

Spatial organization, group living and ecological correlates in low-density populations of Eurasian badgers, *Meles meles*

ELOY REVILLA*† and FRANCISCO PALOMARES*

*Department of Applied Biology, Estación Biológica de Doñana, Spanish Council for Scientific Research-CSIC, Avenida de María Luisa, s/n, Pabellón del Perú, E-41013 Sevilla, Spain; and

†Department of Ecological Modelling, UFZ Centre for Environmental Research, Leipzig-Halle, Permoserstrasse 15, D-04318 Leipzig, Germany

Summary

1. Territoriality and group living are described in a low-density population of Eurasian badgers, *Meles meles* L., by studying the patterns of spatial grouping and territory marking, as well as the differences between individuals in some of their characteristics (body condition and dispersal) and in their space use (seasonally, periods of activity and interaction between pairs of individuals) under strong seasonal fluctuations in the availability of the key resource (young rabbits, *Oryctolagus cuniculus* L.). Finally, the role of the spatial distribution of the main prey (young rabbits) in the development of sociality was also studied in order to test some of the assumptions and predictions of the resource dispersion hypothesis (RDH).

2. Badgers were territorial, showing a flexible system of territory marking, which includes the marking of the most used areas (sett-latrines at the centres of activity) and additionally, at the smaller territories, a system of border-latrines in the areas of contact between territories. The maximum use of border-latrines was associated with the reproductive season, and that of sett-latrines with the season of food scarcity.

3. In the study area where badgers had rabbits as main prey, territories were occupied by small groups of animals, formed by one adult female who reproduced, one adult male who also showed signs of reproductive activity, the cubs of the year (if there was reproduction) and some animals born during previous years, which remained in their natal territory until their dispersal (normally during the mating season of their third or fourth year of life). This system was not strictly fixed as males, given the opportunity, expanded their territories to encompass additional females. Territories in another study site were occupied by one adult female (marked), plus the cubs of the year and another adult individual (unmarked).

4. In winter and spring dominant females and subordinates used only a small fraction of their territories, moved short distances, at a low speed and covering small areas per night. These seasons corresponded with the reproduction of rabbits (highest food availability). Dominant females were the only individuals using all the territory available in the summer (lowest food availability), when badgers had the worst body condition. Food availability increased again in autumn, as did body condition, while range sizes were again reduced. Dominant males used the same proportion of their territories over all seasons. However, in winter (reproductive season) they moved faster, over longer distances, and covered larger areas per period of activity. These results indicate that use of space by dominant males was affected by different factors from that of dominant females and subordinates.

5. RDH does not seem to explain group living in our populations because: (a) territoriality in each pair of primary animals was driven by different factors (trophic resources for females and females for males); (b) dominant males acted as expansionists; and (c) territory size was related to its richness and not to patch dispersion.

6. We propose an integrative hypothesis to explain not only group formation but also interpopulation variability in the social organization of badgers within ecological, demographic and behavioural constraints and in the light of current theory on delayed dispersal.

Key-words: group living, integrative hypothesis, *Meles meles*, resource dispersion hypothesis, social organization, sociality, space use, territoriality.

Journal of Animal Ecology (2002) **71**, 497–512

Introduction

Eurasian badgers *Meles meles* L. can live at very high densities in human-transformed landscapes composed of a mosaic of deciduous woodlots and pastures, where they feed mainly on earthworms, *Lumbricus* spp. (Kruuk 1978a, 1978b). Most of the research on the social organization of badgers has been performed on such populations. In these areas, badgers live in territories occupied by between two and 32 adults of both sex (Woodroffe & Macdonald 1993). These groups are formed by the retention of young individuals in their natal territory (Kruuk & Parish 1982; Cheeseman *et al.* 1987; Silva, Macdonald & Evans 1994). Each territory is centred in a communal burrow (main sett), which is used for resting and breeding (Roper 1992). The mating system is complex (Cresswell *et al.* 1992; Woodroffe & Macdonald 1995a; 1995b; Woodroffe, MacDonald & Cheeseman 1997), and the cubs produced in one territory may belong to more than one female and more than one male (Evans & Macdonald 1989; Silva *et al.* 1994). Territories are defended by occasional fighting and by a system of scent marking with latrines at their border (Kruuk 1989; Roper *et al.* 1993). In these high-density populations cooperation between individuals is rare, and thus the advantages of group living are not evident (Woodroffe & Macdonald 2000). This lack of cooperation and the fact that Eurasian badgers are one of the few social species in the otherwise solitary mustelids, have been interpreted as evidence of a primitive degree of sociality (Macdonald 1983; Woodroffe & Macdonald 1993).

The resource dispersion hypothesis (RDH) in its spatial form (RDHS) is the most frequently used model in explaining the sociality of badgers in high-density populations. It states that, when the key trophic resource is distributed patchily, a pair of animals will choose a minimum territory which may be shared at little or no cost in terms of competition for food (Kruuk & Macdonald 1985; Macdonald & Carr 1989; Woodroffe & MacDonald 1993). RDHS predicts that territory size will be determined by the dispersion of the habitat

patches containing the resource, whereas group size will be determined by their richness (Kruuk & Parish 1982; Macdonald 1983; Woodroffe & Macdonald 1993). Additionally, within the framework of this hypothesis, badgers have been defined as ‘contractors’ because they should maintain the smallest economically defensible territory which encompasses sufficient resources for reproduction, without trying to expand it (Kruuk & Macdonald 1985).

It has been long assumed that understanding the origin of group living in badgers comes through knowledge of the factors promoting and constraining territoriality because territoriality is supposed to be an adaptation to defend a limiting resource (food, mates or refuges; Woodroffe & Macdonald 1993). On the other hand, the quality, distribution and availability of limiting resources do not affect all individuals in the same way, and so we may reasonably expect differences in the patterns of space use between different individuals (Revilla & Palomares 2001). Current theory predicts that group living should evolve when the fitness benefits obtained by one individual within a group outweigh the costs of sharing key resources (Koenig *et al.* 1992; Cockburn 1998; Hatchwell & Komdeur 2000) and/or when there are strong ecological constraints on independent reproduction (Hatchwell & Komdeur 2000). Therefore, the spatial organization of badgers as well as the variability in the use of space shown by different individuals are basic for understanding the sociality of this species, while accommodating all observations of interpopulation variability (also at low-density populations) is a major challenge for any hypothesis aiming to explain the origin of group living. However, current knowledge on the social organization of badgers at low densities is fragmentary and subject to speculation, with populations considered as pair living, non-territorial solitary living or even forming intersexual territories (Kruuk 1989; Woodroffe & Macdonald 1993; Rodríguez, Martín & Delibes 1996; Brøseth, Knutsen & Bevanger 1997).

In this paper we study the social organization of Eurasian badgers in two low-density populations of southern Spain (Coto del Rey and Reserva, both located in Doñana area), and variations in the strategies of individual use of space within the conceptual frame of the RDHS. Specifically, we aimed (1) to determine if badgers are territorial and form groups by describing the patterns of spatial grouping (home range and core area size and stability) and territory marking at latrine

sites. We also aimed (2) to determine if there were differences between individuals in some of the following characteristics and space use strategies under strong seasonal fluctuations in the availability of the key trophic resource (young European rabbits *Oryctolagus cuniculus* L.): (a) seasonal variations in body condition; (b) variations in the seasonal proportion of the territory used; (c) variations in the distance and area covered, as well as the speed of the movement and the number of hours active per period of activity; (d) the interactions between individuals of the same group both during resting and activity periods, measured as attraction or repulsion between pairs of individuals; and (e) patterns of dispersal. Finally, we wanted (3) to know which factors give rise to group formation, as well as the role of the spatial distribution of the main prey in the development of sociality by testing some of the assumptions and predictions of RDHS: (a) a patchy spatial distribution of the key trophic resource is the only necessary factor for explaining group formation, (b) territory size is controlled by the spatial distribution of patches of the habitat holding the key resource (Mediterranean scrubland) and not by its richness, and (c) badgers behave as contractors, never expanding their territories to include an excess of resources.

Methods

STUDY SITES AND BADGER POPULATIONS

We carried out our study in the Doñana region (south-western Spain, 37°9' N, 6°26' W; Revilla, Palomares & Delibes 2001a). Doñana is a subhumid Mediterranean area (i.e. characterized by long dry summers), with an average annual rainfall of 500–600 mm. Landscape is flat with sandy soils, except in marshlands, where they are clayey. Vegetation is characterized by Mediterranean scrubland (*Halimium* spp., *Cistus* spp. and *Pistacia lentiscus* L.); pine (*Pinus pinea* L.) and eucalyptus (*Eucalyptus globulus* Labil.) plantations; marshlands; pasturelands and dehesas (Mediterranean savannahs); and by ash (*Fraxinus angustifolia* Vahl) stands (Revilla, Palomares & Delibes 2000). The core of the area is protected by Doñana National Park, occupying about 550 km², of which 240 km² are habitat suitable for the Eurasian badger (mainly Mediterranean scrubland; Revilla *et al.* 2000, 2001a).

