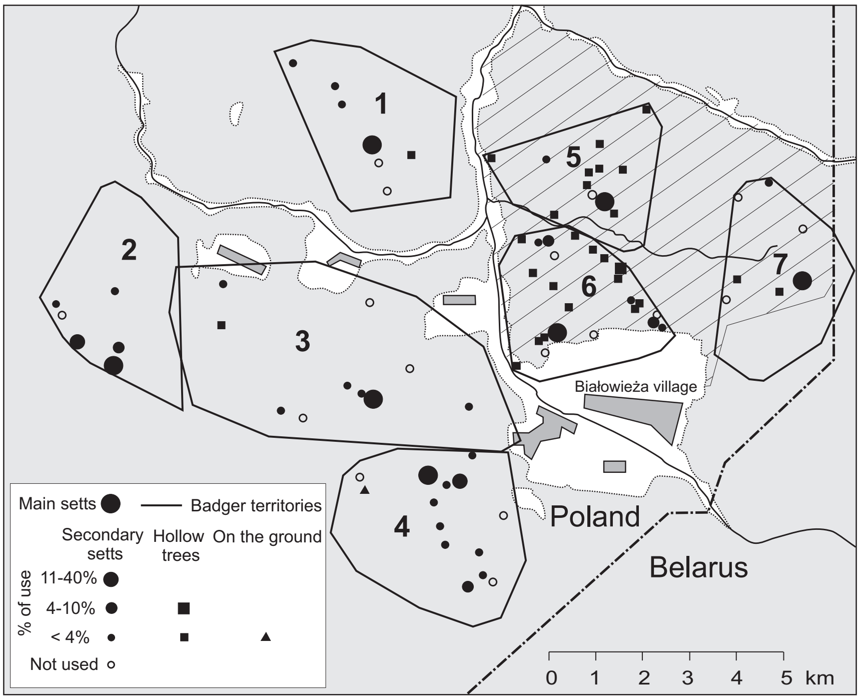

Fig. 2. Distribution of shelters in badger group territories and rates of their utilisation in the protected oldgrowth forests (Strict Reserve of Białowieża National Park – hatched area) and exploited stands of the Białowieża Primeval Forest. Territories are numbered as in Table 1. Shaded area denotes forest.

Table 1. Number and types of day-time shelters used by radio-collared badgers *Meles meles* and characteristics of their main setts in Białowieża Primeval Forest. Territories were occupied by groups of 2–7 badgers (including young), 1–3 of which were radio-collared (subadults and adults only). Territory no. as in Fig. 2. (E) – exploited forests, (P) – pristine forests, * includes the main and the secondary setts.

Territory no.	Number of entrances to the main sett	Area used by badgers within the main sett (m^2)	Number of day-time shelters used in the territory		
			Setts*	Hollow tress	On the ground
1 (E)	8	141	4	1	–
2 (E)	3	29	5	–	–
3 (E)	6	74	6	1	–
4 (E)	10	266	10	–	1
5 (P)	7	117	2	9	–
6 (P)	4	139	6	14	–
7 (P)	6	Not studied	2	2	–
Mean ± SD	6.3 ± 2.4	128 ± 80	5.0 ± 2.8	3.9 ± 5.5	0.1 ± 0.4

Table 2. Use of hollow trees for day-time shelters by badgers in Białowieża Forest, availability of various tree species, and their selection by badgers. BNP – Białowieża National Park. [a] hornbeam *Carpinus betulus*, Norway spruce *Picea abies*, aspen *Populus tremula*, birch *Betula* sp., Scots pine *Pinus silvestris*, black alder *Alnus glutinosa*, elm *Ulmus* sp.

Tree species	Hollow trees used by badgers			Percentage of the species tree stands of BNP	Ivlev's electivity index D
	Standing $n = 9$	Fallen $n = 18$	All $n = 27$		
Lime *Tilia cordata*	4	36	40 (83.3%)	4.8	0.98
Oak *Quercus robur*	5	–	5 (10.4%)	13.0	−0.12
Ash *Fraxinus excelsior*	2	–	2 (4.2%)	9.5	−0.41
Maple *Acer platanoides*	–	1	1 (2.1%)	3.4	−0.24
Other tree species[a]	–	–	–	69.3	−1

setts possessed 6.3 ± 2.4 entrances (range: 3–10, $n = 7$; Table 1), and secondary setts 1.7 ± 1.2 (range: 1–6, $n = 28$). The percentage of days badgers spent in a given sett from spring to autumn depended on its size (expressed by the number of entrances). The correlation was significant for all setts ($r = 0.90$, $n = 35$, $p < 0.0005$). Analysed separately for the main and secondary setts, it was still significant for the secondary setts ($r = 0.84$, $n = 28$, $p < 0.0005$), but not for the main ones ($r = 0.65$, $n = 7$, $p > 0.1$). During the sett surveys (1996–2002), we observed five cases of creating a new sett entrance. In one case, the new entrance was excavated in a main sett with 3 entrances, and in other four cases new holes were created by the collapse of the sett tunnel.

We recorded 48 cases of hollow tree use by badgers (Table 2). Badgers used 18 fallen trees (on 37 days) and 9 standing trees (on 11 days) of four species: lime, oak, ash, and maple. Shelters in fallen trees were located in the main trunks (17) or in a large branch (1). Lime trees were strongly selected by badgers for day-time shelters (Table 2). Of all hollow trees, 74% were used only once, 19% – twice, and 7% – three or more times (maximum 18). Only 3 hollow trees were used by more than one badger from the social group. We noticed one case of joint use of a hollow tree by two radio-collared badgers during the same day. When badgers spent a day in the fallen tree, they rested on average 6.3 m (range: 3–11 m) from the basal part of the tree. We recorded also one case, when badger climbed inside the trunk of the bent standing lime tree to 5–6 m of its height.

