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► **To cite this version:**

G. Molina-Vacas, V. Bonet-Arbolí, E. Rafa Rt-Plaza, J. D. Rodríguez-Teijeiro. SPATIAL ECOLOGY of EurOPEAN badgers (MELES MELES) in Mediterranean habitats of the North -Eastern Iberian Peninsula. I: Home range size, spatial distribution AND SOCIAL ORGANIZATION. *Vie et Milieu / Life & Environment*, 2009, pp.223-232. hal-03253721

HAL Id: hal-03253721

<https://hal.sorbonne-universite.fr/hal-03253721v1>

Submitted on 8 Jun 2021

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SPATIAL ECOLOGY OF EUROPEAN BADGERS (*MELES MELES*) IN MEDITERRANEAN HABITATS OF THE NORTH-EASTERN IBERIAN PENINSULA. I: HOME RANGE SIZE, SPATIAL DISTRIBUTION AND SOCIAL ORGANIZATION

G. MOLINA-VACAS*, V. BONET-ARBOLÍ, E. RAFART-PLAZA, J. D. RODRÍGUEZ-TEIJEIRO

Animal Biology Department, Universitat de Barcelona, 645 Avenue Diagonal, 08028 Barcelona, Spain

* Corresponding author: guillemolina@ub.edu

EUROPEAN BADGER
IBERIAN PENINSULA
MEDITERRANEAN HABITATS
MELES MELES
SOCIAL ORGANIZATION
SPATIAL ECOLOGY
HOME RANGE SIZE

ABSTRACT. – Although there are some radio-telemetry studies on badger spatial organization in sub-humid Mediterranean lowlands, cork oak woods and Atlantic highland forest (in the South, West and North of the Iberian Peninsula respectively), the present study is the first carried out in the Mediterranean forests of the NE Iberian Peninsula in the parks of Collserola and Montserrat, close to Barcelona. The home range of 13 adult badgers (6 males and 7 females) was examined with the aim of providing results to compare with previous studies in order to advance in the understanding of badger social organization with special regard to low density populations in Mediterranean environments. Mean home range size was $307.6 \text{ ha} \pm 96.4$ (\pm SE) and $72.8 \text{ ha} \pm 15.1$ for males and females respectively for MCP95 and 287.4 ± 79.1 and 85.1 ± 26.6 for FK95 with differences between Parks. In addition, the home ranges of Collserola males were over four times larger than those of females, while for Montserrat this figure was 1.5. Moreover, badger groups were formed by one to three individuals in Collserola, and at least three individuals in Montserrat. This discrepancy points to a distinct social organization associated with differences in population densities (0.6 ind./km^2 in Collserola and 1.9 ind./km^2 in Montserrat) and landscape structure conditions. Our results suggest that the home range configuration of males is driven by female distribution in space.

INTRODUCTION

The European badger (*Meles meles*) shows large intraspecific variation in social organization which is understood to reflect ecological, demographic and behavioral plasticity (Palphramand *et al.* 2007). Populations throughout Europe present a two-order of magnitude variation in density, which parallels considerable variation in social spacing. Population density varies from less than one ind./km^2 in Poland (Kowalczyk *et al.* 2000) and the South of Spain (Revilla & Palomares 2002), to over 38 ind./km^2 in some areas of Britain (Johnson *et al.* 2002). In brief, low density populations are found at the northern (e.g. Broseth *et al.* 1997) and southern (e.g. Revilla & Palomares 2002) edges of its distribution range while higher densities occur at medium latitudes, reaching a maximum in the British Isles and Ireland (see review in Johnson *et al.* 2002). In general terms, it seems that badger population density is higher in environments with minor differences between seasonal characteristics (i.e. temperature, rain, etc.) compared to more variable ones. Associated with this, the spatial distribution of individuals within populations is highly variable. In low density populations, groups are usually composed of one (Pigozzi 1987) to 3 individuals (Do Linh San *et al.* 2007a, Revilla *et al.* 2001) and territory size reaches several square kilo-

meters, up to 25 km^2 (Kowalczyk *et al.* 2003). In contrast, in high density populations, groups can include over 25 individuals, including several adults of both sexes (e.g. Rogers *et al.* 1997) and territories rarely reach one square kilometer, being as small as 0.14 km^2 (Cheeseman *et al.* 1981).

The badger has become a model in mammal socio-biology because its plasticity in social organization has been understood as a primitive level of sociality in carnivores (Woodroffe & Macdonald 1993). Sociality in badgers does not seem to be a result of the benefits of cooperative activities, as these have rarely been detected, but rather a result of a resource exploitation strategy. The most persistent ecological theory for the evolution of spatial groups is the *Resource Dispersion Hypothesis* (RDH; Macdonald 1983). In brief, it asserts that, when resources are patchily distributed in space and/or time, the smallest, economically defensible territory able to support its primary holders would usually be rich enough to support additional individuals with little or no cost to the primary holders. Therefore, a benefit is not necessary for spatial groups to develop, or benefits are considered almost negligible. Territoriality is supposed to be an adaptation for the defence of a limiting resource (Woodroffe & Macdonald 1993). Accordingly, different resources have been proposed as the key factors driving badger territoriality,

and their distribution would determine badger spatial organization. In the original form, RDH focuses on food dispersion as the main factor (Macdonald 1983). Doncaster & Woodroffe (1993) argued that the distribution of setts, which are considered a key resource for the species (Roper 1993), rather than food, determines territory size and shape, resulting in territories that are larger than needed in relation to food abundance and, thus, allow more individuals to stay (*Sett Dispersion Hypothesis*, SDH). Finally, the *Anti-kleptogamy Hypothesis* (AKH; Roper *et al.* 1986) proposes that the availability of breeding opportunities is the most important factor in male spatial distribution. Accordingly, territoriality in males would have a mate-guarding function, as also proposed by Revilla & Palomares (2002).