We studied badgers living in two locations of Doñana National Park separated by about 8 km: Coto del Rey, situated at the northern border, and Reserva Biológica, close to the centre of the park (see Fig. 1 in Revilla *et al.* 2001a). In these areas badgers live at the lowest

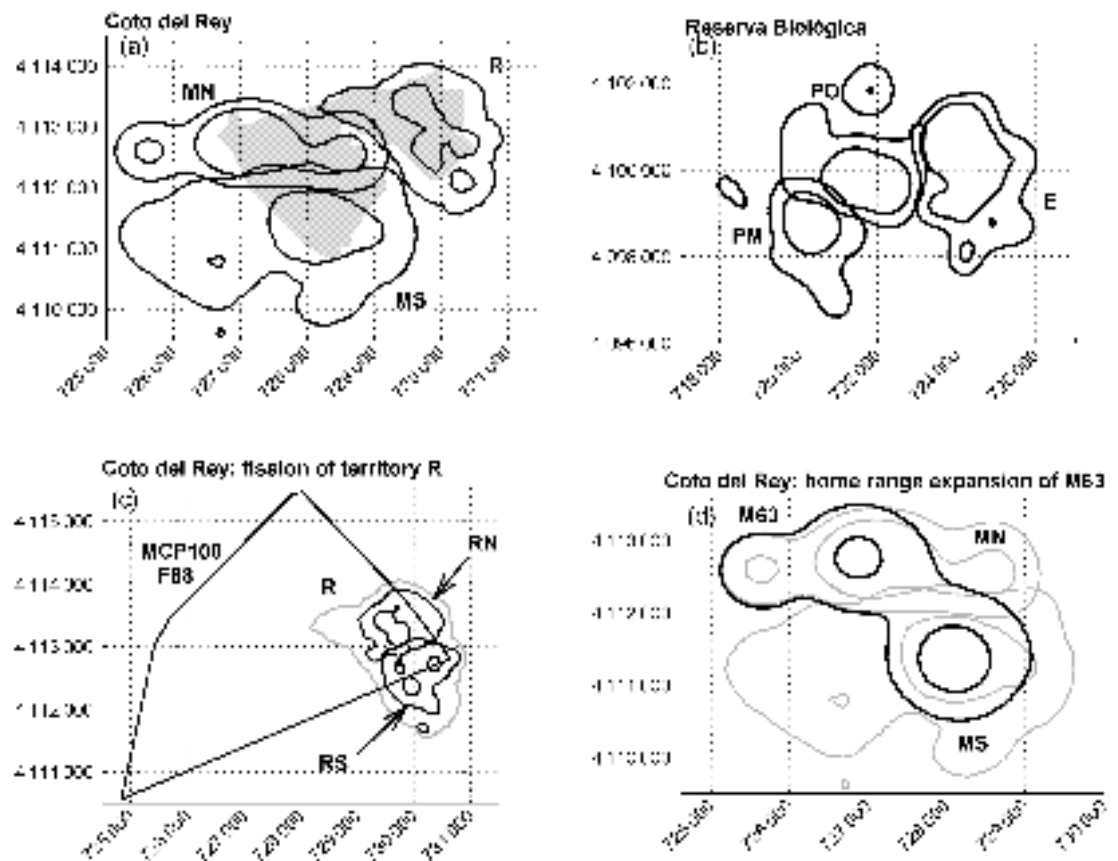


Fig. 1. Group home range outlines defined by KI95 (outer isoline) and KI70 (inner isoline). (a) Territories MN, MS and R in Coto del Rey, Mediterranean scrubland patch is marked in grey. (b) Territories PO, PM and E in Reserva Biológica. (c) Territories RN and RS formed after the fission of territory R (grey isoline). The pre-settlement minimum convex polygon of F68 is also represented (MCP100). (d) Territory expansion by M63 in Coto del Rey. Reference system is in UTM.

Table 1. Home range size and major axis of badger groups in the Doñana study area, south-western Spain, estimated as the minimum convex polygon with 100% and 95% of locations (MCP100 and MCP95, respectively) and as the kernel isoline with 95% and 70% of locations (KI95 and KI70, respectively). Area refers to Coto del Rey (CR), Reserva (RB), Sotos (SO) and Entorno de Doñana (ED)

Territory identifier	Area	Number of animals marked	Number of radiolocations	MCP100 (ha)	MCP95 (ha)	KI95 (ha)	KI70 (ha)	Major axis MPC100 (m)	Major axis of KI95 (m)
R	CR	5	1666	1113	521	380	93	5201	2857
RN	CR	2	637	278	105	114	21	2250	1500
RS	CR	2	301	182	116	109	13	1897	1429
MN	CR	4	556	537	494	453	190	4075	4014
MS	CR	10	1580	1825	981	808	155	5878	4428
M	CR	1	247	819	520	570	91	4163	4000
SO	SO	1	34*	(705)	(403)	(711)	(120)	(4012)	(3723)
PM	RB	1	136	702	580	503	167	4357	4018
PO	RB	1	137	889	706	919	275	4238	3839
E	RB	1	116	1011	893	920	466	4926	4196
ED	ED	1	20*	(425)	(258)	(589)	(206)	(3902)	(3207)

*Insufficient number of radiolocations, home range estimation given only as an indicative figure.

densities recorded (between 0.2 and 1 adults per km², Revilla *et al.* 1999), using up to 41 setts per territory (Revilla, Palomares & Fernández 2001b). Where young rabbits are abundant, such as in Coto del Rey, they are the staple food, with badgers consuming them following a type 3 functional response above one rabbit litter per hectare (then diet is composed by more than 50% of young rabbit in biomass, Revilla & Palomares 2002). Temporally, there are strong fluctuations in rabbit abundance with the maximum occurring in April/June and the minimum from August to February (when there were on average 3.5 times fewer rabbits; Palomares *et al.* 2001). Rabbits are clumped strongly in Mediterranean scrubland, reaching the highest densities in this habitat (Palomares & Delibes 1997; Palomares *et al.* 2001). As a result, badgers in Coto del Rey have a strong preference for Mediterranean scrubland habitat, during both activity and resting periods, while the remaining habitat types are mainly avoided (Revilla *et al.* 2000).

FIELD METHODS

Badgers were captured, anaesthetized, marked individually with a microchip, fitted with a coloured radio collar (with activity and mortality switch; A. Wagener, Herwarthstrasse, Köln, Germany) and released at the point of capture following standard procedures. We distinguished badgers by sex, age and social status (dominant females, dominant males and subordinates). We defined the social status of individuals in terms of their reproductive asymmetry: dominants showed reproductive activity (Revilla *et al.* 1999; Revilla & Palomares 2001). In the case of females, pregnancy and lactation during any of the captures was enough for considering them as dominant, as there was no single case of double reproduction inside any territory (Revilla *et al.* 1999). The oldest males, which also had the largest descended testes, were considered as dominants. Subordinates were animals born at the territory

in previous years, but without reproductive activity (despite sexual maturity). In Coto del Rey we marked 24 individuals between 1994 and 1997, and three in Reserva Biológica in 1997. We also followed two individuals, one in Sotos area and the other in Entorno de Doñana area, where they settled after dispersal (Table 1). We needed a trapping effort of 451 and 407 trap-nights per capture (i.e. including recaptures) for the first and the second area, respectively, making an annual trapping effort of about 5000 trap-nights (including Coto del Rey, Reserva, and Sotos area).

In Coto del Rey we estimated the location of radio-marked badgers once per day during the daylight, and two to three times per week during the night, while in Reserva Biológica we made two to three radiolocations per week both during the day and the night. Additionally, we also radiolocated one to three animals per night from the onset to the end of their period of activity, locating all animals once per hour. These periods of intensive radiotracking were performed once per week. Night locations were carried out via triangulation from two fixed stations, while daylight locations were traced to the animal's resting place (Revilla *et al.* 2001b). In the analysis of home ranges we used only locations separated by at least 4 hours during the activity period and by 1 day during the resting period. We considered these temporal intervals as adequate to avoid auto-correlation between consecutive locations without losing relevant information on the ecology of the animals. We estimated triangulation error in an experimental trial. It was 95% of the times below 245 m, showing, as expected, a positive relationship between location error and distance ($r^2 = 0.46$, $P < 0.0001$, range of distances during the trial between 50 and 2700 m). As 94% of field locations were taken at distances of less than 1 km, location error should always have been far below this upper limit. In total we obtained 7281 locations of badgers in Coto del Rey and 390 in Reserva Biológica.

A minimum number of animals living in each territory was calculated by using a combination of

radiotelemetry and track censuses, and complemented with sighting information. Track censuses were conducted in all territories at least once a year (except in 1994) on previously swept sandy roads (in order to erase old tracks, Palomares *et al.* 1998; Revilla *et al.* 1999). The very high density of roads and fire-breaks in both areas and the absence of grassy plants during most of the year allows the identification of a foraging badger crossing any road just by means of its tracks (in a similar manner to snow-tracking). All radiotagged badgers were radiotracked continuously during the night preceding the track census, in order to assign their movement routes to the footprint trails, and hence to distinguish the ones of unmarked individuals (Revilla *et al.* 1999). In this way we were able to estimate a minimum number of badgers present in each territory. The consistency of these results was assessed by comparison with data obtained using sighting information (both during foraging and sett observations, with the aid of an image intensifier, Empresa Nacional de Optica SA, Spain) and tracks around setts (in the case of cubs). In total we performed 33 track censuses.

We located latrine sites during systematic searches for the collection of badger scats (Revilla & Palomares 2002), as well as opportunistically while performing any activity in the study area. We mapped exhaustively all rabbit warrens in 126 ha of Mediterranean scrubland between April and October of 1995 to determine if there was spatial clumping within this habitat type. Warren mapping consisted of recording the position of every warren using a global positioning system (GPS; model Garmin 75; for further methodological details see Palomares *et al.* 2001).