We found differences in shelter use by badgers between the pristine oldgrowth forest of BNP (territories 5, 6, 7) and exploited stands of BPF (territories 1, 2, 3, 4). In BNP, badgers spent fewer days in setts (79.0%), and rested more often in hollow trees (6.3%), compared to badgers in exploited forests (89.2% and 0.2% of days, respectively) (Table 3, Fig. 2). The difference was statistically significant (G-test for homogeneity of percentages: $G = 10.16$, df = 3, $p < 0.02$). All badgers in pristine forests (6 individuals), but only 2 of 7 individuals in the exploited forests used hollow trees as a shelter.

Table 3. Types of day-time shelters and the relative frequency of their utilisation by radio-tracked badgers in the pristine oldgrowth forests of Białowieża National Park (n = 700 days, 6 individuals) and the exploited stands of Białowieża Primeval Forest (n = 974 days, 7 inds) in 1997–2001 (spring–autumn). [a] badgers rested in shelters other than the main sett.

Shelter type	Percentage of days badgers spent in a given type of day-time shelter	
	Pristine forests of BNP	Exploited stands of BPF
Main setts	70.9	76.4
Secondary setts	8.1	12.8
Hollow trees	6.3	0.2
On the ground	–	0.2
Not found[a]	14.7	10.4

In all territories, the nearest neighbour distance (NND) between shelters [mean 0.88 ± 0.12 km (SE)] was longer than expected (0.65 ± 0.08 km). In five territories, shelter distribution did not deviate from random (R = 1.18 to 1.35, c = 0.79 to 1.77, where R is the measure of the degree to which the observed distribution departs from random expectation with respect to NND, and c is the standard variate of the normal curve; Clark and Evans 1954), whereas in two territories (numbers 5 and 7) it tended to be regular (R = 1.58 and 1.66, c >1.96). The distance from the main sett to other shelters was, on average, 1.65 ± 0.12 km, and in all territories except one (no. 6) it did not differ from the distance between the main sett and random points (mean 1.65 ± 0.17 km) (Mann–Whitney U-test: U = 36 to 144, p = 0.1 to 0.9). Also, NND from territory boundaries to badger shelters (0.57 ± 0.06 km) and to random points (0.51 ± 0.06 km) did not differ significantly (U = 36 to 285, p = 0.2 to 0.9), with the exception of territory no. 4 (U = 69, p = 0.04), where shelters were located further away from territory boundaries than random points. Distance from the main sett to other shelters did not differ from the distance between the main sett and territory boundaries (1.78 ± 0.14 km) (Mann-Whitney U-test: U = 39 to 209, p = 0.3 to 0.9). The mean distance from the main sett to any other shelter constituted 87–100% of average distance from the main sett to the territory boundaries.

Seasonal and individual differences in shelter use

From spring to autumn adult males rested in the main sett on 68% of days, adult females on 81%, and subadults on 76% of days. Adult males utilised shelters other than the main sett from March to October, with a peak in May–September (Fig. 3). Monthly, we recorded on average 2.8 visits of males to other shelters, with a maximum recorded in summer (over 4 visits/month). Subadults were found resting in shelters other than the main sett from March to September with a peak in June

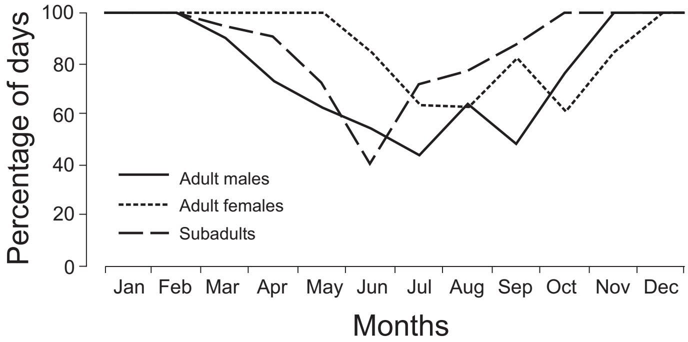

Fig. 3. Monthly changes in the use of main setts by radio-tracked badgers. Average values of percentage of days that badgers spent in the main sett are given.

