

# Characteristics, location and selection of diurnal resting dens by Eurasian badgers (*Meles meles*) in a low density area

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## Abstract

We describe diurnal resting dens (setts) used by Eurasian badgers *Meles meles* L. in Coto del Rey, Doñana National Park, south-western Spain, and analyse the factors that determine sett location and selection in relation to territory outlines, soil type and vegetation structure. Setts were located by tracking radio-tagged badgers daily. Badger setts were mainly underground burrow systems with, on average, 2.6 badger entrances. Frequently, badgers constructed setts by enlarging existing rabbit warrens. Setts were located almost everywhere, but badgers preferred easily dug, well-drained soils with good vegetation cover within foraging habitats. A logistic regression model showed that badgers select sites with high surrounding shrub density, large shrubs covering the burrow and close to the centre of the territory (in Mediterranean scrubland habitat). The small size of badger setts in Coto del Rey is common to other low density areas, and probably relates to the extent of use (i.e. age of the burrows and number of badgers using them) of the burrow system. The number of setts per badger territory is related positively to territory size. The similarity of sett densities between this low density population and high density populations, points to a minimum number of setts being required to maximize territory use, and to offer easily-available protection. The preservation and improvement of Mediterranean scrubland vegetation, as well as of large and old shrubs, are important for the future conservation of the badger in Mediterranean landscapes. In these areas, and given the impossibility of distinguishing main setts, the estimation of absolute densities in population surveys using main sett numbers should be avoided in favour of relative indices of abundance.

**Key words:** *Meles meles*, shelter location, burrow, Mediterranean areas

## INTRODUCTION

The status of the Eurasian badger *Meles meles* L. is insufficiently known in Spain and it is suspected of being endangered, vulnerable or rare (Blanco & González, 1992). The limited information available indicates that the species is rare and declining in some regions (Virgós, 1994). Concern for the conservation of Mediterranean populations of badgers extends to other countries, notably Turkey, Greece, Italy and Portugal (from which there is also no information on population trends or status) and to the endangered endemic Cretan and Rhodian subspecies (Griffiths & Thomas, 1997). Further research on habitat preferences, distribution, population status and trends are strongly advised as being one of the most important conservation and

management actions for the species in Mediterranean countries (Griffiths & Thomas, 1997).

The situation in high density populations of badgers in central Europe and Britain is more hopeful, and here there is no general concern for the future of the species. In these high density populations badgers live in groups, each of which has a communal territory, and the setts can be categorized into main, annexe, subsidiary or outlier. Main setts are large, complex systems with five or more burrow entrances, which individuals of the group use throughout the year and where breeding occurs (Kruuk, 1989; Woodroffe & Macdonald, 1993). There is typically only one main sett per territory, plus a few other burrows of the other types positioned throughout the territory (Kruuk, 1978; Bock, 1986; Thornton, 1988; Roper & Christian, 1992). This sett-centred system has been interpreted as influencing badger behaviour and ecology in many ways, e.g. limiting the distribution of the species to areas where there are suitable soils (Dunwell & Killingley, 1969;

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Harris, 1984; Bock, 1988; Skinner, Skinner & Harris, 1991a), determining the shape and size of territories (Doncaster & Woodroffe, 1993), limiting the number of breeding females per territory (Cresswell *et al.*, 1992; Woodroffe & Macdonald, 1995), and even controlling the number of individuals per social group (Roper, 1992b). Thus, main setts are seen as an important resource for badger survival, maintenance of badger social behaviour, and even as the major evolutionary force of badger sociality (Neal & Roper, 1991; Roper, 1992b; Roper, 1993). This view is frequently regarded as typical for the species, but most information on badger sett characteristics and selection comes solely from high density populations (but see Kruuk, 1989; Broseth, Bevanger & Knutsen, 1997; Feroe & Montgomery, 1999) which, in turn, occupy only a small fraction of the species' large geographical range.

The fact that there is only one main sett per group in high density populations has led to the development of techniques for estimating badger distribution patterns, numbers of groups and individuals, and population trends – all of which are essential to the species' appropriate management and conservation (e.g. Cresswell, Harris & Jefferies, 1990; Reason, Harris & Cresswell, 1993; Smal, 1993; Macdonald, Mitchelmore & Bacon, 1996). The main assumption of these methods is that main setts are distinguished in the field (mostly using only their overt characteristics), and sometimes with little previous knowledge on long-term site use and occupant behaviour. However, the applicability of these methodologies to low density badger populations has not been validated in other environments (Feroe & Montgomery, 1999).

