Hystrix It. J. Mamm. (n.s.) 21(1) (2010): 3-18

SPATIAL ORGANISATION OF BADGERS (*MELES MELES*) IN A MEDIUM-DENSITY POPULATION IN LUXEMBOURG

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Received 4 March 2010; accepted 20 June 2010

ABSTRACT - Any hypothesis aiming to explain the social organisation of Eurasian badgers *Meles meles* has to consider its wide inter-population variability. We used radio-tracking techniques to investigate the spatial organisation and the pattern of space-use by badger in Luxembourg, where badger density can be considered moderate compared to most of Europe.
Eight badgers belonging to five social groups were caught and radio-collared. The size of individual home ranges, as assesses by 100% minimum convex polygons in spring-summer 2002 and 2003, varied from 42.5 ha to 171.8 ha. Core areas corresponded to the 50-70% kernel isopleths and covered an average of 10.1% of individual home ranges. The home ranges of badgers caught at the same sett overlapped largely (average 83.3%), whilst the overlap between neighbouring ranges did not exceed 13.8%. Altogether six boundary latrines were found at the intersection of group ranges. Overall, the spatial system of the Luxembourg badgers is quite flexible, with the boundaries of some group ranges remaining constant over the years, while others may expand or contract.

Key words: territorial behaviour, home range size, radiotelemetry, scent marking

RIASSUNTO - ***Organizzazione spaziale del tasso (*Meles meles*) in una popolazione a media densità del Lussemburgo***. Qualsiasi ipotesi che voglia spiegare l'organizzazione sociale del tasso *Meles meles*, deve tener conto della sua ampia variabilità tra le popolazioni. Tramite la radiotelemetria e il monitoraggio delle latrine, la struttura territoriale e l'uso dello spazio da parte del tasso sono stati analizzati in una popolazione del Lussemburgo, dove la densità della specie può essere considerata intermedia rispetto ai valori noti per il resto dell'Europa.
Sono stati marcati con radio-collari otto tassi, appartenenti a cinque diversi gruppi sociali. Le dimensioni delle aree vitali, stimate con il minimo poligono convesso al 100% per il periodo primaverile-estivo del 2002 e 2003, sono risultate comprese tra 42,5 e 171,8 ha. Le *core areas*, delimitate dalle isoplete al 50-70% ottenute con il metodo kernel, includevano, in media, il 10,1% delle aree vitali individuali. Le aree vitali di individui appartenenti allo stesso gruppo sociale sono risultate nettamente sovrapposte (media: 83,3%), mentre la massima sovrapposizione di home range confinanti è stata pari al 13,8%. In totale sono state individuate sei latrine, posizionate ai margini delle aree vitali di tre gruppi sociali tra loro

confinanti. Nel complesso, i risultati ottenuti suggeriscono che anche in Lussemburgo la struttura spaziale del tasso è basata sulla territorialità, benché tale struttura sia probabilmente abbastanza flessibile, potendosi riscontrare sia confini territoriali stabili nel tempo sia contrazioni o espansioni delle aree vitali dei gruppi sociali.

Parole chiave: comportamento territoriale, dimensioni delle aree vitali, radiotelemetria, marcamento

INTRODUCTION

Within their wide geographic distribution, badgers (*Meles meles*) appear to greatly vary in their behaviour, physiology and degree of prey specialisation, as well as in social organisation (Woodroffe and Macdonald, 1993; Johnson *et al.,* 2002). On the British Isles, they form non-cooperative, mixed-sex groups ("spatial groups", Macdonald, 1983) of up to 27 individuals (Rogers *et al.*, 1997) that share a home range and a main communal sett, but forage alone and do not benefit from alloparental care (Kruuk, 1978; Woodroffe and Macdonald, 2000). In contrast, throughout continental Europe, badgers mostly live in pairs (Spain: Martin-Franquelo and Delibes, 1985; Switzerland: Do Linh San *et al.*, 2007) or small groups, formed by 3-4 resident adults (e.g. Norway: Broseth *et al.*, 1997; Luxembourg: Schley *et al.*, 2004; Italy: Remonti *et al.*, 2006). Badgers in central Italy have been reported to be solitary (Pigozzi, 1987), but this result has recently been criticised and needs confirmation (Revilla and Palomares, 2002).
Compared to the United Kingdom, badger population densities are low or moderate throughout most of Europe (Griffiths and Thomas, 1997). In high density populations in the UK, the whole home range of the group is defended as a territory through direct aggression and a system of boundary latrines marked with faeces and secretions of the sub-caudal gland (Kruuk, 1978; Gorman *et al.*, 1984). At low densities, latrines are mostly associated with setts (Revilla and Palomares, 2002) or are dug along linear features in the centre of activity (core area) of badger groups (Balestrieri *et al.*, 2009). This wide geographic variation in social behaviour has stimulated interest in the badger's sociobiology, leading to a series of models of group formation (Woodroffe and Macdonald, 1993; Johnson *et al.*, 2000, 2002), of which the Resource Dispersion Hypothesis (RDH; Carr and Macdonald, 1986) has been used to explain the grouping behaviour of a wide variety of mammal species (e.g.: Geffen *et al.*, 1992; Kays and Gittleman, 1995).
Any hypothesis aiming to explain the social organisation of badgers in general and territory formation in particular has to take inter-population variability into account. However, a disproportionate number of studies have been performed in the British Isles, where environmental conditions are not typical of all badger populations (Johnson *et al.,* 2002). Because the conclusions and hypotheses based on studies performed in the United Kingdom might not be relevant to continental medium- and low-density populations (see for example Frantz *et al.*, 2010), there is a

need for further studies of badger behaviour and ecology in other parts of the species' geographic range, and especially in central Europe.