In order to improve our understanding on badger socio-spatial organization in low-density Mediterranean populations, and also in a global context, we studied the home range size, group size and population density of two badger populations of the North-Eastern Iberian Peninsula by means of radio-tracking, den-watching, and camera trapping between 1997 and 2007. The specific objectives of the present investigation were 1) to describe badger socio-spatial organization in our study areas to assess which of the above-mentioned explanatory hypotheses fits best with the obtained results, and 2) to compare our data with other European studies.

MATERIALS AND METHODS

Study areas: The Park of Collserola (41°27'N, 2°6'E) is an 85 km² natural space belonging to the Catalan Coastal Cordillera, which spreads over about 100 km in a North-South direction, parallel to the Mediterranean Sea, roughly 10 km away from the coastline. This space is naturally separated from the rest of the cordillera by the rivers Besòs to the NE and Llobregat to the SW. Its south-eastern limit is formed by the city of Barcelona and the rest of its perimeter is almost closed by a belt of cities and highways except for two narrow corridors to the north. It is basically composed of slates with some granite outcrops on the northern side and calcareous outcrops to the south. Altitude ranges from 50 to 512 m above sea level. Mean annual temperature and rainfall are 14°C and 672 mm respectively, with wide seasonal variations in both factors. Summer is usually the hottest and driest season, whereas spring and autumn are the wettest ones and winters are mild. The inner 80 % of the park surface is covered by dense woodland, largely dominated by the Aleppian pine (*Pinus halepensis*) and the holm oak (*Quercus ilex*), with very dense undergrowth. At the periphery, vegetation mostly consists of Mediterranean scrub patches, basically composed of tree heath (*Erica arborea*) and rock rose (*Cistus* sp.). These peripheral areas hold most of the small amount of agricultural activity remaining inside Collserola (8 % of its area). Even though some areas of Collserola can be classified as sub-urban habitats, most of it retains the features of a wild natural space.

The second study area is located on the southern side of Montserrat Mountain Natural Park and in its agricultural surroundings (41°36'N, 1°48'E), 40 km NW of the city of Barcelona (16 km apart from Collserola Park) with an area of over 50 km². The Montserrat massif shows a particular relief with a columnar appearance. It is formed basically by conglomerates created by alluvial sedimentation. Large alluvial cones were raised by Alpine tectonics which originated the Catalan Pre-coastal Cordillera. Altitude ranges from 250 m to 1224 m. Climate is typically Mediterranean, similar to Collserola, but is drier and hotter on the southern side. Wood and scrub are the dominating vegetation types with the same species as in Collserola Park. This vegetation alternates with croplands: olive crops (*Olea europaea*), vineyards (*Vitis* sp.) and cereal crops. The two populations live in similar habitats, however with the following differences. Montserrat is less woody and more patchy and has a higher proportion of fruit crops relative to cereal crops. In addition, these Parks have notable differences in connectivity levels and human pressure. The badgers in Collserola and Montserrat are considered as separated populations owing to the high level of infrastructures that isolate Collserola from the rest of the surrounding natural habitats.

Badger capture and radio-telemetry: Trapping took place between 1997 and 2006. Badgers were captured with padded leg hold traps (Victor Soft Catch 1.5, Woodstream Corp Lititz, PA) placed on well-used badger paths near setts or latrines, which is the most effective method for capturing badgers in Mediterranean landscapes (Bonet-Arbolí 2003, Loureiro *et al.* 2007, Muñoz-Igualada *et al.* 2008, Rafart-Plaza 2005). Traps were checked and defused every day at dawn to avoid trapping domestic animals, and were activated again at dusk. All the Recommendations of the Animal Welfare Protocol of the European Union were followed and no badger was injured during handling. Badgers were anesthetized by intramuscular injections of combinations of ketamine and xylazine hydrochloride (Kreeger 1997), diazepam or medetomidine (Palphramand *et al.* 2007). Sex, body mass to the nearest 0.1 kg and morphometric measurements were taken. We estimated the age of animals on the basis of tooth wear, body mass and date of capture (Da Silva & Macdonald 1989). Only adults were equipped with a radio-transmitter (TW-5, Biotrack Ltd.). We used a portable VHF receiver (R1000, Communications Specialists Inc.) and a hand-held three element Yagi antenna (Biotrack Ltd.) for radio-tracking data collection. Locations were taken with the triangulation method (White & Garrot 1990), as direct observation was impossible in most badger ranges because of the dense undergrowth of the wood.

The radio-tracking protocol was established as follows. The night (19h00-07h00, in solar time) was divided into four periods of three hours each. Each radio-tracking session consisted of one or two periods, during which we recorded as many locations as possible. We recorded all bearings for each radiolocation within a 10-minute interval to reduce error associated with badger movement and within 45-135° intervals for cross bearings. Exceptions to this were the first night after the release of the ani-

mal and when a particular animal was difficult to find. In these cases, radio-tracking took place for the whole night. Each individual was followed for at least one session every ten days when possible.