In order to improve our understanding of the role of setts in the ecology of badgers, define the factors that may limit the presence of setts (and thus of badgers) in Mediterranean habitats and their usefulness as sampling units in population surveys, we studied the sett characteristics and site selection of badgers in a low density, Mediterranean population. We also analysed the factors that determine sett location in relation to territory outlines, soil type and vegetation structure, and discuss our findings in relation to the preferences described for high density populations, as well as the conservation implications of our results.

## MATERIALS AND METHODS

### Study area and badger population

The study area is situated in Coto del Rey, in the north of the Doñana National Park (Fernández-Delgado, 1997; Revilla, Palomares & Delibes, 2000, 2001), south-western Spain. The area covered by the study, about 42 km<sup>2</sup> (defined as the minimum convex polygon encompassing all radiolocations of marked badgers, see below), is flat, with a maximum elevation of 8 m asl, and with a maximum slope of 0.25%. The landscape is composed of a core of Mediterranean scrubland, which

is dominated by large mastic shrubs *Pistacia lentiscus* and scattered cork oak *Quercus suber*, with a high ground cover of *Halimium halimifolium*. There are two bands of ash-stands running from north to south along small streams, where ash *Fraxinus angustifolia*, cork oak, wild olive *Olea europaea*, and white poplar *Populus alba*, form the important tree stratum, and mastic, brambles *Rubus* spp., and tamarisk *Tamarix africana*, are the main shrubs. This core is delimited by plantations of pine *Pinus pinea* and eucalyptus *Eucalyptus* sp. to the north, and by marshland and pastureland to the west, east and south. There is also a large patch of dehesa (a sort of Mediterranean savanna) composed of meadows with scattered cork oak. For more details see Revilla *et al.* (2000). Rabbits *Oryctolagus cuniculus* are abundant throughout the study area, but particularly in Mediterranean scrubland (Palomares, Calzada & Revilla, 1996).

The badgers of Coto del Rey live at low densities (0.67 badgers/km<sup>2</sup>, without considering yearlings, Revilla *et al.*, 1999). They form stable territorial groups composed of a dominant breeding pair and a few subordinates, with territory sizes between 1 and 8 km<sup>2</sup> (Revilla, 1998; Revilla & Palomares, 2001). The population consisted of three groups until 1996, when the easternmost territory broke up into two new ones. Badgers were captured, anaesthetized, individually marked 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 (Cheeseman & Mallinson, 1980; Travaini *et al.*, 1994; Revilla, 1998). Between November 1994 and October 1997 we radio-marked an annual mean of 71.3% ± 13.78 of the entire estimated badger population (Revilla, 1998), which represented a total of 14 marked individuals (considering only those badgers established in permanent territories). We obtained 2770 diurnal radiolocations of these marked animals (considering only one location per animal per day). For more details on the methods used see Revilla & Palomares (2001).

### Sett description

We define the sett as any den or burrow used by badgers as a diurnal resting site. These refuges were found by locating radiomarked badgers on a daily basis, following standard homing practice (see Mech, 1986). Each newly located sett was tagged with an identifying plastic label. Most of the setts found during the first year (i.e. between November 1994 and October 1995) were visited and described during the last 3 weeks of October 1995, and will be referred to as sampled setts. In order to avoid any disturbance, this visit was conducted when no marked badgers were inside. At each sett we counted and measured all entrances (including those assigned to rabbits), distinguishing between active (clean and open), inactive (with cobwebs and vegetation, but without structural modifications), and collapsed

(those with structural modifications) entrances. We also measured the distance to the nearest sett entrance (between badger entrances only). The type of soil, the size of the shrub (if any) under which each sett lay, and the sett's distance from the centre of the territory (see below) were also recorded. Using a 50 m radius circle centred on each sampled sett, we estimated the proportions of tree, shrub and scrub cover by the use of printed patterns of known proportion (Palomares, 2001).

We compared the number of entrances of setts found in Mediterranean scrubland with the number of entrances in a group of 828 rabbit warrens we had mapped during summer 1995 in the same habitat. Soil types were described as sandy (easy to dig), hard-sandy (which produces compact clods when dug), and clayey. Soils are mainly sandy in Mediterranean scrubland, sandy to hard-sandy in dehesa, hard-sandy to clayey along streams, and clayey in marshland. Soil availability was assigned following Castroviejo (1993) and Siljeström *et al.* (1994) and through field validation. Territory outlines were defined, following Revilla (1998), as the 95% fixed kernel isoline, core areas as the 70% fixed kernel isoline, and territory centres as the harmonic mean of all independent radiolocations (including both active and resting periods).