Luxembourg has an estimated minimum overall badger population density of 0.78 animals per km^2, which is a moderate density compared to most of continental Europe, and minimum values of 2.59 adults and 1.85 cubs per social group (Schley *et al.,* 2004). The habitat consists mostly of forest-farmland mosaics, which is typical for much of continental Europe. Badger diet in Luxembourg was shown to be very variable during the summer months, with maize (*Zea mays*), insects, plums (*Prunus domestica*) and earthworms (*Lumbricus terrestris*) as staple foods (Schley, 2000). Badgers in Luxembourg are thus potentially very interesting in terms of sociality, being representatives of a low- to medium-density population with a broad food niche.

We aimed to use radio-tracking techniques to investigate the spatial organisation of a badger population in Luxembourg. Specifically, we wanted to test whether the spatial system consisted of non-overlapping group-ranges and assess the pattern of space-use by badger. Home range boundaries were surveyed for the presence of latrines to look for evidence of territorial defence.

STUDY AREA

The study site was located in the north-east of Luxembourg, east of River Ernz Blanche and between the villages of Ermsdorf and Eppeldorf. The site covered approximately 5.4 km^2, was situated between 225 and 420 m above sea level and consisted of a mosaic of pasture, arable land and woodland (see Schley, 2000 for further details). The study focussed on five adjoining main setts previously identified by Schley (2000): Ermsdorf 1, Ermsdorf 2, Knäipenhecken, Bëlz and Grott.

METHODS

1. Trapping and immobilisation of badgers

Badgers were trapped between April and June 2002 and 2003 using cage traps similar to the model presented in Cheeseman and Mallinson (1979; for trapping dates see Tab.1). Trapping was performed under licence from the Luxembourg Ministry of the Environment. In order to capture badgers successfully, cage traps had to be pre-baited for up to four months using peanuts, placed under a pierced box covered with a stone in order to stop non-target species from reaching the bait. Because badgers did not touch the bait in 2002 when food was plenty, the pre-baiting for the 2003 season was started in winter. At Grott sett, one badger was caught by means of a free-running snare placed over a clearly visible run, following the instructions of Cheeseman and Mallinson (1979).

Box traps were checked just after dawn, and captured badgers were transferred to a holding cage and weighed. After restraining, adult badgers were anaesthetised by intra-muscular injection in the thigh-muscle of 20 mg/kg of ketamine hydrochloride ("Imalgène", Rhône Mérieux, France) using 10 ml syringes and 3 cm long stainless steel needles. When the badgers were motionless and did not respond to tactile stimuli (Pigozzi, 1990), they were sexed, fitted with radio-collars (Biotrack, UK; frequency band: 147 MHz) and released at the site of capture after full recovery from anaesthesia (3-4 hours). Juvenile badgers (weighing between 6 and 7.5 kg) were neither anaesthetised nor radio-collared.

2. Radiotelemetry

The animals were followed by car and on foot using a hand-held, 3-element Yagi antenna (Biotrack, UK) connected to a M57 receiver (Mariner, UK. Following Kenward (2001). A directional fix was recorded on a map only when identical peak signal positions were determined holding the elements of the Yagi antenna both vertically and horizontally. In order to further improve the estimate of an animal's location, the second bearing was always taken as close to 90° from the first as possible and, if possible, a third bearing was taken. In order to make our data set robust to the effects of autocorrelation (de Solla *et al.,* 1999), when following one or two animals at a time, fixes of a specific animal were taken every 30 min, whilst when more than two animals were followed, the location of an animal was recorded once per hour, with a minimum interval of 30 min between fixes.
In order to analyse whether the activity period of the animals was sampled in a representative manner, the temporal distribution of the fixes was plotted. While this was only done in retrospect with the data collected from the animals captured in 2002, in 2003 the relevant graphs were updated regularly and the tracking periods were adjusted accordingly. Unless when moving between feeding patches, it appeared reasonable to assume that badger movement between successive bearings would not cause major inaccuracies in the determination of an animal's position (Kruuk, 1978, 1989).
To investigate whether group ranges were defended as territories by scent marking, in December 2002, the boundaries of the group ranges, as determined by radiotracking, were surveyed for the presence of latrines.