Space use analyses: Radio-tracking data and spatial estimators were calculated with Range VII software (South *et al.* 2005). Thirteen out of the 15 monitored badgers had reached home range stabilization according to the *Incremental Area Plot* method (hereafter IAP; Harris *et al.* 1990), which represents the accumulated area used with the increasing number of fixes. Only active locations outside the sett ($n = 640$) of these 13 badgers were used for the analyses. No major changes in the environment were noted during the 10-year study period, so we analyzed all territories irrespective of the year during which data were collected. To avoid problems in home range estimators caused by unequal time intervals between locations we first randomly deleted locations until they were at least one hour apart in the same night-period (De Solla *et al.* 1999). When individual home ranges overlapped with others simultaneously, a Multi-Response Permutation Procedures test (MRPP, Biondini *et al.* 1988) was performed in order to test for significant differences in space use. If significance was not reached, badgers were considered as members of the same group, the home range of which was obtained by merging all fixes. In spite of criticism (Borger *et al.* 2006), the Minimum Convex Polygon (hereafter MCP) is the method employed most frequently in home range studies. However, MCP requires a subjacent uniform distribution of data, and it is therefore not necessarily optimal for comparing data across studies. Otherwise, the Kernel method seems to be a better index for home range description, but it also has the problem that the bandwidth selection method has a great influence on the results, which prevents robust comparisons between studies (Laver & Kelly 2008). Thus, home ranges were estimated using both methods in order to provide better comparability with other studies: Minimum Convex Polygon with 95% of locations (MCP95) and fixed kernel estimator (Worton 1989) with 95% of the utilization distribution (FK95) as recommended by Laver & Kelly (2008). For fixed kernel estimates an optimal smoothing parameter was created for each home range (Kenward *et al.* 2001) by multiplying the smoothing parameter found by the minimum square method (*hcv*) by a correcting factor (Worton 1995, Seaman & Powell 1996, De Solla *et al.* 1999). This factor was searched, by trial and error, at 0.01 intervals starting from 1 *hcv* and was accepted when K95 was the smallest range that allowed a single shape as a home range (avoiding unconnected patches) as expected for territorial species like the badger (Blundell *et al.* 2001, Borger *et al.* 2006, Hodder *et al.* 1998). Comparisons between sexes and areas concerning mean values of home range estimators (MCP and FK, Table I) were conducted with the Mann-Whitney test using SPSS 15 for Windows (SPSS, Chicago, IL). We obtained similar results for both estimators, so in the text we only show the results of FK to avoid redundant data.

Group size and population density: Group size was estimated

in a systematic way for a wooded area of Collserola only, whereas a coarser estimation was obtained for Montserrat. The procedure for the calculation of group size was based on the simultaneous monitoring of all known setts in each home range on a given night. Badgers were very suspicious and shy, and our previous experience showed that, in most cases, they would not come out of a sett if humans were around. In addition, each individual used between at least three and ten setts during their tracking period (Bonet-Arbolí 2003), so a lot of people would be required to simultaneously watch all setts at night. Therefore sett monitoring was performed by sign surveys during two consecutive mornings in order to ascertain which setts had been used by badgers on a given night and in a given range. The sett watching procedure usually extends for three consecutive nights in order to deal with the possibility of badgers occasionally sleeping away from their usual setts. In our case, we decided to perform the censuses over several non-consecutive nights in the course of one year (07/1998-07/1999) in each territory because, although a clear seasonal pattern of sett use exists in Collserola (Bonet-Arbolí *et al.* 2005), badgers frequently, and unpredictably, move away from their favorite setts for several consecutive days within seasons. This monitoring schedule was also useful to dilute the effect that transients visiting a given range for a few days (particularly males, see results) would have on the overestimation of group size in such a low density population. Therefore, results are given as the mean number of individual \pm standard error across monitoring sessions, in each home range. Censuses started when the limits of each monitored range had been established by means of radio-tracking, and sometimes extended beyond the death of the tracked individual.

The estimation of the number of badgers based on the number of active setts requires knowledge of all setts in a range. Besides the discovery of new setts thanks to the radio-tracking of badgers, a systematic survey (1992-1995) conducted in an area (*A*) of approximately 400 ha before the beginning of the trapping period allowed us to find several setts of interest for that purpose, because *A* was later partially included in three adjacent badger ranges. The area of *A* represented 65 % of the home range of F5 + F6, 20 % of the home range of M7 and 96 % of the home range of F9 (Fig. 1). Sett surveys are highly time-consuming in Collserola owing to the roughness of the landscape and the thickness of the vegetation such that it would have been impossible to complete the survey of each territory within the study period. Therefore we used the number of setts (*S*) found inside *A* during that previous survey to extrapolate the total number of setts (S_{tot}) in each range. All setts were visited several times during the study period and those that were clearly abandoned by badgers were discarded for the subsequent calculations. In order to take into account those setts that would have gone unnoticed during the survey, together with those built since then, we calculated the survey efficiency from the number of setts that the tracked individuals used within *A* and which were already known from the previous survey. This figure was 75 % (i.e. in 1992-1995 we found three out of every four setts present in the surveyed area of Collserola at the time of radio-tracking). Therefore, $S_{tot} = [(S/0.75)/A(\text{ha})] * K95(\text{ha}) + \text{outliers}$.