### Analysis

Data are presented as means  $\pm$  1 standard error, unless otherwise stated; the standard statistical tests used are indicated throughout the text. We used a logistic regression model to determine the effect of several microhabitat and location variables on a binary dependent variable: sett presence. Following Revilla *et al.* (2000) we considered only those setts found in Mediterranean scrubland and ash stands. As a non-selected sample we used information obtained at 100 random points generated in these 2 habitats exclusively (points were found with the aid of a GPS). We considered random points as places non-selected by badgers (i.e. non-occurrences), whilst sampled setts in Mediterranean scrubland and ash stands were considered to be positive or badger selected places (i.e. occurrences). As the badger population had been under an intensive radiotracking control, with daily locations, it is improbable that the random points could be part of the occurrences, and so we considered them to offer a good approximation of non-occurrences. As independent variables we used tree, shrub, and scrub cover around both kinds of points, an index of the size of the shrub under which the setts or the random points were (calculated as the product of the maximum and minimum axes, in metres – if there was no shrub, the value was set to zero), and the distance (in metres) to the territory centre (random points were considered to belong to the nearest centre). The correlation between these variables was weak, varying between 0.16 and 0.43. The model was fitted as a stepwise forward

logistic regression (using the SAS LOGISTIC procedure; SAS Institute, 1990). Goodness of fit was evaluated using  $-2$  log likelihood, which has a chi-squared distribution under the null hypothesis (i.e. all the explanatory variables in the model are zero), and based on the predicted and observed associated probabilities for each case (SAS Institute, 1990). The predictive ability of the model was assessed by the association of predicted probabilities and observed responses (SAS Institute, 1990). The Akaike Information Criterion (AIC) was used to evaluate between submodels of the stepwise procedure, given its ability to detect the most parsimonious of the alternative models (it relates statistical significance with the number of responses and explanatory variables; SAS Institute, 1990). We used 0.1 as the probability criterion for the inclusion of a variable in the model during the stepwise procedure whenever the coefficient of the variables differed from zero (Tabachnick & Fidell, 1996). Given the adequate sample size for both possible responses, which ensured sufficient statistical power, explanatory variables were not transformed (Tabachnick & Fidell, 1996).

## RESULTS

We located 118 badger setts between November 1994 and September 1997, giving sett densities of 2.84 setts/km<sup>2</sup> in the entire study area, and 7.19 setts/km<sup>2</sup> for the area occupied by territory isolines. Sett locations were based on an average effort of 23.5 radiolocations per sett. We found badger latrines in the proximity of 68.6% of the setts. During the first year, we found 83 different setts and visited and described 77 of these (i.e. the sampled setts).

### Sett characteristics

Badger setts were situated in a variety of places, such as inside hollow trees or under concrete constructions. However, most of them (78% of the sampled setts) were totally or partially covered by shrubby vegetation, mainly by large mastic shrubs (with axes of  $17.9 \pm 7.87$  m per  $18.2 \pm 10.35$  m, and  $3.4 \pm 0.69$  m in height). The proportion of setts and rabbit warrens covered by shrubs in Mediterranean scrubland habitat was not significantly different (84.7% and 78.3%, respectively,  $\chi^2 = 1.52$ ,  $df = 1$  with Yates' Correction,  $P = 0.217$ ). Three of the sampled setts were overground shelters located inside dense brambles, two were inside hollow ash trees, and the remainder were underground burrows. The majority of underground setts had between one and four badger entrances (Fig. 1), but those with more entrances were rare (10.5%). The average number of badger entrances per sett was  $2.62 \pm 1.79$  (Table 1); while 82.4% of the sampled setts also had rabbit entrances. Badger setts located in Mediterranean scrubland had a larger number of total

**Table 1.** Mean number  $\pm$  SD of entrances per sett used by badgers (*Meles meles*) in Coto del Rey, Doñana National Park, Spain. Totals do not include collapsed entrances. Range and modes (in brackets) of entrance height and width are also given