ANALYSES

We defined individuals as belonging to the same group when they used the same setts consistently during resting. We determined the size and shape of group and individual home ranges using minimum convex polygons (MCPs), and 95% fixed kernel isolines (KI95s), estimated with least-squares cross-validation and adjusted to the extreme locations (Seaman & Powell 1996). We estimated the minimum number of independent locations needed to calculate group and individual home ranges as 85, using curves of accumulated area (Harris *et al.* 1990), while for seasonal home ranges the minimum number of locations needed was 35. We also used the graphical approach proposed by Harris *et al.* (1990) to establish that the 70% kernel isoline (KI70) defined core areas. We determined the stability of home ranges using the Cole index calculated as:

$$I_C = 100 \cdot \frac{2AB}{(A + B)} \quad \text{eqn 1}$$

where A and B are the areas of consecutive home ranges and AB is the area in common to both periods

(Ferrerias *et al.* 1997). Its value ranges between zero (no coincidence) and 100% (total coincidence). We defined winter from January to March, spring from April to June, summer from July to September and autumn from October to December. For comparative purposes we standardized seasonal home ranges dividing their value by territory size (standardized values are identified by SMCP, SKI95 and SKI70). These coefficients can be interpreted as the proportion of the territory used. During the period of study three of the animals from Coto del Rey changed their initial territory (by dispersal and re-establishment or by range expansion-fission), and thus their tracking interval was split into two distinct periods and, for analytical purposes, considered as new individuals.

We analysed the variability in space use as a function of the season, year and the sex and reproductive status of individuals with generalized linear mixed models, using SAS macro GLIMMIX (version 6.12, 25 September 1998), which iterates procedure MIXED in SAS using a reweighted likelihood algorithm (Littell *et al.* 1996). We considered territories as a random effect in the analyses because they represent only a random sample of a larger set of potential levels (Little *et al.* 1996). Individuals should be considered as a fixed effect because they represent all possible levels of the factor for the territories in which we marked all the individuals, or they represent all levels about which inference is to be made in those territories where not all the individuals were marked (Little *et al.* 1996). However, in the analyses of the seasonal individual home range size we considered individuals also as a random effect due to constraints in sample size (obviously, there is only one value for each individual on each of the combinations of the other variables). Therefore the interpretation of these seasonal models should be undertaken within the constraining frame of the results of the analyses of other movement patterns, where individuals were considered as fixed effects. Additionally, in the analyses of movement patterns during the periods of activity, we included a dummy identifier of the period of activity (date) as a random effect. This is because we can expect similar movement patterns during nights having similar weather conditions (such as heavy rain), irrespective of any other factor. For each model we chose the link function that minimized the deviance corrected by overdispersion (in all cases it was a Poisson distribution with a log-link).

Estimates of levels (treatments) of significant covariates (*post-hoc* contrasts) were calculated with the adjusted means (estimated with the best linear unbiased predictor; Littell *et al.* 1996) from the generalized linear mixed models. Pairwise comparisons for main effects were planned after graphical representation of the adjusted means for the significant covariates and performed using a *t*-test. In the case of significant interactions, we used slice effects (simple effects) to detect the origin of the interaction, and then a pairwise comparison for the planned comparisons derived from

those simple effects. When some of the combinations of treatments were missing, the estimates were calculated with a model with reduced number of treatments for the given factor (in such a case it is indicated in Results).

We investigated the interactions between individuals in their space use both during resting and activity periods using simultaneous locations of pairs of animals from the same territory. During the resting of badgers we considered simultaneously two locations made in the same resting period because it is very improbable that badgers change their resting site once there is daylight. During the period of activity we considered pairs of radiolocations made less than 1 hour apart (decided after considering our maximum radiotracking error and the displacement velocity of badgers; see Results). We used a randomization procedure to determine when a pair of individuals was found significantly closer than expected by a random use of their territory, for each of the seasons when the pairs of individuals were tracked simultaneously. We determined the randomized distribution of distances between individuals by shuffling one of the sets of locations and recalculating the distances between each pair of locations (repeated 10 000 times). In this way we used only those positions in space that were actually used by the individual during that season. We considered a pair of animals to be significantly closer than expected by the null model of no interaction when the observed average distance was smaller and outside the 95th percentile of the randomized distribution.

Body condition of badgers was assessed by calculating a body condition index, already used for badgers (Woodroffe & Macdonald 1995b). Briefly, an expected body mass (W) can be related via the equation $W = \exp(a + b \log L)$ with head-body length (L , in mm without the tail), where a and b are the parameters to be estimated with simple regression (Woodroffe & Macdonald 1995b). Using data obtained from animals coming from all the Doñana area (Revilla *et al.* 1999), the parameters were estimated as $a = 4.706$ and $b = 0.644$ for females ($n = 41$), and $a = 4.210$ and $b = 0.724$ for males ($n = 29$). Body condition index was calculated as the ratio of observed body mass vs. expected body mass (Woodroffe & Macdonald 1995b). Individuals used in body condition comparisons were at least 2 years old. First we studied the variations in the index of body condition using all the animals captured in the Doñana area with an analysis of variance, where sex, season and area (Coto del Rey and Reserva) were fixed effects, and individuals were nested in the model (procedure GLM, SAS Institute Inc.). Then, with data of individuals from only Coto del Rey, we used a generalized mixed model in which we included seasons, sex, social status, individuals and social group (random effect) in the model.

In total we mapped 859 rabbit warrens. We transformed their coordinates into a grid of 10×10 m (using ArcInfo), distinguishing between the cells with and

without warrens. We wanted to know if there was some spatial clumping, its strength, and also the scale up to which there was clumping. For each cell i containing a warren we counted the number of cells also with warrens [$= w(r)$] inside the ring of radius r and the total number of cells in the mapped area within the ring [$= c(r)$]. We calculated the probability of finding cells with warrens at distance r from another arbitrary cell with warren in the mapped area as

$$P(r) = \frac{\sum w_i(r)}{\sum c_i(r)} \quad \text{eqn 2}$$

up to $r = 24$ (i.e. 240 m). For comparison, we generated a null model of warren spatial distribution by randomizing the location of the cells with warrens within the area mapped (1000 times), and recalculating $P(r)$ to generate a 95% interval based on the random null model of no spatial clumping.

Results

GROUP LIVING AND TERRITORIALITY

Groups

We identified a minimum number of 38 different badgers (of which 27 were radiotagged). For one of these animals, we could not determine if was sharing its home range (territory ED, Table 1), while another was living alone (an adult female that settled in an empty area after dispersal; territory SO, Table 1). The rest of the animals were sharing their home range with at least one conspecific.

In Coto del Rey, we distinguished five groups. Two of these originated from the fission of a pre-existing territory. Average number of animals per group and year in this area was 4.56 ± 0.60 (\pm SE, range 2–7 individuals, $n = 9$); or 3.22 ± 0.32 (range 2–4 individuals, $n = 9$), respectively, with and without considering yearlings. One adult female and one adult male formed the basic unit of these groups. These females were the only ones that reproduced while males showed clear signs of reproductive activity (large descended testes). The rest of the individuals were born in the home range of the group, where they stayed until their dispersal or death. In Reserva area, we marked three adult females (two of which were lactating when captured) which occupied adjacent home ranges. During track censuses we identified in each of their home ranges another adult badger. We also detected tracks of two cubs in each of the home ranges of lactating females.

Territories

Overlapping between the home ranges of individuals of the same group was larger (average $60 \pm 29.0\%$) than between animals from different groups ($8 \pm 8.1\%$; $Z = 6.34$, $P < 0.001$). We identified 11 different group

home ranges (defined as KI95, Table 1), which were on average 406 ± 270 ha (\pm 1SD, $n = 6$) in Coto del Rey and 780 ± 241 ha ($n = 3$) in Reserva, with the lasts tending to be bigger ($t = 2.02$, $P = 0.083$, d.f. = 7). Average overlapping between the 95% kernel isolines of adjacent groups was 5.5% (range 0–12.1%). For subsequent analyses we consider this isoline as an approximation to the spatial definition of territories. In Coto del Rey, the interannual stability (Cole index) of territory isolines was on average $70.7 \pm 12.2\%$ (range 50.1–81.8%, $n = 6$), while seasonally the position of the centre of the territories did not change ($n = 26$).

In Coto del Rey there was some change in the number of territories, produced by the fission of one territory and the expansion of two. We tracked animals in territory R from February 1994 to February 1996, when two males (a dominant and a subordinate) were occupying it. In that moment, one adult female, which was living as a floater since the summer 1995 occupying marginal areas between the existing territories (F68, Fig. 1), and an adult male (M70), took the north of the original territory (forming territory RN). The two resident males of territory R used since then only the south (thereafter RS, Fig. 1). This division into two was maintained for 1 year until January 1997, when the dominant male of RS (M44) died. A few days after that, the dominant male of RN (M70) expanded his range to the south, occupying all the former R (Cole index for 1995 vs. 1997, 67% for KI95), and the subordinate of RS (M60) dispersed. There was another case of territorial expansion, also occurring after the death of the dominant male of territory MS, which was related to the takeover of the female by the incoming male (Revilla & Palomares 1999). Thus, the home range of one male (M63) was overlapping two different female territories (Fig. 1d).