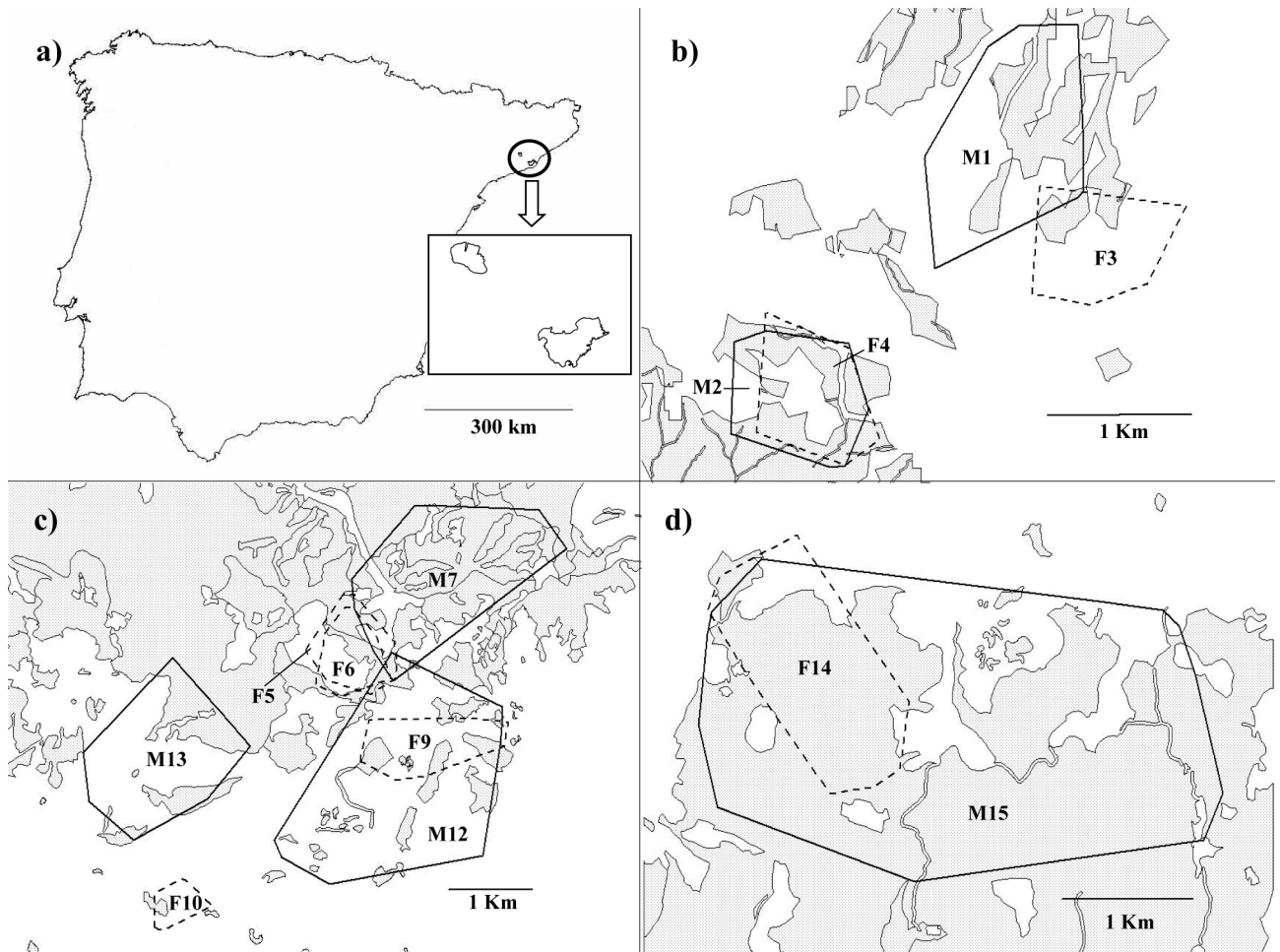


Fig. 1. – a, Location of study areas in the Iberian Peninsula (Montserrat Mountain Park in the upper left corner and Collserola in the bottom right corner). b, c, and d, represent the home ranges of all radio-tagged badgers based on MCP95 contours in the UTM reference system. a, Montserrat study area at a scale of 1:20,000; b, Southern side of Collserola study area (7 individuals) at a scale of 1:33,000, and c, Northern side of Collserola study area (2 individuals) at a scale of 1:21,000. Solid and broken lines represent males and females respectively. Stippled areas represent wooded patches. Only individuals with Incremental Area Plot (the increase in the accumulated used area when adding more fixes) stabilization are represented.

Outliers were setts used by the tracked individuals that were located outside home ranges and setts not used by the tracked individuals and located outside home ranges at a similar distance (mean distance of outlier setts used by the tracked individuals to the border of the home range in question).

Thus, the total number of active setts on a given night (AS_{tot}) as extrapolated from the number of setts actually found active (AS) is: $AS_{tot} = (AS/S) * S_{tot}$.

Finally, two additional factors are needed to estimate the number of badgers based on the number of active setts: the sett changing rate (i.e. the frequency with which badgers change from one sett to another between two consecutive days) and sett sharing frequency.