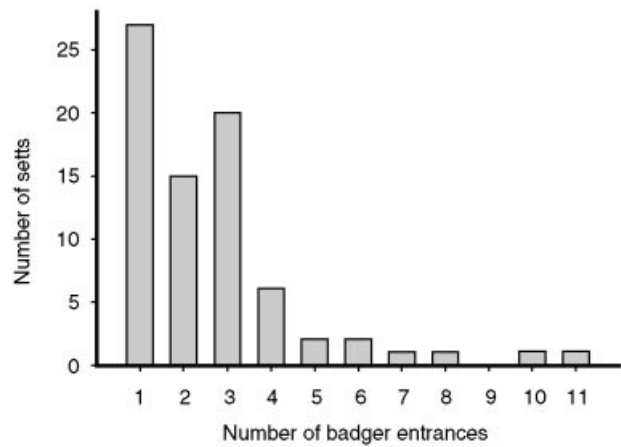
Types of entrances	Mean number of entrances	Entrance height (cm)	Entrance width (cm)
Badger active	0.85 $\pm$ 1.10	22.6 $\pm$ 5.48 11–48 (22)	29.5 $\pm$ 7.46 14–54 (23)
Badger inactive	1.27 $\pm$ 1.39	–	–
Badger total	2.4 $\pm$ 1.79	–	–
Badger collapsed	0.22 $\pm$ 0.60	–	–
Rabbit active	3.23 $\pm$ 3.27	15.2 $\pm$ 4.04 8–32 (11)	15.4 $\pm$ 4.70 8–40 (13.5)
Rabbit inactive	7.00 $\pm$ 13.21	–	–
Rabbit total	8.10 $\pm$ 15.46	–	–
Rabbit collapsed	3.10 $\pm$ 2.66	–	–

entrances than did rabbit warrens in the same habitat (8.88, SD = 14.59,  $n = 69$ ; and 5.96, SD = 5.53,  $n = 828$ , respectively;  $t = 3.496$ ,  $df = 895$ ,  $P < 0.001$ ). However, the mean number of rabbit entrances at setts (6.29, SD = 14.66,  $n = 69$ ) was not significantly different from that found in rabbit warrens ( $t = 0.394$ ,  $df = 895$ ,  $P = 0.693$ ). The aspect of badger entrances (34.1% facing north, 27.1% facing east, 22.5% facing south and 14% facing west) was significantly different from a random orientation ( $\chi^2 = 8.87$ ,  $df = 3$ ,  $P < 0.05$ ), whilst the orientation of rabbit entrances showed no deviation from random ( $\chi^2 = 6.93$ ,  $df = 3$ ,  $P > 0.05$ ). The average distance between badger entrances in the same sett was  $4.78 \pm 2.29$  m.

We determined the presence of signs of badger activity at 74 of the sampled setts. Radio-marked badgers used a total of 24 setts during the 2 weeks previous to sampling, which represents 32.4% of the sampled setts. Active badger entrances were present at all setts used by the marked animals and at 44% of the non-used setts. We did not consider active entrances to be a good indicator of sett use, given the difficulty of knowing which species keeps them active (e.g. unmarked badgers, rabbits, foxes *Vulpes vulpes*, or Egyptian mongooses *Herpestes ichneumon*; Palomares, 1991; Neal & Cheeseman, 1996). A total of 26 setts had other signs of activity (recent tracks, faeces, bedding materials and/or evidence of digging) which gave a better approximation of the number of setts used by the badgers.

**Table 2.** Vegetation characteristics within a radius of 50 m centred at badger setts in Coto del Rey, Doñana National Park, Spain

	Percentage of setts with cover > 0%	Mean cover $\pm$ SD	Range (%)	Dominant species
Tree cover	27.0	9.17 $\pm$ 3.24	3–15	<i>Quercus suber</i> , <i>Fraxinus angustifolia</i> , <i>Olea europaea</i>
Shrub cover	70.0	31.4 $\pm$ 23.7	2–90	<i>Pistacia lentiscus</i> , <i>Phillyrea angustifolia</i> , <i>Rubus</i> spp.
Scrub cover	81.8	15.5 $\pm$ 18.8	1–80	<i>Halimium halimifolium</i> , <i>Cistus</i> spp., <i>Chamaerops humilis</i>



**Fig. 1.** Number of setts with different numbers of badger entrances, considering both active and inactive (but not collapsed ones) in Coto del Rey, Doñana National Park, Spain.

### Sett location

Most of the sampled setts were located on sandy soils (80.3%) with only a few being in hard-sandy or clayey soils (11.8% and 7.9%, respectively). The observed proportions of use were significantly different from availability of soil types throughout the study area ( $\chi^2 = 74.32$ ,  $df = 2$ ,  $P < 0.0001$ ). This was due to most setts being in soft sands as opposed to clayey soils.