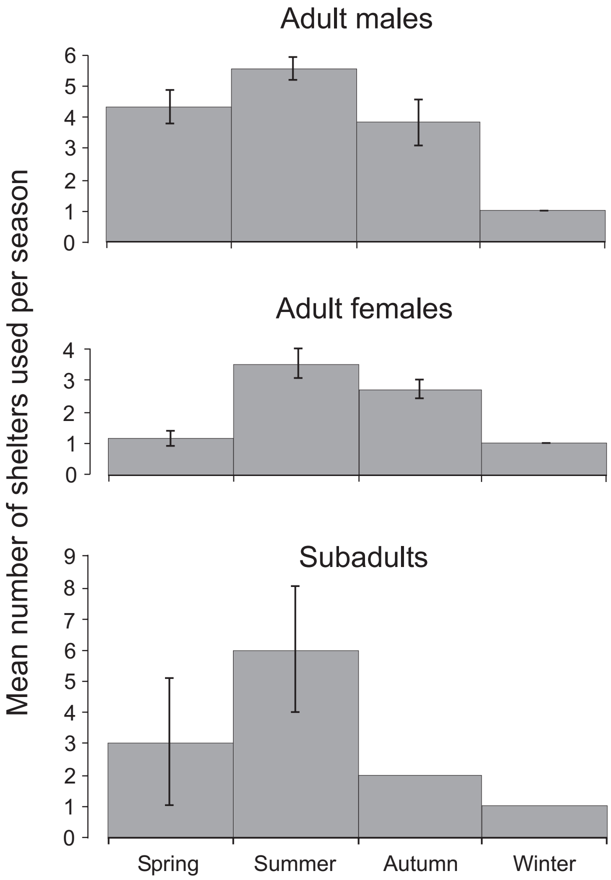

Fig. 4. Seasonal variation in the number of shelters used by radio-tracked badgers of different age and sex. Mean number of shelters in each season (± SE) was calculated on the basis of 1 to 9 badger-seasons.

(60% of days; Fig. 3). They visited other shelters, on average, 1.4 times per month. Adult breeding females behaved differently. They always spent daytime in the main sett in spring (March–May), began to rest in other shelters in June, and continued to do so until November (Fig. 3). Females visited other shelters on average 1.2 times per month, with a maximum in August (4.5 visits/month).

Badgers always spent winters in the main sett. The differences in using the main sett as day-time shelter by badgers of the three age and sex classes were statistically significant ($G = 185.35$, df = 16, $p < 0.001$). They were also significant, when compared pair-wise: adult males vs adult females ($G = 104.83$, df = 8, $p < 0.001$), adult males vs subadults ($G = 22.43$, df = 8, $p < 0.01$), and adult females vs subadults ($G = 141.03$, df = 8, $p < 0.001$).

Each individual utilized from 4 to 13 shelters, on average 7.1 (SD 2.7). Adult males used higher number of shelters (mean 7.8, range: 5–13) than adult females (5.0, range: 4–6) and subadults (6.5, range: 5–8). The highest number of shelters was used by badgers in summer (mean 5.0, range: 3–8), smaller in spring (3.3, range: 1–8) and autumn (3.4, range: 2–7) (Fig. 4). In spring, when cubs were small, adult breeding females most often used the main sett. The differences in the number of shelters used per season were statistically significant between males and females in spring and summer (Mann-Whitney U-test: $U = 35.5$, $n_1 = 9$, $n_2 = 4$, $p = 0.006$ for spring; $U = 26$, $n_1 = 7$, $n_2 = 4$, $p = 0.02$ for summer).

Badgers from one social group (data for 4 pairs of males from 2 social groups) were found resting together in the same sett on 44% of days from spring to autumn (37% of days in the main sett, and 7% in other shelters). They rested separately on 56% of days (46% – one individual rested in the main sett, the second in other shelter, and on 10% of days the two animals rested in different shelters). Badgers from the same social group rested together in the main sett on 45 and 37% of days, respectively, in spring and summer, and on 92% of days in autumn.

When badgers ended their nocturnal foraging, on 74% of cases, on average (range 50–100%), they selected the nearest shelter for resting. On 26% of cases, they moved to further located shelter, usually the main sett.

Use of within-sett space

As the main setts were so important for badgers year round, we analysed the pattern of utilisation of within-sett area, number of chambers, and number of days spent in various chambers. The within-sett range used by badgers differed among the main setts ($n = 6$) from 29 to 266 m^2, mean 128 ± 33 m^2 (SE), and was correlated with sett size, as expressed by a number of entrances ($r = 0.83$, $n = 6$, $p < 0.05$). Individual within-sett ranges of badgers ($n = 10$ inds) varied from 29 to 266 m^2, on average 104 ± 21 m^2, and significantly differed seasonally and between adult males and adult females. Males used larger within-sett ranges than females (115 ± 82 and 92 ± 25 m^2, respectively), and differences were more visible when analysed in seasons (Nested ANOVA, $n = 39$ badger-seasons; effect of season: $F = 4.875$, df = 3, $p = 0.007$; sex: $F = 6.087$, df = 4, $p = 0.001$). The largest ranges

Table 4. Seasonal changes of within-sett use by radio-tracked badgers in Białowieża Primeval Forest: the area used within the main sett, number of underground chambers, and number of days spent in one chamber. Mean values ± SE and ranges (in parenthesis) are given. [a] including subadults, [b] on average, 15 months.

Season	Within-sett range (m^2)			Number of chambers used	Number of days per chamber
	Adult males	Adult females	All badgers[a]		
Spring	69 ± 18 (29–137)	23 ± 15 (4–39)	52 ± 13 (4–137)	12.5 ± 1.6 (5–19)	2.9 ± 0.4 (1–15)
Summer	114 ± 40 (74–199)	50 ± 15 (13–79)	78 ± 21 (13–199)	15.5 ± 0.7 (13–17)	2.3 ± 0.2 (1–9)
Autumn	69 ± 25 (41–151)	44 ± 13 (8–69)	58 ± 15 (8–151)	15.3 ± 2.1 (8–24)	2.4 ± 0.3 (1–10)
Winter	41 ± 8 (8–79)	6 ± 1 (3–9)	31 ± 8 (3–79)	9.8 ± 2.2 (3–17)	4.5 ± 0.9 (1–26)
Whole year	97 ± 25 (28–259)	76 ± 33 (18–141)	89 ± 17 (28–259)	25.5 ± 2.0 (15–37)	2.8 ± 0.3 (1–27)
Whole period of radiotracking[b]	115 ± 33 (29–266)	92 ± 25 (61–141)	104 ± 21 (29–266)	–	–

Table 5. Mean territory size, number and size of setts used by badgers in 12 localities in Europe. * denotes locations, for which detailed data on each territory were available. ? – no data.