3. Data analysis

The size and shape of the home ranges of the animals were determined by the 100% minimum convex polygon (MCP), using the Animal Movement Analyst Extension (AMAE; Hooge and Eichenlaub, 1997) to ArcView®. The area of the MCP delineating all the fixes that were recorded for all the badgers caught at the same sett was calculated and defined, in accordance with Kruuk (1978), as the range of the corresponding badger group. The 100% MCP home range sizes of the two sexes and of members of different setts were compared by ANOVA. The sizes of the respective polygons were obtained using the "Location Statistics" option in AMAE. The graphs of home range size versus number of observations were generated using BIOTAS 1.0.2 (Ecological Software Solutions). The sizes of the areas of overlap between the different home ranges were obtained by modifying the home range polygons by hand in ArcView®.
The internal configuration of the animals' home ranges was investigated using fixed kernel techniques. As suggested by Seaman and Powell (1996), Powell *et al.* (1997), Seaman *et al.* (1998, 1999) and Powell (2000), optimal bandwidths were determined using the LSCV technique. Individual core areas were obtained by plotting graphs of home range area against kernel isopleth value and defined as the point at which the gradient of the slope changed (Ford and Krumme, 1979; Clutton-Brock *et al.*, 1982). Ten kernel density isopleths (10%, 20%, 30%, 40%, 50%, 60%, 70%, 80%, 90% and 95%) were included in the analysis. Spearman's rank correlation test was used to compare the size of home ranges to that of the corresponding core areas.

RESULTS

Altogether eight badgers were caught and radio-collared. For three of the five social groups under investigation, data were available for one animal only (Tab. 1). A maximum number of two

Table 1 - Capture and tracking details of radio-collared badgers.

Animal	Sett	Sex	Date of capture	Weight (kg)	no. of fixes	Tracking period
EMa1	Ermsdorf 2	F	27/05/02	11.5	183	29/05/02-31/07/02
EMa2	Ermsdorf 2	M	11/06/02	13.5	145	12/06/02-07/08/02
EMa3	Ermsdorf 2	F	08/04/03	11.0	181	11/04/03-24/07/03
EMb1	Ermsdorf 1	M	10/04/03	12.0	74	10/04/03-15/05/03
B1	Bëlz	M	08/04/03	12.5	76	10/04/03-15/05/03
B2	Bëlz	F	15/04/03	11.5	402	18/04/03-27/08/03
KH1	Knäipenhecken	F	10/04/03	10.0	40	11/04/03-24/04/03
G1	Grott	F	02/05/03	11.5	154	05/05/03-24/07/03

badgers from each sett was followed at a time. It was possible to collect an average of 157 fixes per animal (SD = 112), with the smallest dataset consisting of 40 and the largest of 402 fixes (Tab. 1). The paucity in the number of fixes recorded for some badgers between 21:00 and 21:59 as well as 05:00 and 06:00 depended on their late exit or early return to the corresponding sett (Fig. 1a).

Incremental area plots suggested that the range sizes of all the animals, calculated as a MCP of the recorded fixes, reached an asymptote during the respective tracking period (Fig. 1b). Six of the eight accumulation curves reached an asymptote after at least 60 fixes had been taken. In the case of animal G1, a minimum of 70 fixes was necessary for home range size to stabilise. It was only possible to collect 40 fixes from animal KH1 before its collar dropped off (Fig. 1b).

The sizes of individual home ranges varied from 42.5 ha to 171.8 ha (100% MCP; Fig. 2, Tab. 2), with an average of 76.5 ha (SD = 49.9). Females had larger home ranges than their male counterparts caught at the same sett and the home ranges of the animals caught at Bëlz sett were the largest. These differences, however, were not significant (Tab. 3). Core areas were equated either to the 50, 60 or 70% inclusion levels (Fig. 3a) and the number of core areas within the range of the eight animals varied from one to five, with an average of 2.9 cores (Fig. 3b). Core ranges had an average size of 7.5 ha (SD = 4.4; range: 3.0-16.4) and covered an average of 10.1% of individual 100% MCP home ranges (SD = 2.6; range: 5.5-13.5%). There was a significant positive correlation between the 100% MCP home range size and the size of the core areas ($r_s = 0.762$, $P < 0.05$), but the negative correlation between the 100% MCP home range size and the percentage of a range that belonged to the core area was not significant. ($r_s = -0.143$, $P = 0.736$). Note that the 95% Kernel home range of animal KH1 does not include the main sett at which the animal was caught. After capture, the animal moved to an outlying sett where it remained until the collar fell off two weeks later.