The majority of setts (72.4%) were located in Mediterranean scrubland. In addition, 8.9% were in ash stands, 7.3% in pasturelands and meadows, 6.5% in dehesas, 4.1% in marshland and only 0.8% inside pine plantations. These observed frequencies were significantly different from those expected, based on the availability of habitats within the study area ( $\chi^2 = 415.67$ ,  $df = 5$ ,  $P < 0.0001$ ). Mediterranean scrubland and ash stands held many more dens than expected, while other habitats had fewer than expected. Most of the setts were surrounded by dense vegetation, 70% by shrubby and 81.8% by scrubby vegetation (Table 2).

The average number of setts used per territory was  $27.0 \pm 6.30$  (range 9–41). There was a positive relationship between this number and territory size ( $r^2 = 0.733$ ,  $F = 11.99$ ,  $df = 1, 3$ ,  $P = 0.04$ ). On average only  $1.4 \pm 0.75$  setts were located outside territory outlines, whilst  $8.0 \pm 1.64$  were situated inside territories but outside core areas. Core areas held a significantly larger number of setts than expected on the basis of their size ( $17.8 \pm 9.26$ ;  $\chi^2 = 103.67$ ,  $df = 4$ ,  $P < 0.0001$ ; Fig. 2).

**Table 3.** Summary of the stepwise forward procedure for the logistic regression on the influence of tree, scrub, and shrub cover, the size of the shrub covering the sett (axis index) and distance to territory centre on setts located in Mediterranean scrubland and ash stands.  $-2\text{Log}$  likelihood is the value of the fitted incomplete model. Wald  $\chi^2$  refers to the entered or removed variable from the model

Step	Variable Entered	Variable removed	$-2\text{Log}$ Likelihood	d.f	$P$	Wald $\chi^2$	$P$	AIC <sup>b</sup>
0 <sup>a</sup>	–	–	230.57	–	< 0.0001	–	–	–
1	Tree cover	–	52.63	1	0.0001	25.41	0.0001	180
2	Scrub cover	–	62.82	2	0.0001	9.22	0.002	172
3	Axis index	–	87.64	3	0.0001	13.42	0.0002	149
4	–	Scrub cover	85.07	2	0.0001	2.47	0.1153	149
5	Distance to territory centre	–	94.62	3	0.0001	8.83	0.0030	142
6	Shrub cover	–	99.93	4	0.0001	4.76	0.0291	139

<sup>a</sup> Null model, represented by the intercept only model

<sup>b</sup> Akaike Information Criterion –AIC, lower values indicate a more parsimonious model

**Table 4.** Parameter values and their standard error, Wald  $\chi^2$  and associated probabilities and odd ratio of variables included in the final logistic model predicting the probability of sett occurrence at Mediterranean scrubland and ash stands in Coto del Rey, Doñana National Park, Spain

	Parameter	Standard error	Wald $\chi^2$	$P$	Odd Ratio
Intercept	–2.502	0.7006	12.75	0.0004	–
Distance to territory centre	0.002	0.0005	11.15	0.0008	1.002
Tree cover	–0.200	0.0439	20.79	0.0001	0.819
Shrub cover	0.029	0.0135	4.76	0.0291	1.030
Axis index	0.010	0.0022	19.88	0.0001	1.010