Location	Mean territory size (km^2)	Mean number of shelters used per territory	Mean size of the main sett (*n* entrances)	Mean percentage of days in the main sett	Source
South Downs, England*	0.28	5.3	22.3	76	Roper *et al*. 2001
Castleward, Ireland	0.50	5.1	?	?	Feore and Montgomery 1999
Wytham Wood, England*	0.66	5.0	10.5	65	Kruuk 1978
East Ofally, Ireland*	0.87	4.4	11.9	?	O'Corry-Crowe *et al*. 1993
Katesbridge, Ireland	1.27	5.0	?	?	Feore and Montgomery 1999
Hakel Forest, Germany	1.39	3.6	?	?	Hofmann 1999
St.-Blaise-Cressier-Thielle, Switzerland*	1.69	4.2	12.2	71	Ferrari 1997
Glenwhirry, Ireland	3.45	3.3	?	?	Feore and Montgomery 1999
Coto del Rey, Spain	4.06	27.0	2.4	29	Revilla *et al*. 2001, Revilla and Palomares 2002, E. Revilla unpubl.
Malvik, Norway*	5.40	12.0	?	32	Brøseth *et al*. 1997
Doñana NP, Spain	7.80	12.0	?	53	Revilla *et al*. 2001, Revilla and Palomares 2002, E. Revilla unpubl.
Białowieża Forest, Poland*	12.80	9.0	6.4	73	This study, and Kowalczyk *et al*. 2003b

were used by badgers in summer (89 m^2), smaller in spring and autumn (61–62 m^2), and the smallest in winter (34 m^2; Table 4, Fig. 5). Mean number of chambers used per season (10–16) did not differ significantly between seasons, but in winter the chambers used by badgers were closer to each other (Fig. 5). In winter, percentage of days spent by a badger in one chamber almost doubled in comparison to the rest of the year (Table 4, Fig. 5).

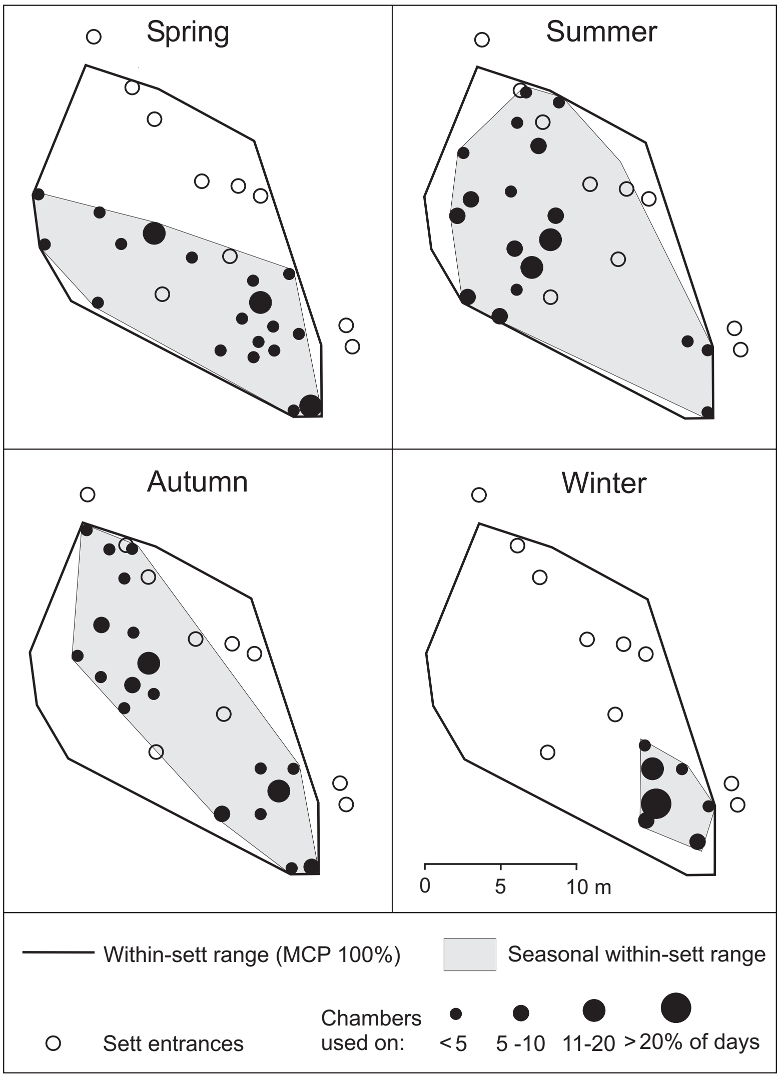

Fig. 5. Example of seasonal changes in utilisation of within-sett space by badgers (sett no. 4, see Fig. 2). Total within-sett space is marked by polygons, shaded areas denote seasonal within-sett ranges, black dots are chambers (see legend for their size), open dots show sett entrances.