Territory marking

We distinguished between latrines located in the proximity of setts (sett-latrines) and others (other-latrines). In Coto del Rey we collected a total of 1005 scats in latrines associated with 56 different setts, and 262 badger scats in 35 other-latrines during 1995 and 1996. In both years, the maximum use of other-latrines occurred in winter and the minimum in summer ($\chi^2_3 = 48.08$ and $\chi^2_3 = 19.42$, $P < 0.0001$, respectively, for 1995 and 1996). Other-latrines were situated preferentially outside the core areas (average of 10.0 latrines ± 2.44 vs. 1.4 latrines ± 0.58 , respectively, outside and inside the core area, $t = 7.66$, d.f. = 3, $P < 0.001$), being in most of the cases, situated in the borders of contact between adjacent territories (e.g. six new latrines appeared in the zone of contact of the territories formed after the fission of territory R), with 71% of them located at less than 200 m from the border defined by KI95. Smaller territories tended to have more other-latrines ($r_s = 0.94$, $P = 0.019$, $n = 5$). The maximum use of sett-latrines occurred in the summer,

and the minimum in spring–autumn ($\chi^2_3 = 22.74$ and $\chi^2_3 = 33.41$, $P < 0.0001$, respectively, for 1995 and 1996). On average, there was 12.4 (SD = 5.13, for five territories) setts with latrines in the centre of activity of the territories, while only 3.6 (SD = 1.14) were outside core areas ($t = 3.75$, d.f. = 3, $P < 0.006$). In the three territories of Reserva we only found one latrine not associated with a sett, which was nevertheless situated in the centre of territory E (Table 1), the rest being sett-latrines (13 setts with latrines per territory, SD = 5).

VARIATIONS IN INDIVIDUAL TRAITS AND SPACE USE

Average home range of resident animals (KI95) was 412 ha, while individual core areas (70% kernel isoline) were on average 114 ha. There were no significant differences in any of the estimators of home range for sex status.

Seasonal home ranges and territory use

Seasonal home ranges (KI95) were 357 ± 219 ha ($n = 43$, range 42–842 ha), while seasonal core areas were 94.9 ± 84.8 ha ($n = 43$). Cole index calculated between consecutive seasonal home ranges was $69.8 \pm 10.95\%$ (range 44.3–90.8%). We did not detect any effect of sex status, season or their interaction, on the stability of seasonal home ranges. On average, seasonal individual home ranges measured as MCP, KI95 and KI70, were, respectively, 85%, 71% and 19% of the territory.

Generalized linear mixed models for the standardized values of MCP and KI95 showed several significant effects; while the model for SKI70 did not (Table 2). In the first case (SMCP, Table 2) there was temporal variation in home range size, between years (in 1995 badgers tended to have larger SMCP while in 1996 they were smaller), between seasons, and with different seasonal trends for 1996 (hence the significant interaction of seasons by years). Seasonally, SMCP tended to be larger in summer than in winter and spring ($t > 3.68$, $P < 0.0036$ for both comparisons) as well as during the autumn ($t > 1.97$, $P < 0.096$ for both comparisons, based on the adjusted mean estimated from a reduced model without considering year 1997).

There was also a significant interaction between the classes of sex status and the seasons (Table 2, Fig. 2): dominant males had a constant home range size over the seasons (simple effects $F = 0.02$, $P = 0.9832$) while that of dominant females (simple effects $F = 11.21$, $P = 0.0066$) and subordinates (simple effects $F = 3.13$, $P = 0.100$, calculated from a reduced model without year 1997) tended to increase from a minimum in winter to a maximum in the summer (Fig. 2). Maximum use of the territory was shown by dominant females in the summer when they moved over areas larger than the actual territory (Fig. 2), and larger than the ones used by dominant males or by subordinates ($t = 2.85$,

Table 2. Results of the generalized linear mixed models for the analyses of the standardized seasonal home range size (measured as the minimum convex polygon SMCP, and the 95% kernel isoline KI95 and the centres of activity KI70), the distance moved per period of activity, distance moved per hour, area covered per period of activity and number of hours active per night. Sex status is defined by dominant females, dominant males and subordinates. Significant effects and interactions are marked in bold. Territory and the number of locations were introduced as random effects in the models

Model – effect	χ^2	d.f.	<i>P</i>
Seasonal home ranges – SMCP			
Year	3.44	2	0.0321
Season	14.30	3	0.0025
Sex status	1.26	2	0.5318
Season × year	11.69	5	0.0393
Sex status × year	4.41	3	0.2204
Sex status × season	21.30	6	0.0016
Seasonal home ranges – SKI95			
Year	1.51	2	0.4698
Season	13.04	3	0.0045
Sex status	1.79	2	0.4086
Season × year	2.90	5	0.7153
Sex status × year	4.35	3	0.2260
Sex status × season	11.57	6	0.0723
Seasonal home ranges – SKI70			
Year	2.15	2	0.3421
Season	3.80	3	0.2836
Sex status	0.16	2	0.9228
Season × year	3.65	5	0.6001
Sex status × year	0.20	3	0.9775
Sex status × season	5.35	6	0.4999
Distance moved per night			
Year	39.98	2	0.0001
Season	11.21	3	0.0106
Sex status	5.55	2	0.0660
Season × year	0.76	5	0.9798
Sex status × year	0.59	3	0.8983
Sex status × season	15.91	6	0.0142
Sex status × year × season	10.42	6	0.1082
Individuals	47.95	15	0.0001
Distance moved per hour			
Year	31.52	2	0.0001
Season	10.06	3	0.0181
Sex status	3.27	2	0.1954
Season × year	2.05	5	0.8418
Sex status × year	0.47	3	0.9255
Sex status × season	9.8	6	0.1331
Sex status × year × season	18.38	6	0.0053
Individuals	46.01	15	0.0001
Area covered per night			
Year	28.38	2	0.0001
Season	8.22	3	0.0469
Sex status	7.29	2	0.0287
Season × year	2.41	5	0.7893
Sex status × year	2.79	3	0.4249
Sex status × season	9.14	6	0.1659
Sex status × year × season	11.82	6	0.0660
Individuals	54.11	15	0.0001
Hours active per night			
Year	1.91	2	0.3839
Season	5.78	3	0.1226
Sex status	2.67	2	0.2631
Season × year	1.68	5	0.8916
Sex status × year	1.30	3	0.7293
Sex status × season	12.90	6	0.0447
Sex status × year × season	5.87	6	0.4377
Individuals	30.30	15	0.0109

$P = 0.0247$ for the comparison with dominant males; $t = 2.07$, $P = 0.0841$ for the comparison with subordinates, calculated from a reduced model without year 1997).

The GLMM for the standardized value of the KI95 showed seasonal variations (Table 2), corresponding to a tendency to have larger SKI95s during the summer (Fig. 2, $t > 2.62$, $P < 0.039$, for the comparison of summer with winter and autumn). There was also a tendency towards a significant interaction between season and the classes of sex status (Table 2). Again, dominant males did not show significant seasonal changes in SKI95 (simple effects $F = 0.01$, $P = 0.9865$), while dominant females tended to have different SKI95 over the seasons (simple effects $F = 4.53$, $P = 0.0054$), having the largest values in the summer, when they used all the territory available (with an adjusted mean of 1.16 and a 95% CI of 0.82–1.63, calculated using the inverse link function).

Movement patterns

On average, badgers moved 4.59 ± 2.09 km per period of activity (± 1 SD, range 0.09–11.57 km, $n = 195$). During 1996 badgers moved smaller distances than in 1995 or in 1997 ($t > 3.07$, $P < 0.0028$). There was an increase in the distance moved per period of activity, from a minimum in winter–spring towards a maximum in summer–autumn. The significant interaction between season and sex status is due to dominant males, which moved larger distances during the winter than any other class of sex status ($t > 3.16$, $P < 0.0020$). In general, males tended to move larger distances than the rest of the individuals ($t = 2.33$, $P = 0.0217$).

Average speed of displacement per night was 0.334 ± 0.160 km/h, range 0.007–0.964 km/h, $n = (195)$. Seasonally there was a minimum speed of 0.299 ± 0.140 km/h in winter, which increased up to a maximum of 0.362 ± 0.170 km/h in summer (Fig. 2). During 1996, badgers moved more slowly than in any other year (0.250 ± 0.09 km/h vs. 0.390 ± 0.150 km/h). Subordinates moved in winter 1995 and 1996 more slowly than dominants (simple effects, $F = 4.11$, $P = 0.0083$; in 1997 we had no subordinates marked), while dominant males tended to move faster than dominant females in winter ($t = 1.70$, $P = 0.0928$; Fig. 2).

The area covered per night (MCP) was 87.2 ± 81.56 ha (range 0.01–479.4 ha, $n = 195$), corresponding to $21.3 \pm 16.4\%$ of the territory (range 0.01–94.18%). During 1996 badgers covered less than half the area than during 1995 or 1997 (adjusted means of 35 has in 1996 vs. 76 has in 1995 and 1997, $t > 3.25$, $P < 0.0016$). We observed the same trend as in previous analyses towards an increase in the area covered per period of activity from winter to summer–autumn (Fig. 2). Dominant males covered larger percentages of their territory, especially in winter ($t > 2.26$, $P < 0.0258$, Fig. 2). The tendency towards an interaction between sex-status, year and season is due to the tendency of