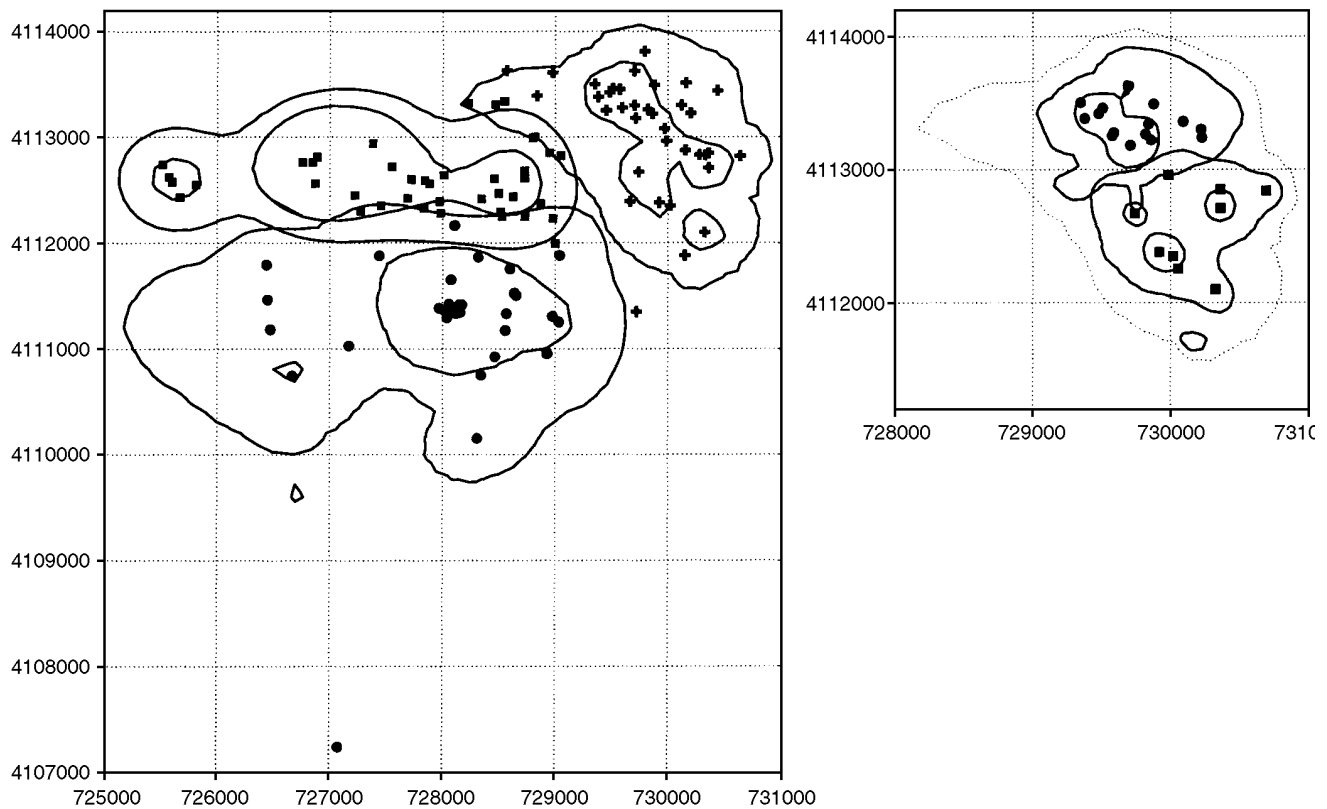
The following variables were included in the final logistic model for sett selection inside Mediterranean scrubland and ash stands ( $\chi^2_{(-2\log L)} = 99.93$ ,  $df = 4$ ,  $P = 0.0001$ ): distance to territory centre, tree and shrub cover, and the size-index of the shrub covering the sett (Tables 3 and 4). All these variables positively affected the probability of selection by badgers, except for tree cover, which had a negative effect (Table 4). The scrub cover around setts was the only variable left outside the model (Table 3). The highest probabilities of sett presence are found in places with low tree cover, high shrub cover in the 50 m surrounding radius, a large shrubby plant covering the burrow itself and in the proximity to the centre of the territory. The association of the predicted probabilities of the final model for the observed responses were 91.2% concordant, 8.8% discordant and 0.1% tied.

## DISCUSSION

Badger dens mostly have been studied within high density populations. As a result, descriptions in the literature distinguish between main setts and other types of sett, notably ‘annexes’, ‘subsidiaries’, and ‘outliers’, depending on the usage of particular authors

(Kruuk, 1978; Thornton, 1988; Cresswell *et al.*, 1990; Roper & Christian, 1992). In general, the setts used by the Doñana badgers were small, with only eight recorded setts having five or more entrances; the largest sett found had fewer entrances than the average main sett in England (Cresswell *et al.*, 1990). This small size also occurs in other medium and low density populations, as in Norway (Broseth *et al.*, 1997), Essex county in England (Skinner, Skinner & Harris, 1991b), the Alpine zone of the Bavarian Alps (Bock, 1986) and Scotland (Kruuk, 1989). None of the setts found in our study area was used all year round with only 30% of radiolocations on average coming from the most-used sett in each territory (Revilla, 1998). Births can occur at different setts in consecutive years within the same territory (Revilla, 1998). Thus, in our study area it is impossible to distinguish between main setts and other types, as found by Feroe & Montgomery (1999) and Virgós & Casanovas (1999) in other low density areas.