Concerning the sett changing rate, the use of the same sett on two consecutive days by an individual results in one active sett/badger whereas sett shifting would result in two active setts/badger. With radio-tracking data and using 23 series of two consecutive days spread over the four seasons (of all individuals in these three territories), the probability of returning to the same sett was 0.48 and the probability of moving to another sett was

0.52. Therefore, we assumed 0.5 frequencies for each situation and we thus obtained $\frac{3}{4}$ badgers/active sett, if $AS_{tot} > 1$.

Sett sharing frequency was estimated by opportunistically setting camera-traps at setts that seemed to be in use all around the ranges of Collserola where the censuses took place. We detected two badgers on only one occasion out of the nine sampled nights (12.5 %). Given this low figure we assumed that each active sett was occupied by a single badger on a given day.

In Montserrat, a camera trapping survey was carried out over two periods: the first one during the trapping sessions in order to confirm badger activity in setts, and the second one, one year later, to detect and identify the maximum number of individuals per group. 373 camera/night were placed near sett entrances, badger paths and latrines, in the three territories (two of them holding one radio-tagged badger and one holding two) as well as in an adjacent control area without tagged animals but with known badger activity (Area O). Each camera was in place for an average of only 3.73 days at a given site, so results were considered together with those obtained by live-trapping and must be considered with caution. The minimum number of recorded

individuals in each home range was used as an estimator of group size.

Population density was calculated on the basis of total recorded individuals across groups, per study area, and two figures are presented, one considering only the area occupied by ranges on the one hand and a wider area encompassing all ranges on the other.

RESULTS

We obtained sufficient data for 13 radio-tracked badgers that had reached home range stabilization as judged from the IAP (6 males and 7 females, Table I, 578 fixes, mean = 44.46 ± 30.17 , range 20-127). These were all of the Montserrat individuals (2 males and 2 females) and 9 badgers from Collserola (4 males and 5 females). In terms of home range size, in Collserola we found differences between the sexes (FK95: $\sigma = 388.1 \pm 72.8$ ha, $\varphi = 95.2 \pm 37.3$ ha; $U = 1$, $P = 0.027$). Two females (F5 and F6) had overlapping home ranges (MRPP test, $\delta = 0.809$, $P = 0.42$, F5 + F6 FK95 67.0 % for F5 and 79.4 % for F6, Fig. 1) and were therefore considered as belonging to the same group. The magnitude of the difference between the sexes did not seem as high in Montserrat Mountain Park (FK95:

$\sigma = 85.9 \pm 32.8$ ha, $\varphi = 59.7 \pm 2.3$ ha), but the small sample size precludes statistical analysis. In Montserrat, the home ranges of M2 and F4 overlapped almost completely (MRPP test, $\delta = 0.809$, $P = 0.79$, M2 + F4 FK95 overlap = 81.7 % for M2 and 75.7 % for F4, Fig. 1). However, in spite of a small overlap between the ranges of M1 and F3, the locations of these two individuals were significantly separated in space ($\delta = 48.287$, $P < 0.001$, M1 + F3 FK95 overlap = 8.8 % for M1 and 5.2 % for F3, Fig. 1). Therefore, M2 and F4 were considered members of the same group, whereas M1 and F3 belonged to separate groups. According to home range size tests, we distinguished three badger groups for further analysis: Montserrat badgers, Collserola males and Collserola females. There was a significant difference between these groups (Kruskal-Wallis test, FK95: $H = 6.89$, $df = 2$, $P = 0.032$): Collserola males have larger home ranges than Collserola females (FK: $U = 1$, $P = 0.032$) and Montserrat badgers (FK: $U = 0$, $P = 0.028$), whereas Collserola females and Montserrat badgers have similar home range sizes (FK: $U = 10$, $P = 1$). According to IAP functions, we found two different patterns of home range exploitation. Females and males M1, M2 (Montserrat) and M13 (Collserola) gradually reached the maximum size of their ranges by regularly moving across their home ranges, whereas the

Table I. – Location, radio-tracking period, cause of the end of tracking, number of radio locations, and home range size (ha). *M* Male, *F* female. * Montserrat Mountain Natural Park, † Southern side of Collserola Park, and ‡ Northern side of Collserola Park.

Badger ID	Tracking period DD.MM.YY	Cause	Fixes	Home Range	
				MCP95	FK95
M1*	18.12.99-02.01.01	Battery ran out	44	117.7	118.7
M2*	07.02.00-17.10.00	Broken collar	29	63.8	53.1
F3*	23.02.00-08.09.00	Battery ran out	22	57.5	62.0
F4*	08.02.00-12.10.00	Battery ran out	24	53.9	57.3
F5†	17.02.97-22.07.97	Death (unknown)	45	77.4	58.1
F6†	17.02.97-03.03.99	Death (unknown)	85	57.8	49.0
M7†	24.01.98-09.07.98	Death (poaching)	34	284.6	314.4
F8†	05.02.99-03.05.99	Death (road-kill)	9	-	-
F9†	03.03.99-19.08.99	Broken collar	28	88.2	135.9
F10†	23.03.00-14.01.01	Death (Poaching)	29	23.7	12.1
M11†	11.11.03-04.12.03	Signal loss	4	-	-
M12†	16.06.04-13.06.05	Broken collar	52	450.3	501.4
M13†	31.07.05-17.11.06	Battery ran out	39	227.0	219.0
F14‡	16.02.06-10.03.06	Broken collar	20	151.0	221.0
M15‡	02.12.06-23.07.07	End of field work	127	702.2	517.7
Mean Montserrat males \pm SE ($n = 2$)			37 \pm 8	90.8 \pm 27.0	85.9 \pm 32.8
Mean Montserrat females \pm SE ($n = 2$)			23 \pm 1	55.7 \pm 1.8	59.7 \pm 2.3
Mean Collserola males \pm SE ($n = 4$)			63 \pm 22	416 \pm 106.5	388.1 \pm 72.8
Mean Collserola females \pm SE ($n = 5$)			41 \pm 12	79.6 \pm 20.9	95.2 \pm 37.3
Mean males \pm SE ($n = 6$)			54 \pm 15	307.6 \pm 96.4	287.4 \pm 79.1
Mean females \pm SE ($n = 7$)			36 \pm 9	72.8 \pm 15.1	85.1 \pm 26.6