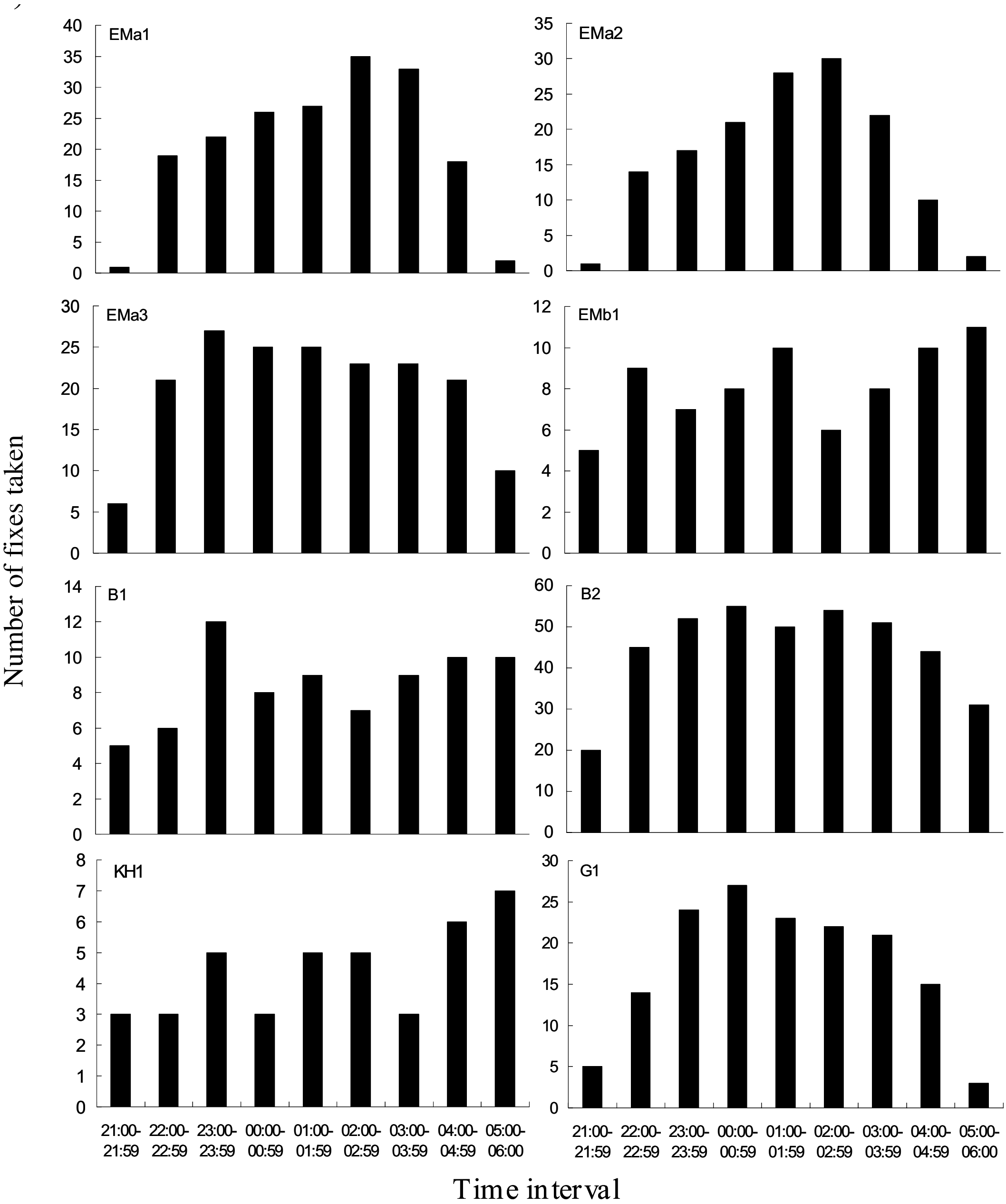

Figure 1a - Temporal distribution of the radio fixes recorded for the eight radio-collared badgers. The minimum time interval between fixes was 30 min.

Overlap of 100% MCP home ranges of badgers caught at the same sett varied from 66.6 to 97.6% (average 83.3%) and the largest home range recorded for