Nevertheless, why do badgers in low density areas not construct larger setts? Some of the proposed adaptive advantages of large setts also can be achieved with more, but smaller, burrows, notably defence from predators and reduced exposure to ectoparasites (Roper, 1992a; Butler & Roper, 1996). Shelter from bad weather conditions (such as the extreme summer temperatures typical of south-western Spain) can easily be avoided in small underground burrows, particularly below a large shrub (Fernández & Palomares, 2000). Another stated advantage of living in large setts is the greater probability of reproduction for more females of the group due to reduced intraspecific interference (Roper, 1992b; Stewart, Bonesi & Macdonald, 1999). Also it may be that by having many widely dispersed setts, interference would be less likely (Cresswell *et al.*, 1992). Thus the only reason remaining for having one large sett instead of several small ones is that the most-used setts (i.e. older ones) are larger. If badgers living in small territories need fewer setts these would be more frequently used, and so setts would tend to be larger because the amount of work invested in their maintenance and digging would be larger (see Ostler & Roper, 1998; Stewart *et al.*, 1999).



**Fig. 2.** Spatial position of setts located between November 1994 and September 1997 at territories (outer isolines) and core areas (inner isolines), defined respectively as 95% and 70% fixed kernel isolines. The eastern-most territory of the left figure broke into two new territories in 1996 (represented on the right). In both graphs the setts of every territory are represented by different symbols. Co-ordinates are UTM (in metres), and grid represents cells of 1 km<sup>2</sup>.

Badgers located setts in a wide variety of places – almost everywhere, including areas with hard soil, without cover, or with a high water table (e.g. the marshland). Furthermore, sett sites included underground burrows, hollow trees, concrete constructions or brambles. But even with this variability there is a pattern of selection following an order of priorities, which gives a good picture of the places preferred by badgers for locating their setts. The first step is given by the sort of soils: badgers have a strong preference for friable, easy-to-dig soils. These in turn do not flood during the winter; as already shown for other populations (e.g. Dunwell & Killingley, 1969; Harris, 1984; Neal & Roper, 1991). This soil requisite is fulfilled in Mediterranean scrubland and pine plantations and partially so in ash stands. In Mediterranean scrubland and ash stands there is a high density of rabbit warrens (11.5 warrens per ha in the first habitat; Palomares *et al.*, 1996; Revilla *et al.*, 2000); probably because rabbits have similar soil requirements to badgers (Rogers & Myers, 1979; Kolb, 1991; Palomares *et al.*, 1996). Given that most of the setts had rabbit entrances, it seems that badgers use rabbit warrens as initial ‘seeds’ during the construction of their new setts (Neal & Cheeseman, 1996). On several occasions, we observed different badgers enlarging pre-existing warrens where, in turn, they slept the following day. Many of the setts con-

tinued to contain rabbits, even when they were used simultaneously by badgers. Both the preference for easily dug soils and the use of pre-existent rabbit warrens can be interpreted as a behavioural response for conserving energy when digging a new sett.

The second factor that, on a large scale, influenced badger sett selection was habitat: they built setts preferentially in Mediterranean scrubland and ash stands but not in pine plantations, despite their favourable soil composition. In this case, the protection offered by vegetation cover can be seen as one of the main reasons for the preference (pine plantations have no undergrowth). However, it is also possible that this habitat preference is simply a result of the spatial location of trophic resources (mostly rabbits and fruits), because sett location at these habitats could reflect the best way of saving energy when travelling to the foraging grounds.

We conducted the logistic regression using only setts found in Mediterranean scrubland and ash stands, which had more setts than expected. Tree cover surrounding the sett was the variable with the strongest influence on the probability of selection, affecting it in a negative way. Ash stands have a higher tree cover density than Mediterranean scrubland, so the negative effect on the probability of site selection may be related to its harder soil and the higher frequency of flooding

during winter. The role of this variable is also evident in a significantly lower use of setts located in ash stands, as shown by Revilla *et al.* (2000). Shrub cover was the following variable in importance with a positive effect, with badgers showing a preference for sites with a higher surrounding shrub density. Shrubs covering the sett itself were also important. The larger the 'umbrella shrub' the larger the probability of being selected. This result again points to the need for protective cover both around and over the sett (Thornton, 1988; Neal & Roper, 1991; Skinner *et al.*, 1991a; Macdonald *et al.*, 1996). This variable is also important in a highly protected national park such as Doñana, where the disturbance of setts by people is expected to be low. Apart from the protection that it gives, building a burrow beneath a large mastic bush has two other advantages. The strong roots can consolidate the soft sandy soil and thus reduce the risk of collapse for chambers and tunnels, and also provides a buffer effect on microclimatic conditions over the burrow (Fernández & Palomares, 2000).