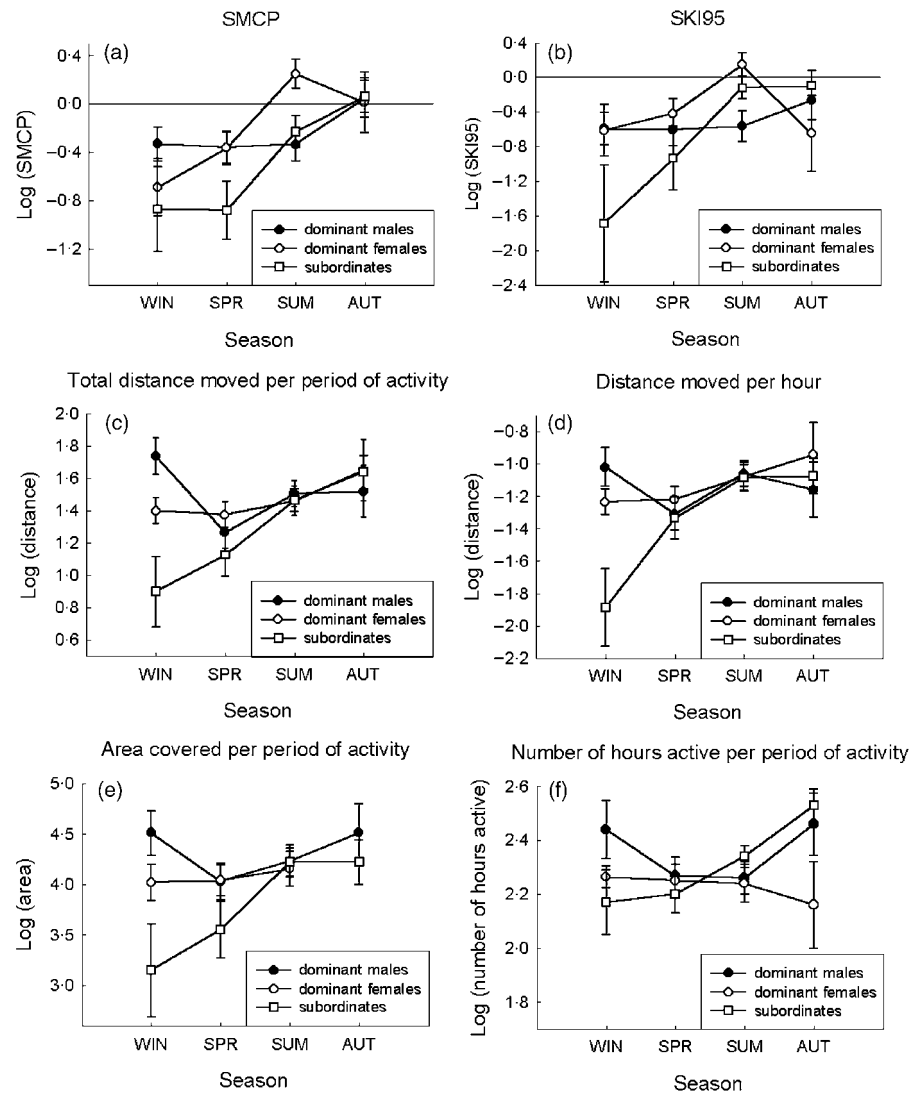


Fig. 2. Variations in standardized seasonal home ranges measured as the minimum convex polygon SMCP (a) and 95% kernel isoline SKI95 (b), the total distance moved per period of activity (c), distance moved per hour (d), area covered per period of activity (e) and numbers of hours active per period of activity (f). Values are the adjusted means and their standard error calculated from the generalized linear mixed models. Seasons are represented as WIN for winter, SPR for spring, SUM for summer and AUT for autumn.

dominant males to cover larger areas than the other animals during the winter (Fig. 2).

The number of hours active per period of activity was 9.7 ± 2.70 h (range 1–20 h, $n = 195$), corresponding to a proportion over the total radiotracking effort performed per period of activity of 0.71 ± 0.19 (range 0.04–0.94 number of hours active/total number of locations). There was a significant interaction between the season and the sex status of the animal (Table 2). The number of hours active was stable along the seasons and years for both dominant males and dominant females (simple effects $F < 1.30$, $P > 0.2781$). However, subordinate individuals increased the number of hours active from a minimum in winter to a maximum in autumn (simple effects $F = 4.46$, $P = 0.0059$, calculated with a reduced model without year 1997, autumn adjusted mean was larger than winter and spring values, $t > 2.66$, $P < 0.0089$).

Interactions between individuals

Badgers slept with another individual(s) in the same sett on 28% of days (the rest sleeping alone, Fig. 3). However, the only pair of dominant animals that we tracked together in winter slept together on 80% of days (Fig. 3). During the period of resting we detected a total of seven significant interactions ($n = 21$) between pairs of individuals of the same territory. Pairs composed of a dominant female and a dominant male slept significantly closer than expected by a random use of the selected setts than any other combination of individuals (71% vs. 14% of the pairs, Fisher's exact test, $P = 0.017$). Only two pairs of animals (one dominant female and her young of the year; and two subordinates) that slept significantly closer than expected did not consist of a dominant pair. During the period of foraging, the pairs of dominant individuals of the same territory

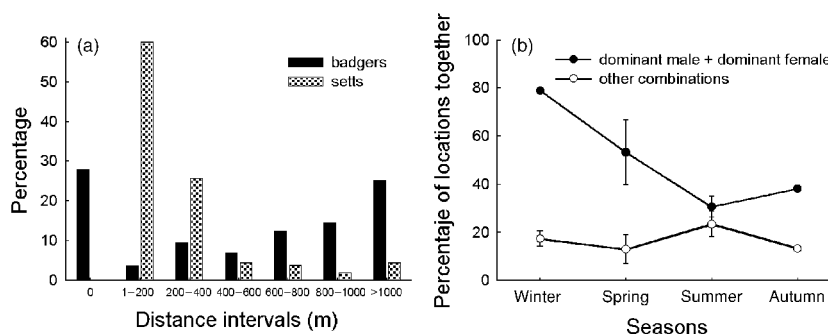


Fig. 3. (a) Distribution of the minimum distance between setts in Coto del Rey and the distribution of minimum distances at which badgers slept in Coto del Rey, both measured in distance intervals of 100 m. (b) Seasonal percentage (± 1 standard deviation) of days in which a given pair of individuals of the same group slept together in the same sett, as a function of the sex status of the individuals.

were again more frequently closer than expected than any other combination of individuals (88% vs. 11% of the pairs, Fisher exact test, $P = 0.003$).

Individuals and their body condition

The general linear model for the index of body condition of all individuals measured in the Doñana area ($F_{4,59} = 4.24$, $P = 0.0044$) showed significant main effects for the area ($F_{1,59} = 7.12$, $P = 0.0098$), and the season ($F_{3,59} = 4.01$, $P = 0.0115$). The index of body condition was lower for animals captured in Reserva than for animals in Coto del Rey (0.959 and 1.035, respectively, $P < 0.05$, Tukey's test). Body condition was also significantly lower during the summer than in the spring (0.959 and 1.035, respectively, $P < 0.05$, Tukey's test).

In Coto del Rey, subordinate individuals had a lower index of body condition than dominants (0.9396 and 1.108, respectively; $\chi^2 = 7.33$, $P = 0.007$, $t = 2.71$, $P = 0.013$). Seasons were not significant in this model ($\chi^2 = 3.46$, $P = 0.326$), due probably to the low number of animals that we captured in the summer (only three individuals, with an adjusted mean of 0.912, while estimated body condition was 1.028, 1.077 and 1.074, during winter, spring and autumn, respectively).

Dispersal

In total, we recorded eight dispersal events (six females and two males), all of them in Coto del Rey (32% of the animals marked). Five of these animals were born in territories of this area, while the other three were already dispersing when captured. All the animals born in Coto del Rey dispersed when 2 or 3 years old, coinciding with the time of oestrus (January–February, Revilla *et al.* 1999). Annual dispersal rate was between 0.14 and 0.33 per territory. Half of the animals that dispersed from Coto del Rey settled, while the rest died (killed by humans or by dogs). Successful dispersers settled at distances between 2.5 and 32.0 km from their natal territory, while animals that died reached distances between 7.5 and 8.8 km. One 8-year-old female (F68)

of unknown origin lived in marginal areas of Coto del Rey as a floater during at least 6 months, until her settlement, together with one 4-year-old male of unknown origin (M70), in territory RN in February 1996.

KEY TROPHIC RESOURCE AND SPATIAL ORGANIZATION

All badger territories in Coto del Rey held a single patch of Mediterranean scrubland of between 71 and 219 ha per territory (between 17% and 84% of their area, Fig. 1a), and all of them but one (which had no access to the marshland) had only one line of ecotone between scrubland and pastureland–marshland. Rabbit warrens were negligibly clustered within Mediterranean scrubland (~1% increase in the probability of finding a rabbit warren) up to distances of about 150 m.

Territories where badgers consumed a higher proportion of young rabbit biomass tended to be smaller ($r^2 = 0.84$, $F_{1,5} = 25.7$, $P = 0.004$, Fig. 4). Seasonally, dominant females used a larger proportion of their territories when a smaller proportion of their diet was composed of young rabbits ($r^2 = 0.60$, $F_{1,8} = 11.4$, $P = 0.0098$, Fig. 4). This relationship was even stronger when considering the actual availability of rabbit litters ($r^2 = 0.91$, $F_{1,5} = 48.6$, $P = 0.0009$, for 1996 and 1997 only; Fig. 4). However, the correlation of the proportion of young rabbits consumed and the seasonal proportion of territories covered by subordinates and dominant males was poorer ($r^2 = 0.16$, $F_{1,20} = 5.0$, $P = 0.036$, without considering dominant males during the winter Fig. 4), and the relation with the litters per hectare in 1996 and 1997 was not significant ($r^2 = 0.17$, $F_{1,6} = 1.23$, $P = 0.3$, again without considering dominant males during the winter; Fig. 4).