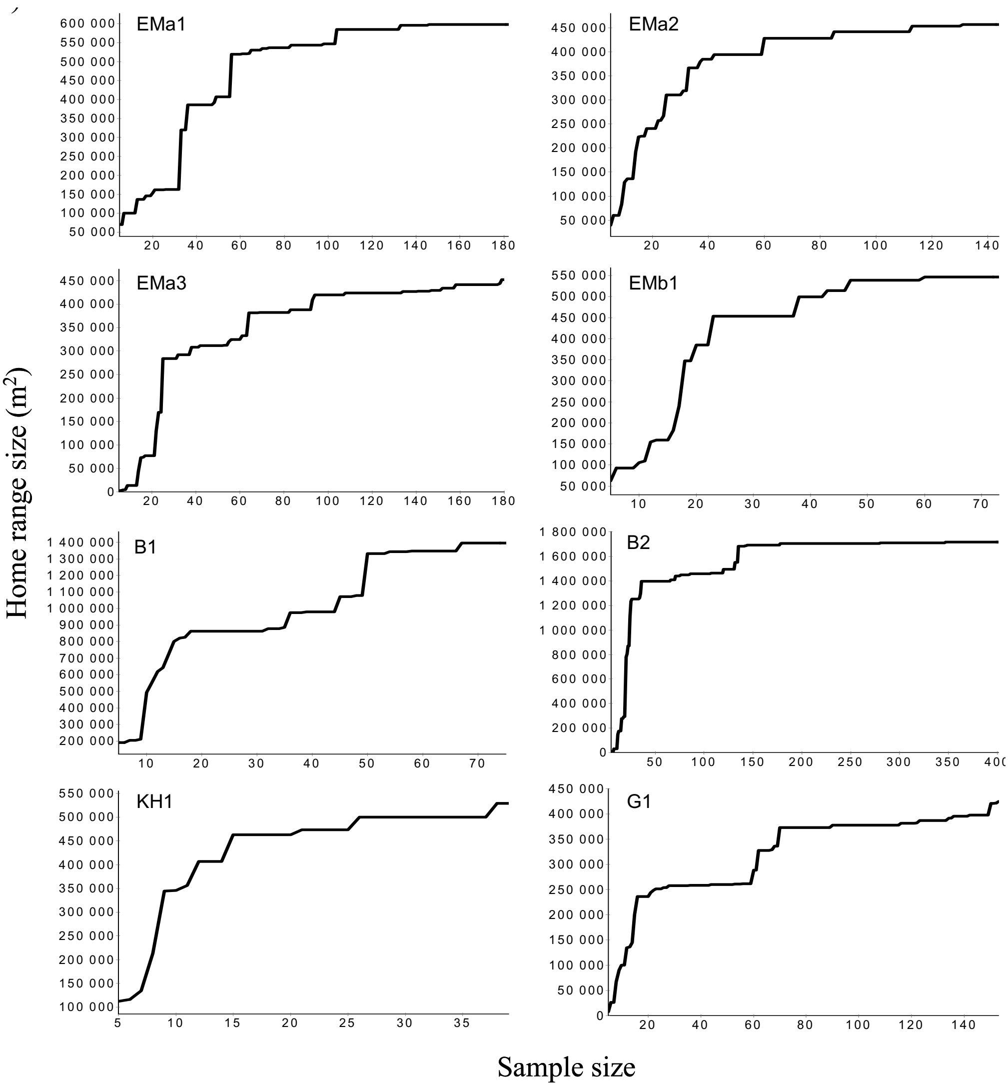

Figure 1b - Cumulative home range area as a function of radio-tracking effort for eight badgers. The range size was calculated using MCP.

both social groups contained almost completely the ranges of the other animals caught at the respective setts (>85% shared area; Fig. 2). In the largest overlap between neighbouring ranges, 13.8 and 8.8% of the home range of animal KH1 overlapped with the home ranges of animals B1 and B2, respectively, and 10% of the fixes recorded for animal KH1 were located in the area of overlap. In contrast, the combined number of fixes from the two other animals in this area was three (out of a total of 478) and there was little or no overlap between pairs of the remaining neighbouring ranges (<4% share

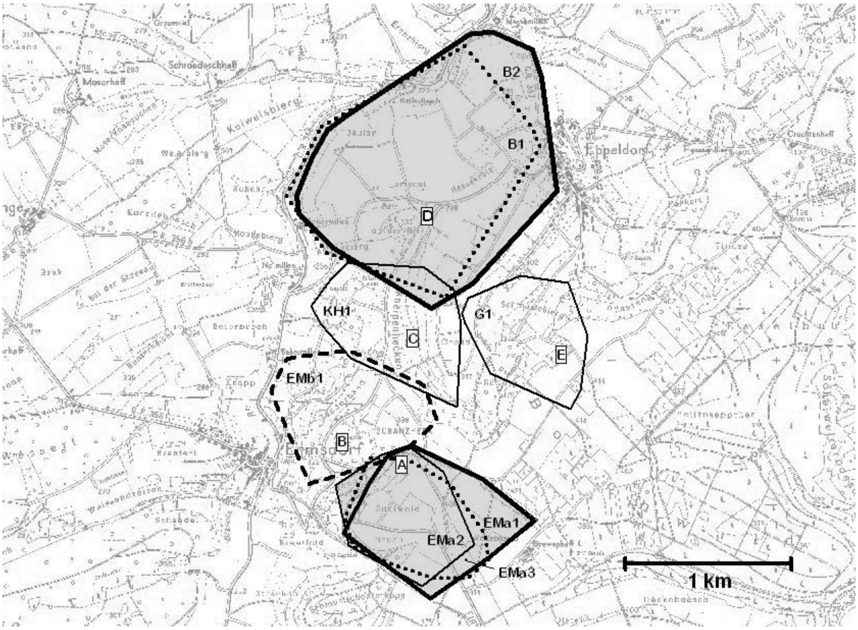

Figure 2 - Spatial arrangement of the home range (100% MCP) of eight badgers in the study area in Luxembourg. The combinations of letters and numbers identify the individual whose home range is represented. Capital letters indicate the location of the main sett: A = Ermsdorf 2; B = Ermsdorf 1; C = Knäipenhecken; D = Bëlz; E = Grott. Each area shaded in grey represents a group's home range, whenever more than one member of the group was captured.

Table 2 - Home ranges estimates of eight Luxembourg badgers calculated using MCP and 95% Kernel analysis and determined by radio-tracking locations. Determination of the Kernel inclusion level that was taken to represent the core area of each home range is summarised in Figure 3a; % = percentage of total home range that belongs to core.

		Home range area (ha)			
Animal	Social Group	MCP 100%	Kernel 95%	Core area (ha)	%
EMa1	EM2	59.8	57.0	8.1	13.5
EMa2	EM2	45.7	40.7	5.5	12.0
EMa3	EM2	45.2	42.3	4.7	10.4
EMb1	EM1	54.7	48.9	3.0	5.5
B1	Bëlz	139.5	95.2	13.7	9.8
B2	Bëlz	171.8	126.7	14.6	8.5
KH1	KH	52.9	46.5	6.7	12.7
G1	Grott	42.5	36.6	3.7	8.7

Table 3 - Results from an ANOVA comparing the 100% MCP home range sizes of the different sexes and of members of different setts.