The individual within-sett ranges of badgers covered, on average, 76% of group ranges (min–max: 55–95%, for setts with more than one radio-collared badger). Annually, badgers used, on average, 64% of all available within-sett area (calculated as MCP with 100% of locations). The overlap of within-sett area used by badgers occupying the same main sett was, on average, 82% (range: 78–87%, n = 5 pairs). If two badgers rested together in the main sett, they were localised in the same chamber on 48% of cases, but some seasonal differences were observed. In spring and summer, badgers shared the same chamber on 33–34% of days, in autumn on 46%, and in winter in 72% of days.

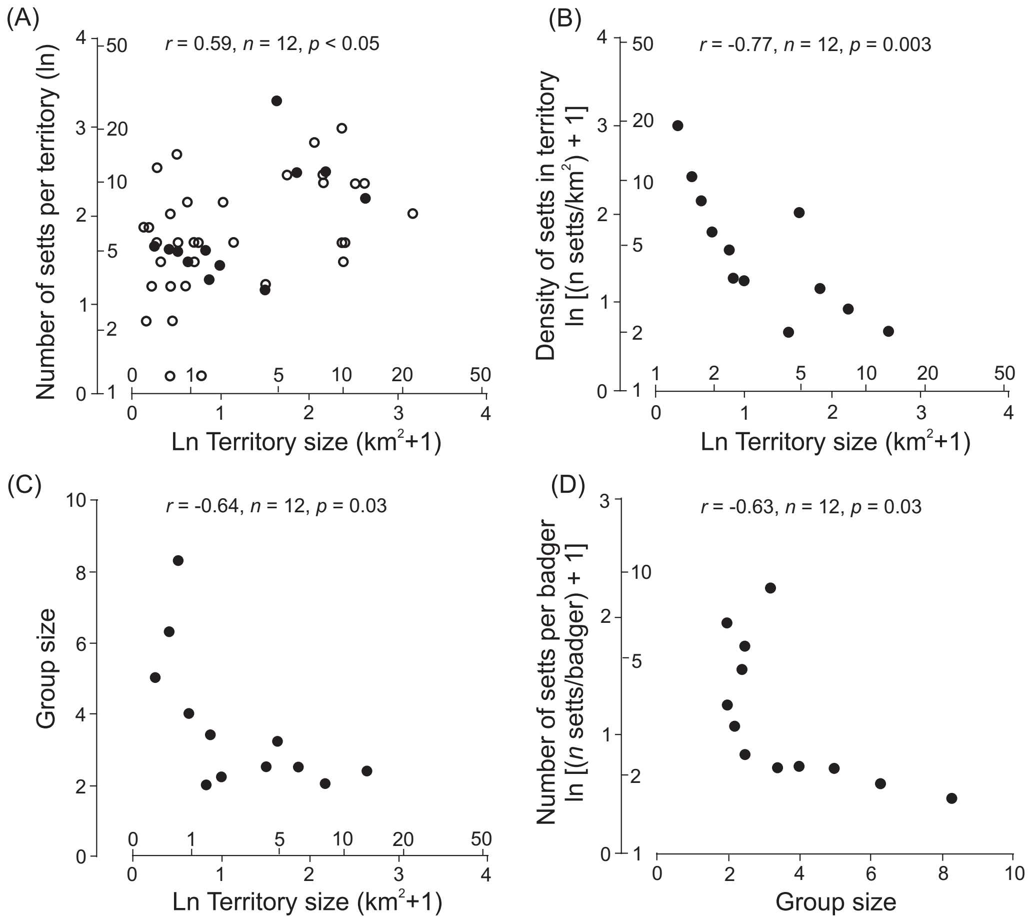

Fig. 6. Biogeographical variation in sett and shelter number and density in relation to badger territory and group size in 12 localities in Europe. (A) The number of setts in a territory in relation to territory size. Open circles denote detailed data from 6 localities, and black dots are average values from all 12 localities. Correlation was calculated based on mean values (see Table 6). (B) The density of setts (n setts per 1 km^2 of territory) in relation to territory size. (C) Correlation between territory size and group size of badgers. (D) Number of setts per badger in relation to group size. In log-transformed variables, axes show both log-scaled and absolute values.

Biogeographical variation in shelter use by badgers in Europe

We reviewed data available from Europe on sett use by badgers. The studies conducted in 12 localities ranging from Ireland and Spain to Norway and Poland gave detailed data (6 localities) or average values (6 localities) on number and size of setts used, territory size, badger group size or time spent in the main setts (Table 5). We used the mean values in further analyses. The number of setts occupied by social groups of badgers increased with growing size of their territory (Fig. 6A). However, the density of setts (n setts per 1 km^2 of territory) decreased with increasing territory size (Fig. 6B). One can expect that the number of setts will increase with number of badgers occupying a territory. However, badger group size was negatively correlated with territory size (Fig. 6C), and the mean number of setts per individual badger was negatively correlated with group size (Fig. 6D).

As the number of setts used per territory increased, badgers spent fewer days in the main sett ($r = -0.83$, $n = 7$, $p = 0.02$, x-values log-transformed), and the size of the main sett (expressed by the number of entrances) became significantly smaller ($r = -0.91$, $n = 6$, $p = 0.01$, both x and y-values log-transformed).

Discussion

In Białowieża Primeval Forest, badgers showed strong seasonal changes in territory use and activity as a result of varying supply of earthworms, their main food. In summer (poor availability of earthworms), badgers moved over large home ranges and showed long daily activity compared to other seasons (Kowalczyk *et al*. 2003a, b). The parallel seasonal changes were observed in shelter utilisation by badgers. Summer increase in the number of shelters used was related to wider territory penetration and longer activity of badgers in that season.