Discussion

TERRITORIALITY IN LOW-DENSITY POPULATIONS

At low densities, badgers are territorial showing a flexible system of territory marking that includes the

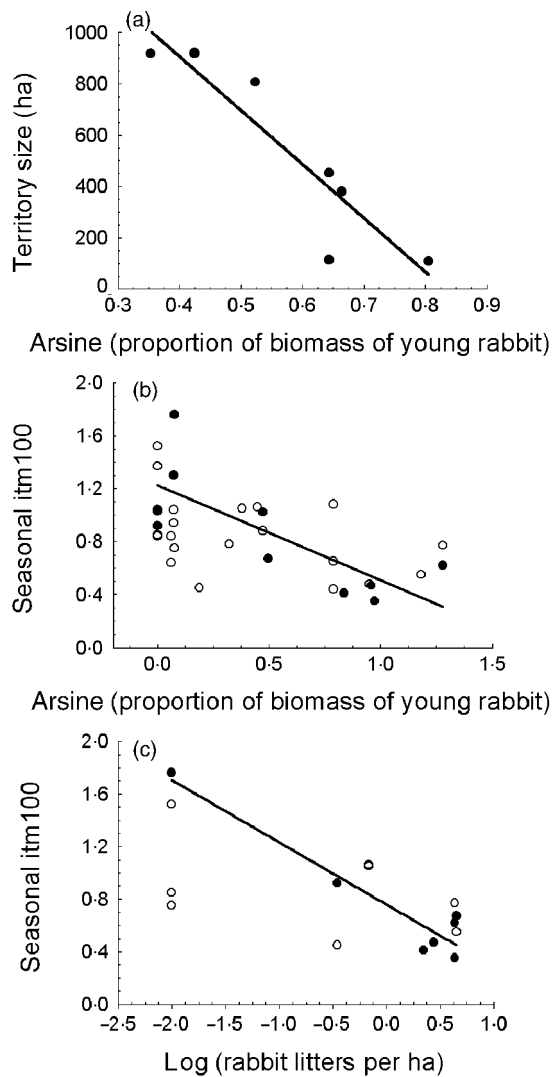


Fig. 4. (a) Relationship between territory size and the amount of young rabbits consumed by badgers (measured during the same study period 1995–97, Revilla & Palomares 2002). (b) and (c) Relationship between the proportion of the territory used seasonally and the seasonal amount of young rabbits consumed by badgers (Revilla & Palomares 2001, 2002) and the availability of rabbit litters in Mediterranean scrubland (Revilla & Palomares 2001, 2002), respectively. Empty dots represent dominant males and subordinates. Regression lines correspond to dominant females (black dots).

marking of the most used areas (sett-latrines at the centres of activity), and additionally, when territories are smaller, a system of border-latrines in the areas of contact between territories. The intensity of use of border-latrines was associated with the reproductive season, and that of sett-latrines with the season of food scarcity, which suggest that the first is associated with mate defence by dominant males (Roper, Shepherdson & Davies 1986; Roper *et al.* 1993), and the second with the defence of trophic resources (but see Woodroffe & Macdonald 1993 for an alternative explanation), as described in other areas, where adult males perform most of the marking (Kruuk, Gorman & Leitch 1984; Roper *et al.* 1986, 1993; Pigozzi 1990).

The system of hinterland marking might be an important part of the defence of large territories, where avoiding intruders in the centre of activity might be more important (and efficient) than the actual delimitation of a clear border (Gorman 1990; Gorman, Kruuk & Leitch 1984). This lack of border-latrines might have been the reason for defining other low-density populations as nonterritorial (e.g. Woodroffe & Macdonald 1993; Feore & Montgomery 1999), and also why the use of bait marking to determine the borders of large territories fails.

Some low-density populations of badgers have been considered as having intersexual territories defended by merely one individual against any other badger. The only support for the existence of this territorial system comes from Pigozzi 1987 (cited in Woodroffe & Macdonald 1993), in La Maremma Natural Park, where territories are described as very small (only 78 ha). These contrasting results are surprising, since La Maremma National Park is very similar to our Reserva study site (and so is badger diet; Pigozzi 1988; Revilla & Palomares 2002). However, we have no information on the number of badgers marked (Pigozzi 1989 in the same area reports only three marked individuals, which ‘foraged together with other unmarked badgers’), the amount of time tracked and the methodology used in the estimation of territory size. Therefore, the existence of individual territories requires confirmation.

GROUP VS. SOLITARY LIVING IN LOW-DENSITY POPULATIONS

In Coto del Rey, territories were occupied by small groups of animals. These groups were formed by one adult female who reproduced, one adult male who also showed signs of reproductive activity and, if there was reproduction, the cubs of the year. Additionally, individuals born in previous years remained in their natal territory until their dispersal during the mating season of their third or fourth year of life. Territories in the Reserva study site were occupied by adult females, plus the cubs of the year and another adult individual. By analogy with the territories in Coto del Rey it seems likely that this individual was an adult male (supported also by the existence of reproduction). Interestingly, we did not detect additional adults. This could be due to our small sample size, which together with a high mortality rate may result in finding territories with just two adults. However, mortality rates in Reserva are very low (Revilla *et al.* 2001a), and badgers there can live for many years (up to 14 years, authors unpublished). Another possible explanation is a failure in the detection of additional individuals due to the method used. Nevertheless, we applied the same method in Coto del Rey (where the number of territories studied was also small), and so we would expect the same problems there. The last possible explanation might be the early dispersal of the badgers born in the territories of

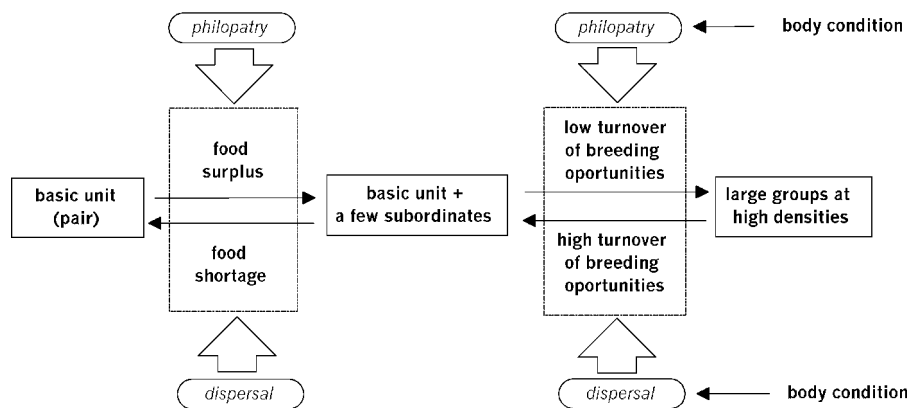


Fig. 5. Scheme with an integrative view of the constraints affecting the social organization of Eurasian badgers, focusing on the three levels of complexity (boxes) ranging from the basic unit formed by one pair of animals to the large groups living at high densities. Ecological and demographic constraints (dotted boxes) affect the change between these levels of complexity through individual decisions (philopatry or dispersal; for more details see Discussion).

Reserva. If this interpretation holds, dispersal should occur in this area between their first summer and the first reproductive season.

Previous studies support the interpretation of badgers living in territorial pairs at low densities, such as in some parts of Scotland (Kruuk 1989), Scandinavia (Brøseth *et al.* 1997), and also in another site of the Doñana area (Rodríguez *et al.* 1996). Therefore, current evidence suggests that the basic pattern of social organization of badgers living at low densities can be described as territories occupied by a core pair of individuals (one female and one male, the 'basic unit' in Fig. 5) with, occasionally, a few additional adults born in the same territory. This system is not strictly fixed because males, given the opportunity, may expand their territories to encompass additional females (Roper & Lüps 1993; Tuytens *et al.* 2000a, 2000b), despite which dominant males still spend a large amount of time with the dominant female (Revilla & Palomares 1999).

INDIVIDUAL DIFFERENCES IN SPACE USE

In winter and spring dominant females and subordinates used only a small fraction of their territories, moved short distances, at a low speed and covering small areas per night. These seasons correspond with the reproduction of rabbits (beginning with the first rains), which is the moment of highest food availability, when rabbit kittens form more than half of the consumed biomass (Revilla & Palomares 2001, 2002). At the other extreme, dominant females were the only individuals using all the territory available. They did so during the summer, when food availability is the lowest (Revilla & Palomares 2001, 2002) and also when badgers had the worst body condition. Dominant females are probably the individuals with the highest energetic requirements (Creel & Creel 1991; Woodroffe & Macdonald 1995a), and therefore it is reasonable that in summer (when young are still dependent) they

need to move over larger areas, using all the space available (even out of the outline of their territory) and using areas normally avoided such as the marshland (Revilla *et al.* 2000). With ripening of the fruits of dwarf palms (*Chamaerops humilis* L.) and wild pears (*Pyrus bourgaeana* Decne) in the autumn (Revilla & Palomares 2002), food availability increases again, and so does body condition, while the spatial requirements are reduced again.

Dominant males showed a completely different pattern of space use. They covered a stable proportion of their territories along the seasons (also in winter). During the winter they moved faster, for longer distances, and covered larger areas per period of activity. All these results indicate that space use of dominant males was affected by different factors to that of dominant females and subordinates. In Doñana reproduction occurs in winter (Revilla *et al.* 1999), which is also the season with the highest use of border-latrines. The most reasonable interpretation is that dominant males engage in some kind of territory patrolling, which is especially evident during the reproductive season. This winter territorial behaviour is probably directed to mate defence, and not to resource defence (otherwise they should also show it in the spring, which, from the point of view of resource availability, is very similar to winter; Revilla & Palomares 2001, 2002). The interpretation of mate-guarding behaviour by dominant males is further supported by the fact that males were closer to dominant females than expected by chance during both the resting and activity periods.

TERRITORIALITY AND GROUP LIVING IN DOÑANA VS. RESOURCE DISPERSION HYPOTHESIS

The resource dispersion hypothesis (RDHS) is considered the most probable explanation of group living in badgers and other species (Macdonald 1983; Geffen

et al. 1992; Silva *et al.* 1993; Woodroffe & Macdonald 1993; Johnson, Macdonald & Dickman 2000). One of the main assumptions of RDHS is that territoriality is a response to intraspecific competition to defend limiting resources. However, territoriality can be simply a maximization of space use (Stamps & Krishnan 1999), and not necessarily a way to exclude conspecifics (or at least not only or not initially). We have shown that dominant females are the only individuals using all the available territory during the summer and also that the correlation between the size of the seasonal home range of dominant females and territory richness is much stronger than for any other category of animals. Dispersing females are the first animals to settle in empty areas (Tuytens *et al.* 2000a, 2000b), deciding how large their stable home range should be to allow survival and reproduction. All this indicates that females may be the ones determining the initial size of territories. Furthermore, territory size was correlated with the overall consumption of young rabbits, which should be a good indicator of territory richness.