Source of variation	d.f.	Sum of squares	Mean square	F	P
Sex	1	4.4×10^{10}	4.4×10^{10}	4.098	0.292
Sett	4	1.7×10^{12}	4.2×10^{11}	39.439	0.119
Sex*Sett	1	1.9×10^{10}	1.9×10^{10}	1.743	0.413
Error	1	1.1×10^{10}	1.1×10^{10}		
Total	8	6.4×10^{12}			
Corrected total	7	1.7×10^{12}			

area). Individual home ranges covered, on average, 79% of the area of a group range - 68.3 and 177.2 ha for Ermsdorf 2 and Bëlz, respectively (Fig. 2). While animal EMa3 had the smallest home range compared to the group range size (66% of overlap), the home range of animal B2 corresponded almost completely to the group range (97% of overlap).

A total of six boundary latrines - associated with Ersmdorf 1, Ermsdorf 2 and Knäipenhecken -, was found (Fig. 4). No such feature was identified at the intersections of Bëlz, Knäipenhecken and Grott group ranges. The largest latrine (n° 1 in Fig 4b) consisted of more than 30 dung pits and covered an area of about 500 m^2.

DISCUSSION

Because the temporal distribution of the fixes was regularly monitored, important biases in the data set could be avoided, thereby fulfilling an important condition for home range estimates to be robust and analyses of home range utilisation patterns to be meaningful (McNay *et al.*, 1994; Swihart and Slade, 1997; De Solla *et al.*, 1999; Otis and White, 1999). Analyses of incremental area plots suggested that all the eight home ranges are accurately represented by means of a 100% MCP for the total period the respective animals were followed (spring and summer of 2002 and 2003). An additional increase in the home range size of KH1 would probably have been observed had it been possible to track the animal for longer.

Considering both the spatial arrangement and the size of individual and group home ranges, even when only a single animal could be captured at a specific sett, analysis of its telemetry data provided a good indication of the corresponding group range size. If we assume that, according to Kowalczyk *et al.* (2003) and Balestrieri *et al.* (subm.), badger home ranges are largest in spring-summer, the values reported here may broadly correspond to the total annual range size of each group.

Bearing in mind that, similarly to other carnivores (Macdonald, 1983; Kruuk and Macdonald, 1985), the estimated sizes of badger home ranges can substantially vary between studies due to

