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Home-ranges and patterns of spatial use in territorial Bonelli's Eagles *Aquila fasciata*

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Bonelli's Eagle *Aquila fasciata* is one of the rarest birds of prey in Europe, where it has suffered a significant decline in recent decades. We present information on the home-ranges and spatial parameters of 18 Bonelli's Eagles radiotracked in 2002–2006 in Catalonia (northeast Spain) and describe the home-range probability kernel, distances moved, breeding area eccentricity, territorial overlap, nearest neighbour distance and breeding site fidelity, and assess the influence of sex, breeding status, season and geographical area on these parameters. Median home-range according to the minimum convex polygon (MCP) and 95% kernel were 50.3 and 36.1 km^2, respectively. The median breeding area eccentricity was 1477 m. There was considerable overlap in the home-range of both sexes within pairs (MCP: 71.4% and 95% kernel: 98.5%), indicating close pair bonding and similar foraging patterns. Overlap in home-ranges of up to 15% between neighbouring individuals also occurred and was positively related to breeding pair density. There was no difference in spatial parameters between sexes or with breeding status, but during the non-breeding season Eagles had larger home-ranges and stayed further from nests. The high consistency across birds suggests a pattern of spatial use that is characteristic of this species. The high level of use of breeding areas and their surroundings (50% kernel) throughout the year makes it important that these areas be protected from human disturbance. Additionally, it is necessary that heavily used areas away from nesting sites, which are used for foraging and roosting, are identified, protected and managed in a sustainable fashion.

Keywords: habitat selection, *Aquila fasciatus*, raptors.

Bonelli's Eagle *Aquila fasciata* is a medium-sized raptor whose distribution ranges from India and western China to the western Mediterranean (del Hoyo *et al.* 1994). The estimated European population of 920–1100 pairs (BirdLife International 2004) has declined over the last three decades by 20–50% (Rocamora 1994, Real & Mañosa 1997, Real 2003). The bulk (*c.* 80%) of this population is concentrated in the Iberian Peninsula, where this raptor has suffered an average decline of 50% over the last three Eagle generations. Because of this,

the species is considered endangered in Spain (del Moral 2006) and is regarded as a Species of European Conservation Concern and Endangered in Europe by BirdLife International (2004).

Various factors have been put forward to explain this decline. A demographic imbalance related to increased adult and sub-adult mortality and/or decreased fecundity have been proposed (Real & Mañosa 1997, Rico *et al.* 1999, Real *et al.* 2001, Carrete *et al.* 2002a, Penteriani *et al.* 2003, Moleón *et al.* 2007). Interspecific competition with other raptors such as Golden Eagle *Aquila chrysaetos* for breeding sites and home-ranges is another possibility (Fernández & Insausti 1990, Fernández

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et al. 1998, López-López *et al.* 2004, Carrete *et al.* 2006). The loss of suitable habitat caused by changes in land-use including urban development, infrastructure projects and a decline in traditional extensive farming may also have had an impact (Carrete *et al.* 2005, Balbontín 2005, Martínez *et al.* 2007).

To improve the poor conservation status of this and many other species, the European Union created the Natura 2000 Network and a network of Special Protection Areas (SPAs) (Directives 79/409/EEC and 92/43/EEC). To implement conservation measures effectively it is necessary to target sufficient territories and birds in viable populations (Taylor & Gerrodette 1993) and identify key areas used by birds to address specific conservation problems and develop active management plans (Fabrizio *et al.* 2006). If the policies in place for Bonelli's Eagle are to work, it is necessary that core areas, territorial boundaries and habitat selection be elucidated (White & Garrott 1990, Kenward & Walls 1994).

For birds of prey, our knowledge of spatial patterns is often limited to nest-sites and breeding birds (Newton 1979, Kenward 1987), either because breeding is believed to be the most important period or because this kind of information is the most readily available (Newton 1979). However, studies of raptors indicate that their reproductive success and survival often depend on large areas, known as home-ranges (Morse 1980). These include nest-sites but also other areas where birds forage and feed, advertise the occupation of their territory and interact with the rest of the population (Burnham *et al.* 1989, Mañosa *et al.* 1998, Balbontín 2005). The size of home-ranges and the factors that influence their variation are important both in terms of biological knowledge and for conservation purposes. However, in birds of prey, knowledge of spatial use is limited to just a few species, geographical areas and environmental conditions (Newton 1979, Gargett 1990, Marzluff *et al.* 1997).

Bonelli's Eagle is a monogamous and sedentary species that lives in pairs in the same territory throughout the year. Pairs are usually tied to a specific area that is used to rear young each year (del Hoyo *et al.* 1994). Although the behaviour of this species in relation to its nest-sites and the breeding season is well known (Blondel *et al.* 1969, Cheylan 1972, Arroyo *et al.* 1995), knowledge regarding home-ranges and the spatial parameters of territorial birds is limited (Cheylan 1981, Mure 1999, Sanz *et al.* 2005).