In winter, due to scarcity of earthworms, badgers stayed inactive in their main setts for over 3 months (Kowalczyk *et al*. 2003a). The depth and complex structure of main setts can secure survival in severe and long winters. Moreover, in winter, badgers occupied very small within-sett space, and tended to huddle together. The same behaviour of badgers was observed in South Downs in England (Roper *et al*. 2001). It can be explained by thermoregulatory advantages, as observed in other animals (eg marmots, Blumstein and Arnold 1998). Roper (1992) observed, that usually only few chambers in the sett contained bedding, and therefore, were suitable for overwintering. In BPF, most of the active main setts of badgers were occupied by raccoon dogs in winter (Kowalczyk *et al*. 2000). Raccoon dogs decrease their activity in the cold season and – to survive periods of food shortage in winter – often settle in badger setts. The presence of raccoon dogs might force badgers to use limited within-sett space in order to avoid contacts with their ‘usurpatory lodgers’. Concurrent radio-tracking of individuals of both species wintering in the same setts showed that badgers and raccoon dogs used different parts of the sett (R. Kowalczyk, unpubl.).

Shelter use by badgers was also influenced by sex and reproduction. In spring, reproducing females had to return to the main sett at dawn every day to feed cubs. When cubs started to follow their mother, her use of daily shelters was similar to that observed in other badgers. The same behaviour of adult females was reported from Norway (Brøseth *et al.* 1997).

Forest structure influenced the type and number of shelters. In pristine oldgrowth forests of BNP, badgers often rested in hollow trees, whereas in the exploited part of BPF, they used mainly underground setts. Similar effect of forest protection regime on availability and use of hollow trees was reported for Asiatic black bears *Ursus thibetanus* (Huygens *et al.* 2001). The use of hollow trees by badgers was also noticed in Transcaucasia by Rukovskii (1968) and in Spain by Revilla *et al*. (2001). Strong preference of badgers for lime trees results from special features of that tree. In BPF, old limes reach a diameter of the trunk up to 200 cm and, due to very soft and easily decaying wood, their trunks are usually empty inside from the base to branches, what creates spacious hollow (Faliński 1977). When downed, they make excellent shelters, used also by other animals such as raccoon dogs and foxes (R. Kowalczyk, unpubl.).

In contrast to other low-density populations (Brøseth *et al.* 1997, Revilla *et al.* 2001), each badger territory in BPF contained a main sett, which was utilised by all group members more often than other shelters. The number of shelters used by badgers was lower than in other low-density populations, but still higher than in high-density areas (review in Table 5). Smaller number of setts used by Białowieża's badger compared to other low-density population may result from lower sett availability. In BPF, large areas of unsuitable habitats (wet forests, marshy river valleys) affected the distribution of setts and territories of badgers (Kowalczyk *et al.* 2003b).

Butler and Roper (1996) proposed that badgers use many setts and many chambers within a sett to defend themselves against ectoparasites. Although we have not studied ectoparasite load in badgers in our study area, we think that parasites may have a small effect on within-sett use by badgers. In BPF, social groups were small (on average 3.9 badgers per group, Kowalczyk *et al.* 2003b), and they utilised more shelters and larger within-sett space than badgers studied by Butler and Roper (1996) and Roper *et al.* (2001) in South Downs, England. Two badgers captured by us in spring were checked for ectoparasites following the procedure described by Butler and Roper (1996); we found comparable numbers of ticks and fleas, but 6-fold lower number of lice.

Badgers are strictly territorial animals, which intensively mark their territories (Kruuk 1978, Roper *et al.* 1986, Stewart *et al.* 2001). In large territories, long boundary (on average 13 km in BPF) and long distance from the main sett to the boundaries (mean 1.8 km) should lead to wide dispersion of latrines (cf Stewart *et al.* 2001). As shown by Gorman and Mills (1984), animals adopt a strategy of territory marking from border to hinterland as territory size increases. Also, the proportion of marks placed in the peripheral parts of territory is smaller than in the core area (cf Zub *et al.* 2003), and it declines as territory size increases (cf Roberts and Lowen 1997). We propose that in large territories, setts and hollow trees may be used as territorial markers – regularly visited, refreshed, and scent-marked. Such behaviour of badgers was previously observed in another low-density population in Doñana, Spain, where 80% of all scats found were associated with sett-latrines (Revilla and Palomares 2002). Animals often localize scent-marks in places guaranteeing their discovery by other individuals of the species (Macdonald 1980, Gorman and Mills 1984, Gosling and Roberts 2001). Setts may play a role of such objects, as they are essential components of badger territories. It was frequently reported that setts are marked by badgers, and defecation also occurs inside the setts (Kruuk 1978, Roper 1992, Buesching and Macdonald 2001). The proposed function of shelters as territory markers is further supported by different pattern of sett use by males and females. In BPF, males which are engaged more often than other individuals in territory defence (visiting and marking latrines; Pigozzi 1990, Brown *et al.* 1992, Roper *et al.* 1993), used bigger number of shelters and spent less time in the main setts than females.

Excavation of burrows is energetically costly and takes time (Vleck 1979, Roper *et al.* 1991). As indicated by Bevanger and Brøseth (1998), use of shelters other than underground burrows may be the way of saving energy. This is especially important in areas with limited and seasonally varying food resources, such as BPF. Utilisation of hollow trees by badgers increased the number of potential shelters and allows badgers save energy during territory exploring.