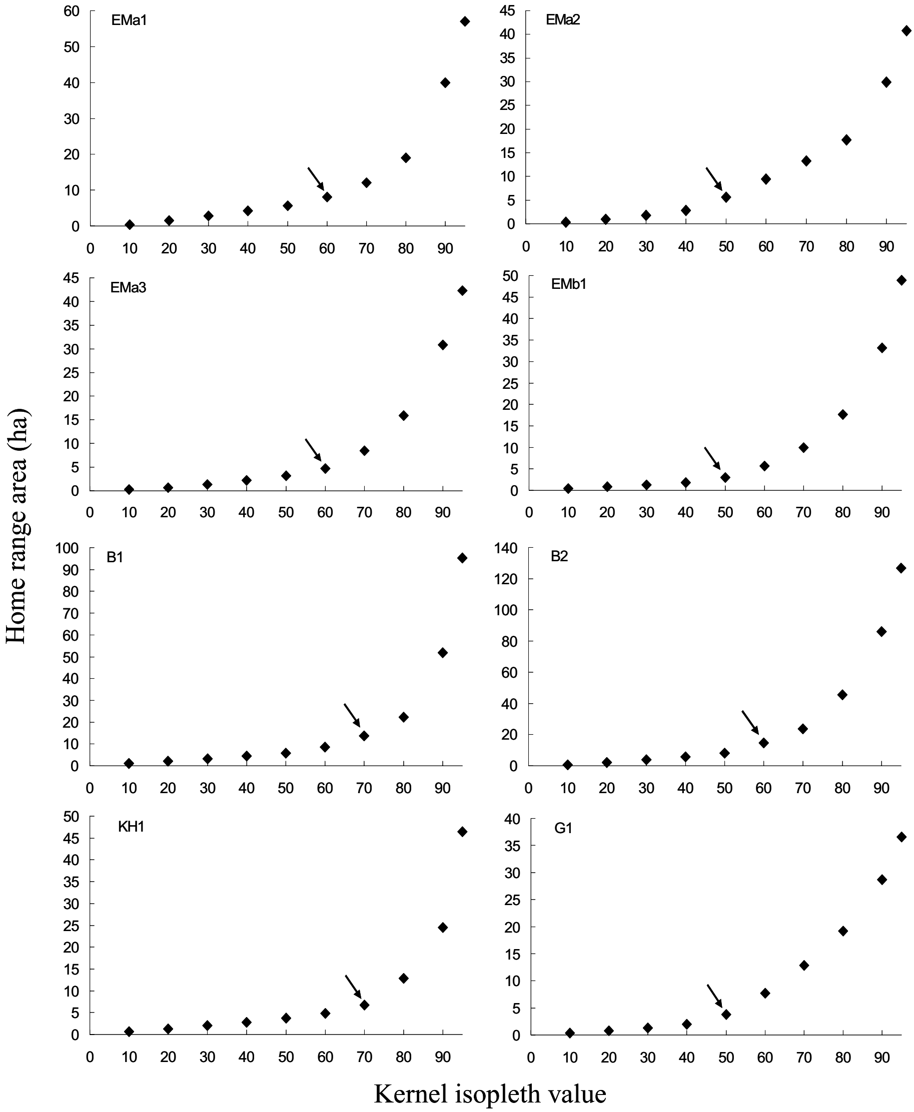

Figure 3a - Home range areas against kernel isopleth values for eight radio-collared badgers. Core ranges are defined as the inflection point of the corresponding curves (determined visually and arrowed).

differences in the analyses, our results are in the lower end of the spectrum of home range (and territory) sizes reported from the medium- to low-density populations on the European mainland (see Hofmann *et al.*, 2000). The mean size of group ranges in summer ranged between 3.6 in Italy (Balestrieri *et al.*, subm.) and 7.7 km^2 in Poland (Kowalczyk *et al.*, 2003).
In Germany (Bock, 1986) and Spain (Revilla and Palomares, 2002), the

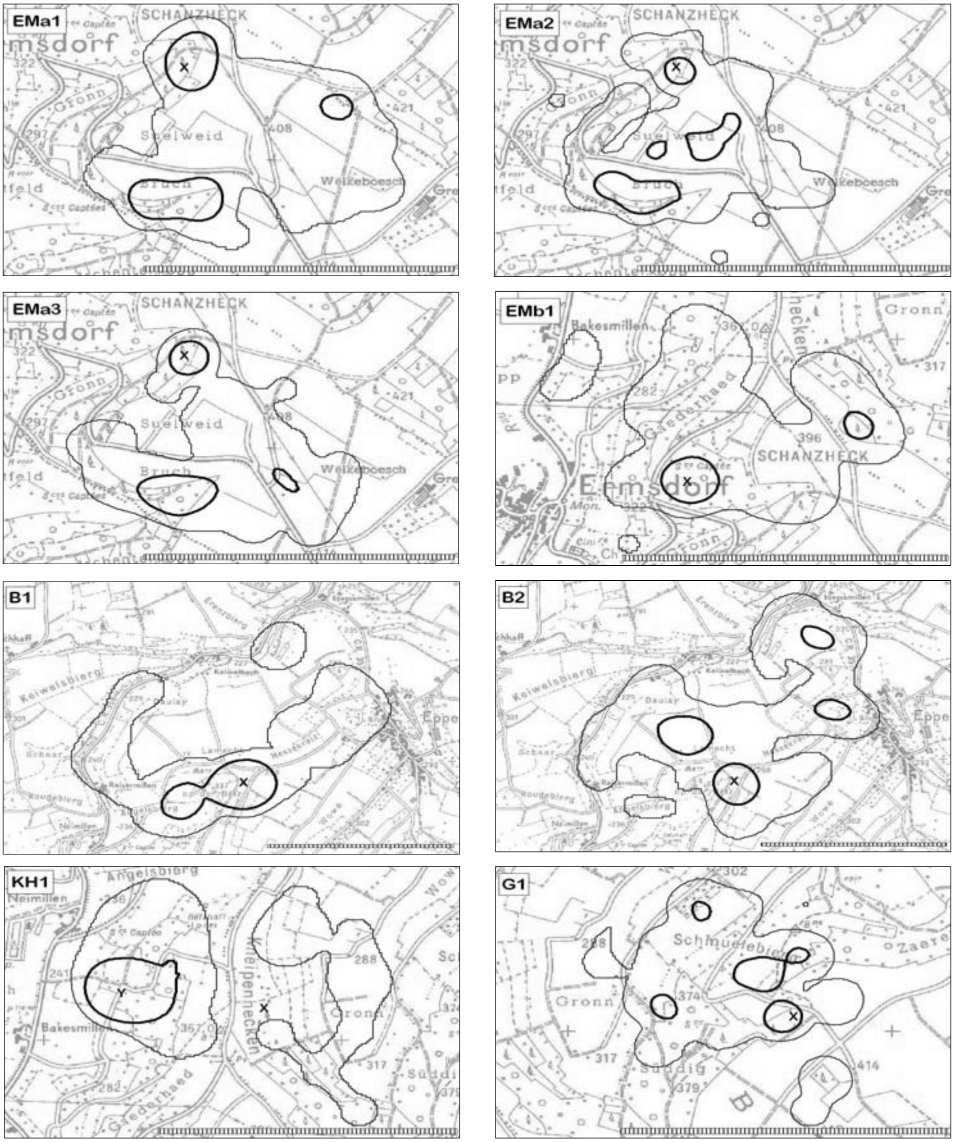

Figure 3b - The position of the 95% Kernel home range (thin outline) and the Kernel inclusion level representing the core of the home ranges of the eight investigated badgers (bold outline). “X”: location of the main sett. “Y”: location of outlying sett. The bar at the right-hand bottom of each map corresponds to a length of 1 km.