The last important variable was distance to the centre of the territory, with the probability of selection being higher closer to the centre. Its importance is in agreement with the unequal distribution of setts in territories (sett density is higher in core areas). Territory centres are situated at the core of the Mediterranean scrubland within each territory, which on the other hand is the most important foraging habitat (Revilla *et al.*, 2000). This spatial configuration can be expected as an energetic maximization of territory because the centre of the territory is the point closer to all the foraging grounds. If this interpretation holds true, in large territories, where the energy required for travelling to foraging increases, badgers would also need other scattered setts, as is the case in Coto del Rey.

To the best of our knowledge, the Doñana case, with an average of 27 setts, is the largest average number of setts per territory recorded to date. Kruuk (1989) comments that in Ardnish Peninsula, Scotland, badgers used a large number of small 'refuges', whilst in Norway, Broseth *et al.* (1997) found an average of 12 setts per territory. Thus, despite the large differences in environmental conditions between these populations, there seems to be more setts in larger territories. This relationship is confirmed by a significant correlation in Doñana between sett number and territory size. Using the regression function obtained, we could predict that, for example, a badger territory of 50 ha, as in Wytham Wood (Kruuk, 1978), should have seven different setts. This value is close to the observed number of 5.3 setts per territory (Kruuk, 1978). In another high density population, in east Offaly, Ireland (O'Corry-Crowe, Eves & Hayden, 1993), the result predicted again is slightly larger than that observed. This slight overestimation can result from several factors: there are more suitable places to build setts in Doñana, where we made a large effort to find the majority of the dens used in our study population (attained with the aid of the radio-tracking of an important fraction of the population, and

with locations recorded every day), and/or it could be due to the different environmental conditions of those populations. Sett density in Coto del Rey is not far from that in Wytham Wood or east Offaly (6.48 and 3.63 setts/km<sup>2</sup>, respectively) or, at least, the difference is not on the same scale as the large variation between territory sizes. As already stated, effective exploitation of a large territory can be achieved with many scattered setts, which may allow badgers to reduce the energetic costs of travelling long distances when feeding in areas far from the centre of the territory and also reduce the risk of predation. A few small setts can be very important for the survival of badgers when they are under high predation pressure (as could happen with poachers, wolves *Canis lupus*, or packs of feral dogs, e.g. Revilla *et al.*, 2001). In any case, the extent of the relationship between territory size and number of setts should be further investigated in other low density areas.

Mediterranean scrubland is the key habitat for the location of badger setts in this Mediterranean area. Large, old shrubs, such as mastic, which can cover more than 100 m<sup>2</sup>, grow very slowly (several hundred years), making recovery very difficult after loss. Extensive afforestation historically has replaced Mediterranean woods and scrubland by plantations of eucalyptus and pine in which the shrub layer is virtually absent or periodically removed. The main reasons argued for this systematic shrub elimination are to reduce the probability of fire, to increase pasture for cattle and wild ungulates, and to increase timber production. Regionally, scrubland is also being eliminated in the Doñana area and replaced by intensive crops of strawberries. Scrubland is classified as non-productive agricultural land and thus being replaced by quick-growing trees (mainly conifers). This is presently the case in Spain and Portugal (Delibes, Rodríguez & Ferreras, 1999). These afforestation programs, as well as many of the associated activities, are financed by the European Union. Paradoxically, their aim is to promote the conservation of endangered species such as the Iberian lynx *Lynx pardinus* which depends also on the conservation of this habitat (Rodríguez & Delibes, 1992; Delibes *et al.*, 1999, Palomares, 2001). The elimination of these vegetation types should be avoided or, when this is impossible, alternative treatments should be considered such as the sett-aside of several hectare patches, and to allow the development of undergrowth in pine plantations.

The spatial distribution and status of badger main setts has been used successfully to survey distributions, and to estimate absolute abundances and population trends in high density badger populations. Our results point to the unsuitability of this technique in Mediterranean habitats and, probably, also in other low density areas (e.g. Feroe & Montgomery, 1999). The consideration of active burrows with five or more entrances as main setts in our study area would have led to the overestimation of the number of territories present (eight – double the number existing in 1994, 1995 and 1997). In Mediterranean environments, any survey should avoid trying to estimate the absolute abundance

of badgers from the number of 'large burrows'. A more conservative approach should be used, whereby the presence of signs of activity such as faeces and tracks, either alone or at burrows, would be an equally useful estimation of the relative abundance of badgers. A similar approach has been suggested for high density populations, when only a single sampling can be conducted because of the difficulty of distinguishing main setts using only their structural characteristics (Wiertz, 1993).

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