As suggested by Roper (1992), Brøseth *et al.* (1997) and Revilla *et al.* (2001), effective exploitation of a large territory can be achieved by using many scattered setts, which allow badgers to reduce the energetic costs of travelling between the feeding patches and the main sett. In BPF, badgers most often hid in the nearest shelter available in a vicinity of a last foraging patch. It indicates that many setts scattered in the territory allow badgers to avoid long-distance returns to the main sett every night, what is especially important in territories as large as those in BPF. Avoiding predation risk by use of multiple setts may also count. In BPF, badgers fell as a prey to wolves (Jędrzejewska and Jędrzejewski 1998), and inspections of badgers sett by wolves and lynxes *Lynx lynx* were recorded (Kowalczyk *et al.* 2003b).

Our analysis of badger sett use in biogeographical scale indicates that different factors may influence the pattern of sett utilisation in relation to population density. In high-density populations, social factors such as large groups, aggressive interactions among individuals, and ectoparasite infestation force badgers to use multiple setts (Kruuk 1978, Butler and Roper 1996). Moreover, more setts available in a territory enable more than one female in the social group to breed, as was observed in some populations in England (Rogers *et al.* 1997, Woodroffe and Macdonald 2000). In high-density populations, abundance of food allows badgers to spend extra energy on sett digging, so they excavate more setts per unit area and make them more complex, with larger number of entrances. However, we showed that in high-density populations, the number of setts per badger appeared smaller than in low-density populations, most probably due to limited space and conditions for sett excavation in small territories.

In low-density populations with limited and seasonally varying food resources, spatio-energetic factors are more important in determining the shelter use: big number of shelters in a territory allow badgers to exploit their large territories more efficiently and save energy. In such conditions, badgers excavate smaller number of setts per unit area and often utilise other available shelters (such as hollow trees in this study; man-made structures in Norway, Brøseth *et al.* 1997; rabbit warrens and hollow trees in Spain, Revilla *et al.* 2001). It leads to a different pattern of shelter use and decreases the role of a 'main sett' as such, as observed in low-density populations in Spain and Norway (Brøseth *et al.* 1997, Revilla *et al.* 2001). Despite those differences, in their whole geographic range, badgers strongly depend on setts, which are essential components of their life, guaranteeing successful reproduction, survival in severe climates, and security from large predators.

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References

Bevanger K. and Brøseth H. 1998. Body temperature changes in wild-living badgers *Meles meles* through the winter. Wildlife Biology 4: 97–101.

Blumstein T. D. and Arnold W. 1998. Ecology and social behavior of golden marmots (*Marmota caudate aurea*). Journal of Mammalogy 79: 873–886.

Bobiec A. 2002. Living stands and dead wood in the Białowieża forest: suggestion for restoration management. Forest Ecology and Management 165: 125–140.

Brøseth H., Bevanger K. and Knutsen B. 1997. Function of multiple badger *Meles meles* setts: distribution and utilisation. Wildlife Biology 3: 89–96.

Brown J. A., Cheeseman C. L. and Harris S. 1992. Studies on the spread of bovine tuberculosis from badgers to cattle. Journal of Zoology, London 227: 694–696.

Buesching C. D. and Macdonald D. W. 2001. Scent-marking behaviour of the European badger (*Meles meles*): resource defence or individual advertisement? [In: Chemical signals in vertebrates 9. A. Marchlewska-Koj, J. J. Lepri and D. Müller-Schwarze, eds]. Kluwer Academic/Plenum Publishers, New York: 321–327.

Butler J. and Roper T. J. 1996. Ectoparasites and sett use in European badgers. Animal Behaviour 52: 621–629.

Clark P. J. and Evans F. C. 1954. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology 35: 445–453.

Faliński J. B. 1977. Białowieża Primeval Forest. Phytocoenosis 6: 133–148.

Feore S. and Montgomery W. I. 1999. Habitat effects on the spatial ecology of the European badger (*Meles meles*). Journal of Zoology, London 247: 537–549.

Ferrari N. 1997. Eco-éthologie du blaireau européen (*Meles meles* L., 1758) dans le Jura Suisse: comparison de deux populations vivant en milieu montagnard et en milieu cultivé de plaine. PhD thesis, University of Neuchâtel, Neuchâtel, Switzerland: 1–252.

Gorman M. L. and Mills M. G. L. 1984. Scent marking strategies in hyaenas (Mammalia). Journal of Zoology, London 202: 535–547.

Gosling L. M. and Roberts S. C. 2001. Testing ideas about the function of scent marks in territories from spatial patterns. Animal Behaviour 62: F7–F10.

Hofmann T. 1999. Untersuchungen zur Ökologie des europäischen Dachses (*Meles meles*, L. 1758) im Hakelwald (nordöstliches Harzvorland). PhD thesis, Martin-Luther-University Halle-Wittenberg, Halle, Germany: 1–102.

Huygens O., Goto M., Izumiyama S., Hayashi H. and Yoshida T. 2001. Denning ecology of two populations of Asiatic black bears in Nagano prefecture, Japan. Mammalia 65: 417–428.

Jacobs J. 1974. Quantitative measurement of food selection. A modification of the forage ratio and Ivlev's electivity index. Oecologia 14: 413–417.

Jędrzejewska B. and Jędrzejewski W. 1998 Predation in vertebrate communities. The Białowieża Primeval Forest as a case study. Ecological Studies 135. Springer-Verlag, Berlin – Heidelberg – New York: 1–450.