In summary, territoriality in the pair of primary animals seems to be driven by different factors (richness of trophic resources for the female, and the females for the male); dominant males may act as 'expansionists' (*sensu* Kruuk & Macdonald 1985); we could not distinguish more than one clearly defined patch of the key habitat inside each territory, and territory size was related to its richness and not to patch dispersion. Therefore we conclude that RDHS cannot be the explanation of group living in Coto del Rey. Why, then, do badgers form groups in that area? Badger groups in Coto del Rey and elsewhere are formed by philopatry of individuals born in the territory beyond sexual maturity (Kruuk & Parish 1982; Cheeseman *et al.* 1987; Silva *et al.* 1994). If these individuals remain in their natal area it is because there are enough food resources to sustain them and the rest of individuals of the group. If territory size is determined initially by the needs of the breeding female during the harsh summer of Doñana, those territories having Mediterranean scrubland with healthy rabbit populations may have a surplus of resources during at least half of the year. Rabbit reproduction begins explosively after the first autumn–winter rains, lasting until the end of the spring, with female rabbits breeding several times during this period. As a result, badgers experience a fast shift from having no young rabbits available to having an excess of them. This excess of resources allows badgers to improve their body condition during winter and spring; improved body condition that permits them to survive a summer with few resources. In autumn, there is again a sudden overabundance of food, in the form of ripened–fall wild pears and dates. If this interpretation holds, it would be the strong seasonality of this Mediterranean ecosystem that reduces the competition for food between individuals during most of the year.

RDHS and the strong seasonality of the Doñana ecosystem are the factors permitting the formation

of groups, but neither explains group formation in low- and high-density populations at the same time. It is reasonable to think that they are not the causal factors of group formation, because the key question (i.e. why badgers are philopatric) remains unanswered. Furthermore, the existence of important costs associated with a reduced probability of reproduction for the individuals within the group (Cresswell *et al.* 1992; Silva *et al.* 1994; Woodroffe & Macdonald 1995a; 1995b; Tuytens *et al.* 2000a, 2000b) will challenge any hypotheses assuming that there are no (or very low) costs for individuals living in a group (such as RDHS).

AN INTEGRATIVE HYPOTHESIS

Most of the models used to explain group living in badgers assume that there is only one main factor responsible for sociality, ecological factors controlling territoriality being the most commonly invoked, while the behavioural strategies of individuals, such as individual dispersal and mating strategies (but see territory inheritance hypothesis, Lindström 1986), have been neglected frequently (e.g. Johnson *et al.* 2000). As a result, current hypotheses fail in the explanation of the available knowledge on the social organization of badgers, and there is a need for a more integrative hypothesis that takes into account the three main types of factors influencing the social organization of badgers: (1) ecological constraints determined by the availability of key resources which shape the degree of competition between individuals; (2) demographic constraints defined by mortality rates of dominant individuals and of animals during dispersal; and (3) behavioural constraints that under the same conditions may favour philopatry over dispersal.

The basic unit in the social organization of badgers is one pair of territorial adult animals (Fig. 5). If territory richness is low we may expect strong competition during periods of food stress, with young animals dispersing from their natal territory. Under this scenario we should observe very large territories occupied by one adult female and one adult male, together with the cubs of the year, but no additional subadults (as seems to be in Reserva), because philopatry is constrained by competition for food with the breeding animals (Fig. 5). Also, in Coto del Rey, after a crash in the rabbit population, we observed that subordinates reduced their use of the key habitat, which may be interpreted as a spatial exclusion of subordinates by dominants from the limiting trophic resources (Revilla & Palomares 2001).

However, if the ecological frame is such that, during most of the year, competition for food is low, subadults adopt a philopatric strategy (e.g. Coto del Rey). The low competition can be explained by the RDHS, by strong seasonal variations in food abundance or by any other mechanism that leads to a surplus of food resources. Current theory on the evolution of delayed

dispersal states that constraints on independent breeding can be a result of (1) a shortage of vacant breeding territories of sufficient quality for independent reproduction; (2) a high mortality risk during dispersal; (3) a low probability of finding a mate; and/or (4) a low probability of successful independent reproduction once a territory has been established (Hatchwell & Komdeur 2000). In the case of badgers, the first reason probably occurs in many areas saturated with territories with a low turnover of breeding opportunities (note that the carrying capacity of breeding opportunities differs from the population carrying capacity), while we may expect high mortality rates while moving in an unknown area during dispersal. Under this scenario, philopatric individuals entering the reproductive status face the decision of staying in their natal territory without breeding, or dispersing to find an empty territory or outcompeting a resident (becoming a floater would be strongly avoided if mortality during dispersal is high). However, a good body condition is needed for successful reproduction, as well as for taking over an occupied territory successfully (Cresswell *et al.* 1992; Woodroffe & Macdonald 1995a; 1995b; Woodroffe *et al.* 1997; Tuytens *et al.* 2000b). Therefore, remaining in the natal territory until gaining the maximum body condition seems a safe decision when the probability of finding one empty territory is low. In this discussion we are assuming that dominant individuals are able to suppress the breeding of subordinates, both males and females. If this suppression is mostly successful (as might be the case in small groups, such as in Coto del Rey), the only chance of gaining reproductive status would be dispersal. A relatively high turnover of territory vacancies caused by a high human-induced mortality in some areas of Doñana (Revilla *et al.* 2001a) may favour dispersal of fully grown (and hence fully competitive) individuals (Fig. 5).

Territories occupied by many individuals may develop (up to a limit set by territory richness) in the interplay of these demographic and behavioural trade-offs; territories where the complete suppression of the reproduction of 'subordinates' would no longer be possible, and hence the distinction of fully dominant individuals (Fig. 5). Female badgers may then adopt two different strategies to gain reproductive status: dispersal towards a known territory where a higher reproductive probability may be gained (i.e. a better body condition in comparison with other members of the group). Alternatively, they may remain philopatric and try to reproduce whenever there are enough resources available in their current territory. In the case of males, reaching reproductive status would be less conflictive as they can try to mate not only with females in their own territory, but also in the neighbouring ones. The final strategy adopted by individuals under this scenario of high density would depend on: (1) the probability of finding an empty territory (turnover of breeding opportunities); (2) the probability of overtaking a territory

occupied by other animals (own physical condition in comparison with the more dominant animals in close territories – where individuals can actually assess it); and (3) the probability of reproducing in the natal territory (own physical condition in comparison with other individuals and in relation with the social status – importance of the availability of food in determining the body condition).

The scheme proposed here is only a first attempt to put together the current knowledge on the life history of badgers into a single integrative hypothesis explaining why badgers live in groups. The discussion on the origin of sociality in badgers has been centred for a long time in the mechanisms producing an oversized territory containing more resources than needed by the pair of primary individuals. Such excess of resources is needed as a prerequisite of delayed dispersal. However, acknowledging this prerequisite represents only one part of our understanding of badger social organization. Groups appear when individuals reaching sexual maturity decide to remain in their natal territory and when their parents allow them to do so. Therefore, to be able to understand group formation fully we have to focus on the alternative strategies adopted by individuals when deciding between dispersing and staying.

Acknowledgements

This research was funded by DGICYT and DGES (projects PB94-0480 and PB97-1163) and sponsored by Land Rover España. ER was supported by a predoctoral grant from the Spanish Ministry of Education and Culture and by a Marie Curie Fellowship from the European Commission (Energy, Environment and Sustainable Development Contract EVK2-CT-1999–50001). Fieldwork was conducted with the permission of Doñana National Park (Spanish Ministry of Environment) and Consejería de Medio Ambiente (Junta de Andalucía). P. Stewart, H. Kruuk, T. Roper and D. Macdonald helped in the initial design of the project. We are extremely grateful to S. Alís, J. Ayala, J. V. Baños, J. Calzada, A. Devenoges, J.M. Fedriani, N. Fernández, G. Janss, A. de Jong, R. Laffitte, G. Lariccia, J. A. López, P. Martín, A. Meijers, J.M. Pérez, L. Polderman, F. Ponga, J. C. Rivilla, C. Rodríguez, M. Rodríguez, A. de Roos, V. Salvatori, M. Smith and N. Zabala for their help with fieldwork. We also thank S. Schadt for GIS expertise and M. Delibes, A. Travaini, P. Ferreras, J.M. Fedriani, J. Calzada and T. Wiegand for their many comments and suggestions. T. Roper, P. Doncaster, E. Virgós and two anonymous referees kindly reviewed a draft of this work.

References

- Brøseth, H., Knutsen, B. & Bevanger, K. (1997) Spatial organization and habitat utilization of badgers *Meles meles*: effects of food patch dispersion in the boreal forest of central Norway. *Zeitschrift für Säugetierkunde*, **62**, 12–22.