remaining males (all of them belonging to *Collserola*) and female F3 (Montserrat) increased their home range by exploiting different areas at different times, which entails a sharp rise in the IAP curve (Fig. 2).

Census and group size in the wooded area of Collserola

During the census period, one to three badgers were detected in home range F5 + F6 (mean: 1.5 ± 0.3 , $n = 7$ monitoring sessions); zero to two individuals were detected in home range M7 (1.8 ± 0.5 , $n = 4$, M7 was not found during one of the censuses) and one individual was detected in home range F9 in the two monitoring sessions carried out (F9). In home range F5 + F6, the monitoring sessions were carried out after the death of F5. Therefore, while this home range was used by at least two females in 1997, the number of animals during the following two years was normally one (F6), although we detected two individuals on one occasion and three individuals on another. In home range M7, the most frequent number of badgers detected was two, while it is clear that F9 ranged alone during its tracking period. Taking into account the size of the home ranges, badger density in the wooded part of *Collserola* during the study period was 1.6 ind./km² (considering only the area occupied by the three territories). Given that these territories were adjacent, the density within the MCP100 drawn around all locations of all individuals (720 ha) was 0.6 individuals/km².

In Montserrat at least three badgers were detected in home range M1 : M1 and two other non-tagged adults, which could be distinguished by the different tonality of their hair. In home range F3 we found a minimum of three badgers as well: F3 and two subadults, which were probably her previous year's offspring. Home range M2 + F4 also contained three animals: M2, F4 and one non-tagged adult. Finally, in Area O we again identified a minimum of three individuals (one adult, one sub-adult and one cub) by camera trapping. So we obtained a minimum group size of three individuals (adults and sub-adults) per home range and a population density of 1.9 individuals/km².

Ranging patterns

Males seem to range over larger areas than females in *Collserola*. For example, M7 was caught in January 1998 and was consistently detected within the eastern half of its home range (Fig. 1) and slept in dens within that part of the home range. In April, it started to exploit the neighboring female home range (F5 + F6) and slept in a den in the overlap zone, while occasionally returning to its former range to forage and rest. In July it disappeared from the study area, returning in October to the F5 + F6 home range, when it was shot by a poacher. Similarly, individual M12 was caught near a sett in June 2004, in the western part of its home range and its signal was lost after release. In August, it was found foraging and sleeping in the oppo-

site (eastern) corner of its home range, and in February 2005 it returned to the original home range inhabited by at least one female (as judged from the presence of signs made by cubs). Finally its collar was broken when it moved to a new area in June 2006.

Although one-night excursions far away from the normal range were performed by several individuals in both study areas, no such movements lasting for several weeks were observed for the Montserrat individuals or *Collserola* females. The high mobility of males is further illustrated by the fact that two males disappeared from the area in which they were caught, shortly after release. One of them was caught the same day at the same sett that F10 was caught, the signal of its transmitter having been lost the night of its release. Another one was caught inside the home range of M12, 8 months before M12, and after a few days of tracking, it disappeared. Although a failure in the radio system cannot be ruled out, this never happened to Montserrat individuals or *Collserola* females. Indeed, the sole *Collserola* female for which we could not gather enough data to calculate its home range was followed for two months before it was killed by a car. This female was consistently using the western third of the F5 + F6 home range (when F6 was already dead) but it slept outside the limits of this home range.

In Montserrat the three studied territories contained at least three members, with at least one of them containing individuals of both sexes (M2 + F4). In contrast, in *Collserola*, F9 was solitary in its home range, as revealed by the systematic census carried out. Several one-day visits at all known setts in the small range of F10 suggested that this female was living solitarily as well. On the other hand, F6 sometimes shared its home range with one or, occasionally, two additional individuals (one of them was F5 in 1997), but the census revealed that it was sometimes ranging alone.

DISCUSSION

For both study areas we found population density values close to those obtained for the South and West Iberian Peninsula (Revilla & Palomares 2002, and Rosalino *et al.* 2004 respectively). These results are also comparable to those obtained by Kowalczyk *et al.* (2000) in Białowieża Primeval Forest, and place our populations at the corresponding low population density level of the sclerophyllous Mediterranean dry forests (Virgós & Casanovas 1999) in contrast to badger populations inhabiting the British Isles (Johnson *et al.* 2002). Along with the low population densities, territories were large, particularly in the case of *Collserola* males. Only badgers from Poland and the south of the Iberian Peninsula (Revilla *et al.* 2001) have larger home ranges than *Collserola* males at a lower population density (Kowalczyk *et al.* 2003).