Kowalczyk R., Bunevich A. N. and Jędrzejewska B. 2000. Badger density and distribution of setts in Białowieża Primeval Forest (Poland and Belarus) compared to other Eurasian populations. Acta Theriologica 45: 395–408.

Kowalczyk R., Jędrzejewska B. and Zalewski A. 2003a. Annual and circadian activity patterns of badgers *Meles meles* in Białowieża Primeval Forest (E Poland) compared to other Palaearctic populations. Journal of Biogeography 30: 463–472.

Kowalczyk R., Zalewski A. Jędrzejewska B. and Jędrzejewski W. 2003b. Spatial organization and demography of badgers *Meles meles* in Białowieża Forest (Poland) and the influence of earthworms on badger densities in Europe. Canadian Journal of Zoology 81: 74–87.

Kreeger T. J. 1997. Handbook of wildlife chemical immobilization. Wildlife Pharmaceuticals Inc., Fort Collins: 1–342.

Kruuk H. 1978. Spatial organization and territorial behaviour of the European badger *Meles meles* L. Journal of Zoology, London 184: 1–19.

Kwiatkowski W. 1994. Vegetation landscapes of Białowieża Forest. Phytocoenosis (N.S.), Supplementum Cartographiae Geobotanicae 6: 35–87.

Macdonald D. W. 1980. Patterns of scent marking with urine and faeces amongst carnivore communities. Symposia of the Zoological Society of London 45: 107–139.

Nilsson S. G., Niklasson M., Hedin J., Aronsson G., Gutowski J. M., Linder P. Ljungberg H., Mikusiński G. and Ranius T. 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. Forest Ecology and Management 161: 189–204.

O'Corry-Crowe G., Eves J. and Hayden T. J. 1993. Sett distribution, territory size and population density of badgers (*Meles meles* L.) in east Offaly. [In: The badger. T. J. Hayden, ed]. Royal Irish Academy, Dublin: 35–56.

Ostler J. and Roper T. J. 1998. Changes in size, status, and distribution of badger *Meles meles* L. setts during a 20-year period. Zeitschrift für Säugetierkunde 63: 200–209.

Pigozzi G. 1990. Latrine use and the function of territoriality in the European badger, *Meles meles*, in a mediterranean coastal habitat. Animal Behaviour 39: 1000–1002.

Revilla E., and Palomares F. 2002. Spatial organization, group living and ecological correlates in low-density populations of Eurasian badgers, *Meles meles*. Journal of Animal Ecology 71: 497–512.

Revilla E., Palomares F. and Fernández N. 2001. Characteristics, location and selection of diurnal resting dens by Eurasian badgers (*Meles meles*) in a low density area. Journal of Zoology, London 255: 291–299.

Roberts S. C. and Lowen C. 1997. Optimal patterns of scent marks in klipspringer (*Oreotragus oreotragus*) territories. Journal of Zoology, London 243: 565–578.

Rogers L. M., Cheeseman C. L. and Mallinson J. 1997. The demography of a high-density badger (*Meles meles*) population in the west of England. Journal of Zoology, London 242: 705–728.

Roper T. J. 1992. Badger *Meles meles* setts – architecture, internal environment and function. Mammal Review 22: 43–53.

Roper T. J. 1993. Badger setts as a limiting resource. [In: The badger. T. J. Hayden, ed.]. Royal Irish Academy, Dublin: 26–34.

Roper T. J. and Christian S. F. 1992. Sett use in badgers (*Meles meles*). [In: Wildlife telemetry: remote monitoring and tracking of animals. I. G. Priede and S. M. Swift, eds]. Ellis Horwood, Chichester: 661–669.

Roper T. J., Conradt L., Butler J., Christian S. E., Ostler J. and Schmid T. K. 1993. Territorial marking with faeces in badgers (*Meles meles*): a comparison of boundary and hinterland latrine use. Behaviour 127: 289–307.

Roper T. J., Ostler J., Schmid T. K. and Christian S. E. 2001. Sett use in European badgers *Meles meles*. Behaviour 138: 173–187.

Roper T. J., Shepherdson D. J. and Davies J. M. 1986. Scent marking with faeces and anal secretion in the European badgers (*Meles meles*): seasonal and spatial characteristics of latrine use in relation to territoriality. Behaviour 97: 94–117.

Roper T. J., Tait A. I., Fee D. and Christian S. E. 1991. Internal structure and contents of three badger (*Meles meles*) setts. Journal of Zoology, London 225: 115–124.

Rukovskii N. 1968. [Badger]. Okhota i okhothnichie khozyaistvo 6: 20–21. [In Russian]

Stewart D., Macdonald D. W., Newman C. and Cheeseman C. L. 2001. Boundary faeces and matched advertisement in the European badger (*Meles meles*): a potential role in range exclusion. Journal of Zoology, London 255: 191–198.

Vleck D. 1979. The energy cost of burrowing by the pocket gopher *Thomomys bottae*. Physiological Zoology 52: 122–136.

Woodroffe R. and Macdonald D. W. 2000. Helpers provide no detectable benefits in the European badger (*Meles meles*). Journal of Zoology, London 250: 113–119.

Zub K., Theuerkauf J., Jędrzejewski W., Jędrzejewska B., Schmidt K. and Kowalczyk R. 2003. Wolf pack territory marking in the Białowieża Primeval Forest (Poland). Behaviour 140: 635–648.

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