- Cheeseman, C.L., Wilesmith, J.W., Ryan, J. & Mallinson, P.J. (1987) Badger population dynamics in a high-density area. *Symposia of the Zoological Society of London*, **58**, 279–294.
- Cockburn, A. (1998) Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology and Systematics*, **29**, 141–177.
- Creel, S.R. & Creel, N.M. (1991) Energetics, reproductive suppression and obligate communal breeding in carnivores. *Behavioral Ecology and Sociobiology*, **28**, 263–270.
- Cresswell, W.J., Harris, S., Cheeseman, C.L. & Mallinson, P.J. (1992) To breed or not to breed: an analysis of the social and density-dependent constraints on the fecundity of female badgers (*Meles meles*). *Philosophical Transactions of the Royal Society of London B*, **338**, 393–407.
- Evans, P.G.H. & Macdonald, D.W. (1989) Social structure of the Eurasian badger (*Meles meles*): genetic evidence. *Journal of Zoology, London*, **218**, 587–595.
- Feore, S. & Montgomery, W.I. (1999) Habitat effects on the spatial ecology of the European badger (*Meles meles*). *Journal of Zoology, London*, **247**, 537–549.
- Ferreras, P., Beltrán, J.F., Aldama, J.J. & Delibes, M. (1997) Spatial organization and land tenure system of the endangered Iberian lynx. *Journal of Zoology, London*, **243**, 163–189.
- Geffen, E., Hefner, R., Macdonald, D.W. & Ucko, M. (1992) Habitat selection and home range in the Blandford's fox, *Vulpes cana*: compatibility with the resource dispersion hypothesis. *Oecologia*, **91**, 75–81.
- Gorman, M.L. (1990) Scent marking strategies in mammals. *Revue Suisse Zoologie*, **97**, 3–29.
- Gorman, M.L., Kruuk, H. & Leitch, A. (1984) Social functions of the sub-caudal scent gland secretion of the European badger *Meles meles* (Carnivora: Mustelidae). *Journal of Zoology, London*, **204**, 549–559.
- Harris, S., Cresswell, W.J., Forde, P.G. & Trehella, W.J. (1990) Home-range analysis using radio-tracking data: a review of problems and techniques particularly as applied to the study of mammals. *Mammal Review*, **20**, 97–123.
- Hatchwell, B.J. & Komdeur, J. (2000) Ecological constraints, life history traits and the evolution of cooperative breeding. *Animal Behaviour*, **59**, 1079–1086.
- Johnson, D.D.P., Macdonald, D.W. & Dickman, A.J. (2000) An analysis and review of models of the sociobiology of the Mustelidae. *Mammal Review*, **30**, 171–196.
- Koenig, W.D., Pitelka, F.A., Carmen, W.J., Mumme, R.L. & Stanback, M.T. (1992) The evolution of delayed dispersal in cooperative breeders. *Quarterly Review of Biology*, **67**, 111–150.
- Kruuk, H. (1978a) Foraging and spatial organisation of the European badger, *Meles meles* L. *Behavioral Ecology and Sociobiology*, **4**, 75–89.
- Kruuk, H. (1978b) Spatial organization and territorial behaviour of the European badger *Meles meles*. *Journal of Zoology, London*, **184**, 1–19.
- Kruuk, H. (1989) *The Social Badger*. Oxford University Press, Oxford.
- Kruuk, H., Gorman, M., L. & Leitch, A. (1984) Scent marking with the subcaudal gland by the European badger (*Meles meles* L.). *Animal Behaviour*, **32**, 899–907.
- Kruuk, H. & Macdonald, D. (1985) Group territories of carnivores: empires and enclaves. *Behavioural Ecology: ecological consequences of adaptive behaviour* (eds R.M. Sibly & R.H. Smith), pp. 521–536. Blackwell Scientific Publications, Oxford.
- Kruuk, H. & Parish, T. (1982) Factors affecting population density, group size and territory size of the European badger, *Meles meles*. *Journal of Zoology, London*, **196**, 31–39.
- Lindström, E. (1986) Territory inheritance and the evolution of group living in carnivores. *Animal Behaviour*, **34**, 1825–1835.
- Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS System for Mixed Models*. SAS Institute Inc., Cary, NC.
- Macdonald, D.W. (1983) The ecology of carnivore social behaviour. *Nature*, **301**, 379–384.
- Macdonald, D.W. & Carr, G.M. (1989) Food security and the rewards of tolerance. *Comparative Socioecology. The behavioral ecology of humans and other mammals* (eds V. Stanley & R.A. Foley), pp. 75–99. Special Publication no. 8. British Ecological Society, Blackwell Science, Oxford.
- Palomares, F. & Delibes, M. (1997) Predation upon European rabbits and their use of open and closed patches in Mediterranean habitats. *Oikos*, **80**, 407–410.
- Palomares, F., Delibes, M., Revilla, E., Calzada, J. & Fedriani, J.M. (2001) Spatial ecology of Iberian lynx and abundance of European rabbits in southwestern Spain. *Wildlife Monographs*, **148**, 1–36.
- Palomares, F., Ferreras, P., Travaini, A. & Delibes, M. (1998) Co-existence between Iberian lynx and Egyptian mongooses: estimating interaction strength by structural equation modelling and testing by an observational study. *Journal of Animal Ecology*, **67**, 967–978.
- Pigozzi, G. (1988) Diet of the European badger (*Meles meles* L.) in the Maremma Natural Park, Central Italy. *Mammal Review*, **18**, 73–75.
- Pigozzi, G. (1989) Digging behaviour while foraging by European badger, *Meles meles*, in a Mediterranean habitat. *Ethology*, **83**, 121–128.
- 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., Delibes, M., Travaini, A. & Palomares, F. (1999) Physical and population parameters of Eurasian badgers (*Meles meles* L.) from Mediterranean Spain. *Zeitschrift für Säugetierkunde*, **64**, 269–276.
- Revilla, E. & Palomares, F. (1999) Changes in the behaviour of a male Eurasian badger: evidence in favour of the anti-kleptogmy hypothesis? *Acta Theriologica*, **44**, 471–476.
- Revilla, E. & Palomares, F. (2001) Differences in key habitat use between dominant and subordinate animals: intra-territorial dominance payoffs in Eurasian badgers? *Canadian Journal of Zoology*, **79**, 165–170.
- Revilla, E. & Palomares, F. (2002) Does local feeding specialization exist in Eurasian badgers? *Canadian Journal of Zoology*, **80**, 83–93.
- Revilla, E., Palomares, F. & Delibes, M. (2000) Defining key habitats for low-density populations of Eurasian badgers in Mediterranean environments. *Biological Conservation*, **95**, 269–277.
- Revilla, E., Palomares, F. & Delibes, M. (2001a) Edge-core effects and the effectiveness of traditional reserves in conservation: Eurasian badgers in Doñana National Park. *Conservation Biology*, **15**, 148–158.
- Revilla, E., Palomares, F. & Fernandez, N. (2001b) 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.
- Rodríguez, A., Martín, R. & Delibes, M. (1996) Space use and activity in a Mediterranean population of badgers (*Meles meles*). *Acta Theriologica*, **41**, 59–72.
- Roper, T.J. (1992) The structure and function of badger setts. *Journal of Zoology, London*, **227**, 691–698.
- Roper, T.J., Conradt, L., Butler, J., Christian, S.E., Ostler, J. & 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. & Lüps, P. (1993) Disruption of territorial behaviour in badgers *Meles meles*. *Zeitschrift für Säugetierkunde*, **58**, 252–255.
- Roper, T.J., Shepherdson, D.J. & Davies, J.M. (1986) Scent marking with faeces and anal secretion in the European

- badger (*Meles meles*): seasonal and spatial characteristics of latrine use in relation to territoriality. *Behaviour*, **97**, 94–117.
- Seaman, D.E. & Powell, R.A. (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, **77**, 2075–2085.
- da Silva, J., Macdonald, D.W. & Evans, P.G.H. (1994) Net cost of group living in a solitary forager, the Eurasian badger (*Meles meles*). *Behavioral Ecology*, **5**, 151–158.
- da Silva, J., Woodroffe, R. & Macdonald, D.W. (1993) Habitat, food availability and group territoriality in the European badger, *Meles meles*. *Oecologia*, **95**, 558–564.
- Stamps, J.A. & Krishnan, V.V. (1999) A learning-based model of territory establishment. *Quarterly Review of Biology*, **74**, 291–318.
- Tuytens, F.A.M., Delahay, R.J., Macdonald, D.W., Cheeseman, C.L., Long, B. & Donnelly, C.A. (2000a) Spatial perturbation caused by a badger (*Meles meles*) culling operation: implications for the function of territoriality and the control of bovine tuberculosis (*Mycobacterium bovis*). *Journal of Animal Ecology*, **69**, 815–828.
- Tuytens, F.A.M., Macdonald, D.W., Rogers, L.M., Cheeseman, C.L. & Roddam, A.W. (2000b) Comparative study on the consequences of culling badgers (*Meles meles*) on biometrics, population dynamics and movement. *Journal of Animal Ecology*, **69**, 567–580.
- Woodroffe, R. & Macdonald, D.W. (1993) Badger sociality-models of spatial grouping. *Symposia of the Zoological Society of London*, **65**, 145–169.
- Woodroffe, R. & Macdonald, D.W. (1995a) Cost of breeding status in the European badger, *Meles meles*. *Journal of Zoology, London*, **235**, 237–245.
- Woodroffe, R. & Macdonald, D.W. (1995b) Female/female competition in European badgers *Meles meles*: effects on breeding success. *Journal of Animal Ecology*, **64**, 12–20.
- Woodroffe, R. & Macdonald, D.W. (2000) Helpers provide no detectable benefits in the European badger (*Meles meles*). *Journal of Zoology, London*, **250**, 113–119.
- Woodroffe, R., Macdonald, D.W. & Cheeseman, C.L. (1997) Endocrine correlates of contrasting male mating strategies in the European badger (*Meles meles*). *Journal of Zoology, London*, **241**, 291–300.

Received 17 August 2001; revision received 11 January 2002