Even though the small sample size in Montserrat pre-

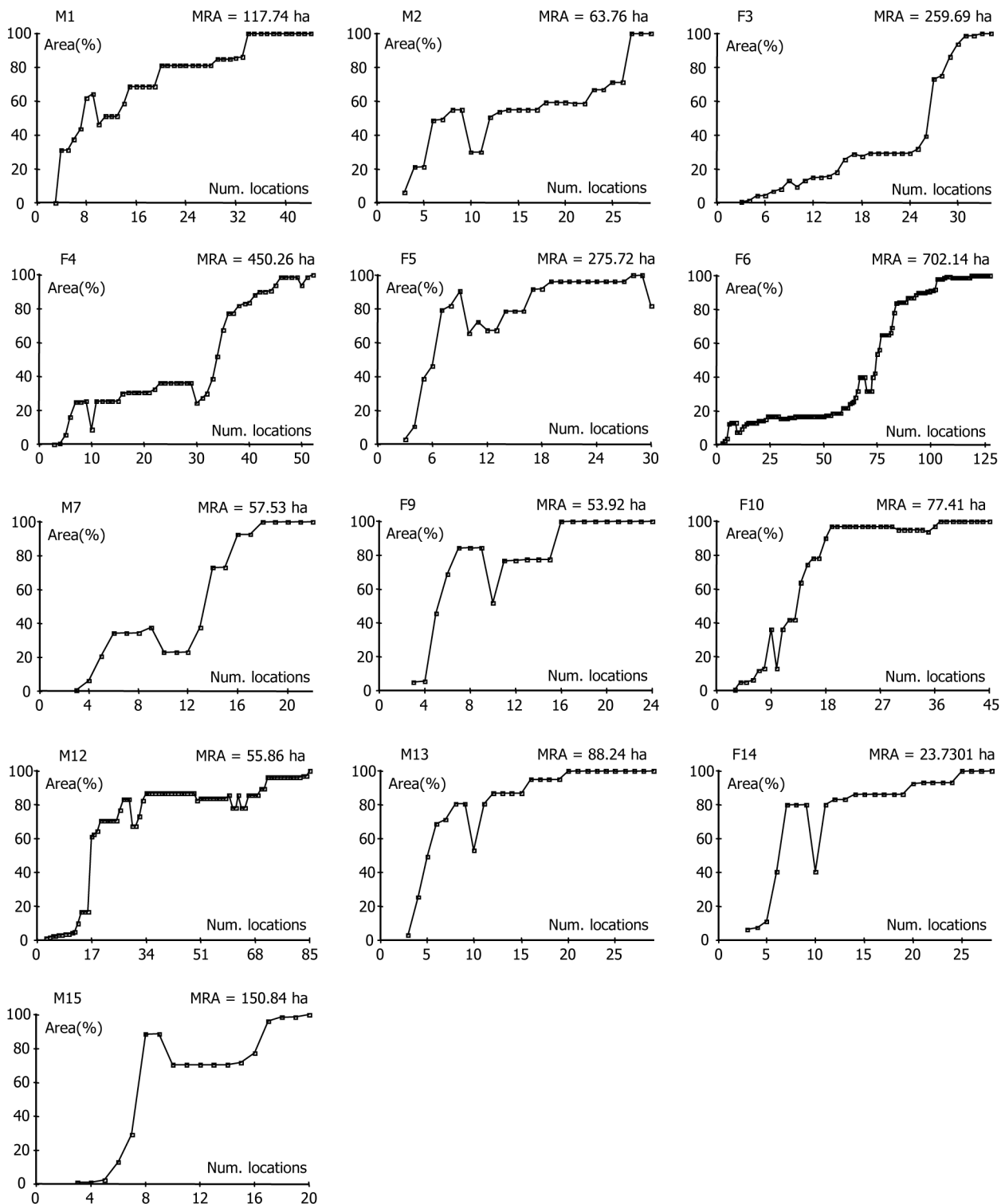


Fig. 2. – Incremental Area Plot for MCP95 for individuals which reached the home range stabilization (M1 to M15). Same plotting was conducted for FK95 with similar results (MRA= Maximum Range Area).

cludes statistical analysis, it is clear that the magnitude of the difference between male and female home range sizes is much greater in *Collserola* than in *Montserrat* (Table I): *Collserola* males had a mean home range size over five times that of females for MCP95 and over four times for

FK95, whereas for *Montserrat* this figure was less than two for both estimators (Table I). In addition, for MCP95 the smallest male home range in *Collserola* (M13) was 1.5 times larger than the largest female home range (F9) while in *Montserrat* the smallest male home range (M2)

had a size comparable to that of females.