smallest home ranges were larger than the largest range reported in our study. Additionally, home ranges larger than 5 km^2 have been reported from Norway (Brøseth *et al.*, 1997), Poland (Kowalczyk *et al.*, 2003) and Switzerland (Do Linh San *et al.*, 2007). Contrarily to results reported from studies in Europe, the home range sizes reported in our study fall well within the

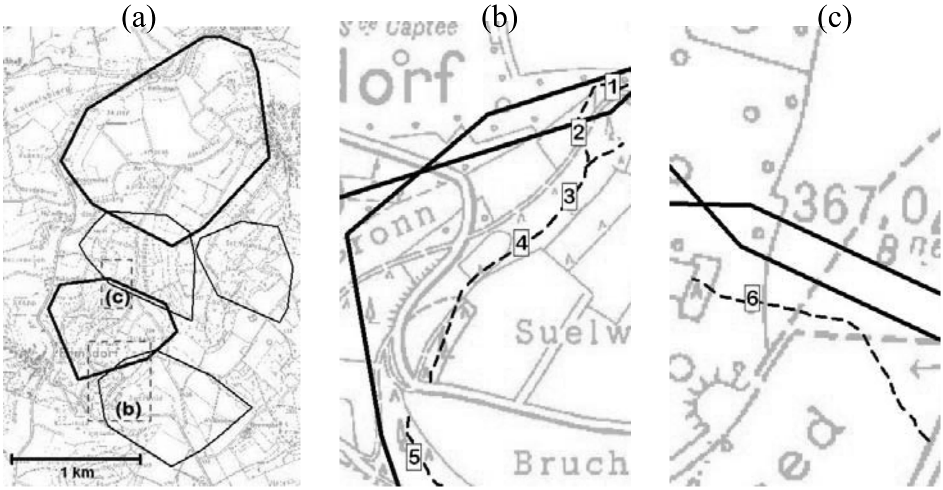

Figure 4 - (a) Location of the investigated latrines at the boundaries of three group ranges. (b), (c) exact location of the six latrines. Dashed lines in (b) and (c) show visible badger paths.

range reported for populations in rural Britain (Woodroffe and Macdonald, 1993; Krebs *et al*., 1997).

It is believed that the sizes of badger home ranges are determined by access to food resources (Kruuk and Parish, 1982; Hofer, 1988; da Silva *et al*., 1993; Kowalczyk *et al*., 2003; Rodriguez *et al*., 1996; Brøseth *et al*., 1997) and den sites (Doncaster and Woodroffe, 1993; Roper, 1993). In our study area, Schley (2000) showed that maize was the food eaten most frequently by badgers during a 5-month study period (July-October) and cereals were shown to be an important food in July and August. Earthworms also frequently occurred in the scats (Schley, 2000). The relatively small home range size observed in our study might thus be explained by the high concentration of high quality resource patches within the study area, a mixture of pasture and cereal and maize fields. This conclusion is supported (1) by the small mean size of the core area, which, in other continental areas, has been reported to range between 27% (Spain: Revilla and Palomares, 2002; Switzerland: Do Linh San *et al.,* 2007) and 30% (Italy: Balestrieri *et al*., subm.) of the total home range, compared to the 10.1% reported here, and (2) by the fact that there was a significant positive correlation between the size of core areas and home range sizes, but not between the total home range size and the percentage of a home range that was the core area

Analysis of the overlap between the different 100% MCP home ranges suggested a pattern of mutually exclusive group ranges. While the home ranges of animals caught at the same sett overlapped to a large extent, exactly the opposite was the case for animals caught at different setts. Schley (2000) reported results from three badgers captured and radio-tracked in 1998 and 1999 in the same study area. The size and shape of the home ranges of a male captured at Ermsdorf 2 and a female from Knäipenhecken are similar to the results for the same setts presented in our study. However, the home range of the third animal, a male captured at Knäipenhecken sett, roughly encompassed both the Knäipenhecken and Bëlz home ranges presented here. Possibly, in the three years between the two studies, a large territory consisting of Knäipenhecken and Bëlz split into two separate territories.

The total number of identified boundary latrines was rather small when compared to other studies performed on low-density populations (Pigozzi, 1990; Graf *et al*., 1996; Hutchings *et al*., 2001; Revilla and Palomares, 2002; but see Kruuk and Parish, 1982). The almost exclusive presence of latrines inside the core area of a badger group has been reported for northern Italy (Balestrieri *et al*., subm.), outlining that the marking behaviour of badgers at low- and medium-density is very variable and needs further investigation.

The fact that the badgers in our study area appeared to inhabit group-specific home ranges, and that scent marks were found on some of their boundaries, suggest that, in principle, the spatial system of the Luxembourg badgers may be based on territoriality. However, comparison with the results obtained by Schley (2000) suggests that the spatial system is quite flexible, with the boundaries of some territories remaining constant over the years, while others expanded or contracted. It appears that those boundaries that contained latrines remained more stable than those where no such scent-marks could be identified.

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