Similar, but less marked, tendencies for male home ranges to be larger than those of females have been reported for some other low density populations (Do Linh San *et al.* 2007b, Kowalczyk *et al.* 2003). No such striking differences in home range size between sexes have been reported for any other European population (e.g. Bodin *et al.* 2006, Palphramand *et al.* 2007, Kowalczyk *et al.* 2003, Remonti *et al.* 2006). Nevertheless, the situation in Collserola is similar to that of Hinode in the suburbs of Tokyo where male badgers have territories three times larger than females (Kaneko *et al.* 2006). This difference in home range size is attained by males by exploiting different areas of their territories at different times of the year (as judged from IAP patterns). Therefore, all evidence strongly suggests that males are more mobile than females and exploit or occasionally visit different areas at different times. In Montserrat, even though the sample size was small, all evidence points to the fact that badgers form classical mixed-sex groups of small size like other European low density populations. In Collserola, the basic territorial unit seems to be a solitary female, which would be the first animal to settle in an empty area based on the richness in trophic resources (Tuytens *et al.* 2000b, Tuytens *et al.* 2000a). It may subsequently associate with other individuals under unknown conditions, probably females, as suggested by the fact that the only two individuals tracked at the same time that completely overlapped their ranges were two females (F5 and F6). Assuming that both sexes have similar overall metabolic requirements, and therefore the difference in home range size can not be explained by differences in energetic needs, the large difference in home range size in Collserola suggests that females are the key resource in male spatial organization, as predicted by the AKH (Neal & Cheeseman 1996, Roper *et al.* 1986).

We found a notable difference in population density between the two Parks (Collserola 0.6 individuals/km², Montserrat 1.9 individuals/km²), in spite of them having similar habitat, weather and soil conditions. This may reflect the fact that, even though there are few habitat differences between Collserola and Montserrat when grouping habitats into main categories, Montserrat Park has a higher proportion of fruit crops than cereals, which could provide higher food availability. In addition, the Collserola badger population is physically isolated from other surrounding natural reserves and suffers a higher influx of people than Montserrat, which means higher levels of badger sett disturbance, poaching and road-kill risk. Nevertheless, it has to be borne in mind that the systematic census was carried out in a wooded part of Collserola and, even though this is representative of 80 % of the Park's area, several indications suggest that density may be higher in the agricultural periphery. For example, visual observations on one night revealed at least three badgers wandering around a sett used by M12 in the agricultural

periphery of Collserola (G Molina-Vacas pers obs). This suggests that group size in agricultural areas may be higher than in wooded areas. Given that territories were similar in size, density may be higher as well. In contrast, we found a strikingly small home range in that agricultural part of Collserola (the range of F10 was less than half the size of the range of the other females) and its female inhabitant was apparently living solitarily. Therefore, a higher density could also be reached by the juxtaposition of very small territories in the richest parts of the Park (i.e. the agricultural ones, see Molina-Vacas *et al.*, this issue) inhabited by one, or a few females. More research in the agricultural periphery of Collserola is needed in order to ascertain which the prevailing mode is.

Although it was not the aim of the present paper to discuss territoriality in our populations, all indications suggest that badgers of Montserrat and Collserola are indeed territorial, as is the case for all the studied populations of any density to date, with the possible exception of the Bristol population (Harris 1984). First, the intrasexual home range overlap is almost a case of all or nothing (c.f. Fig. 1). Second, F9 and F6 were tracked simultaneously for 2 months without trespassing over their common range borders. Shortly after F6 died, after which its range remained empty for some months, F9 made a two-night excursion deep into the F5 + F6 range. Finally, a fight between two unknown individuals was observed on the border of the F5 + F6 range, which was marked with a combination of visual (i.e. paths) and chemical (i.e. latrines) signs (Bonet-Arbolí 2003).

At first glance, the spatial organization of badgers in Collserola is similar to the typical mustelid spacing pattern (Powell 1979), with the likelihood of females forming groups, probably due to the greater tolerance between females of this species compared to other mustelid species (Woodroffe & Macdonald 1995). The pattern observed in Collserola was first observed by Kruuk (1978) in Wytham Woods. Kruuk observed that 45% of the studied individuals belonged to a specific kind of social group, which he named *joint ranges*, in which the males' ranges overlapped with those of females from different main setts.

We suggest that, at low densities, where females range alone or in very small groups, males need to encompass several female territories in order to increase their mating opportunities, and this could be achieved at low risk for males of encountering other aggressive males. This spatial strategy in males is only achievable if female territories are not too large, which is the case in both study areas, probably due to the existence of sufficient food resources. Where home range richness is very low and females need to have large territories to satisfy their nutritional needs (Broseth *et al.* 1997, Rodriguez *et al.* 1996, Revilla & Palomares 2002) males would be unable to encompass more than one female home range, thus giving rise to pairs as a basic unit of social organization. In contrast, at high den-

sities, where several females cohabit, one home range is enough to ensure a high number of mating opportunities, and the probability of encountering aggressive neighboring males is high, so that it would be advantageous for a male to be a permanent member of a multi-female group.

ACKNOWLEDGEMENTS. – We thank Professor T J Roper and three anonymous referees for their helpful comments that greatly improved an earlier version of the manuscript. We are grateful to Collserola Park for financial support and Barcelona Zoo veterinary services and Can Balasch Biological Station for their veterinary and logistical support. VBA and ERP received fellowships from the Generalitat de Catalunya during part of the work. We also appreciate the help of A Barroso and the Montserrat Mountain Park guards for their help with the trapping and radio-tracking tasks. Badgers were trapped and manipulated with permission of the Departament de Medi Ambient i Habitatge of the Catalan government, the ethical inter-universities commission of Catalonia, the Parks' authorities and the hunters' associations. The English version of this manuscript has been revised by R Rycroft from the UB's Linguistic Advice Service.

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Received October 30, 2008

Accepted February 9, 2009

Associate Editor: E Magnanou