Demographically, territorial birds are the most important section of a population and conservation policies should prioritize their protection (Real & Mañosa 1997, Carrete *et al.* 2005). Given the importance of understanding the biology of this raptor and of implementing effective conservation policies in their European populations, it is necessary to obtain accurate knowledge of spatial use by territorial adults. This study provides data on the year-round spatial patterns of 18 territorial Bonelli's Eagles, obtained by standardized radio-tracking methods. The aims of this study were to describe the size of the home-ranges and spatial patterns of territorial adults, to evaluate the influence of sex, breeding status, season, geographical area and distances of conspecifics on home-range size and other spatial parameters, to evaluate the Eagles' fidelity to breeding areas, and to propose spatial management and conservation measures.

METHODS

Study areas

Three areas in Catalonia (northeast Spain) with different environmental and ecological features were selected: the Northern Pre-littoral Range (NPR), the Coastal Range (CR) and the Southern Pre-littoral Range (SPR) (Fig. 1).

Home to four pairs of Bonelli's Eagle, the NPR is situated in the northern part of the range of Bonelli's Eagle in Catalonia (centred on 41°39′N, 2°0′E). This area consists of steep mountain ranges with altitudes between 400 and 1200 m, extensive *Quercus ilex* and *Pinus halepensis* forest cover (60–80%), and high levels of human disturbance. The density of Bonelli's Eagle here is low following a sharp decline during the 1980s and 1990s (Real 2003, Real *et al.* 2004); nesting Golden Eagles are absent.

The CR, which holds six pairs of Bonelli's Eagle, is located near the sea (centred on 41°19′N, 1°53′E) in coastal hills with altitudes between 300 and 650 m, where the climate is dry and mild. This area is mainly covered by scrub and dry meadows and has high levels of human disturbance. The density of Bonelli's Eagle here is intermediate (see Table 3) and nesting Golden Eagles are absent.

There were 15 pairs of Bonelli's Eagle in the SPR, an inland area with a more continental
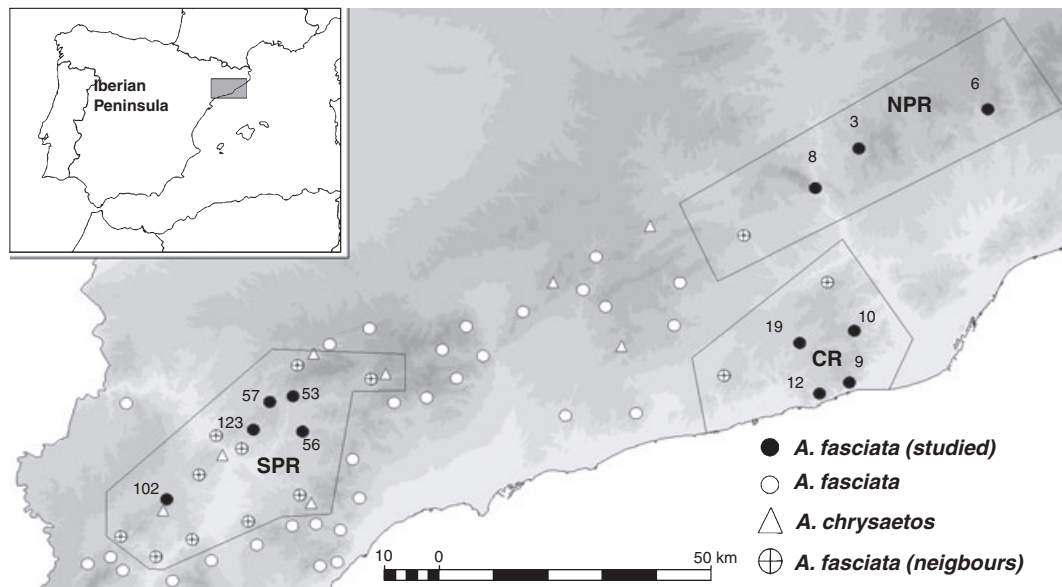
Figure 1. Study area. Northern Pre-littoral Range (NPR), Coastal Range (CR) and Southern Pre-littoral Range (SPR), Catalonia (Spain). Symbols indicate the approximate location of territorial pairs of Eagles (locations are modified to prevent nests from being located).

climate (centred on 41°11′N, 0°41′E). This area is characterized by steep mountain ranges, with altitudes ranging from 400 to 1100 m; land cover consists mainly of scattered non-irrigated cultivation, secondary pinewoods and scrub, although human presence is low. The density of Bonelli's Eagle here is high (see Table 3) despite a decline during the 1990s (Real 2003, Real *et al.* 2004); five nesting pairs of Golden Eagle were also present.

Trapping and radiotracking

During the years 2002–2006, we radiotagged 18 territorial Bonelli's Eagles: six (four males and two females) in NPR, five (three males and two females) in CR and seven (four males and three females) in SPR. Eagles were trapped with a radio-controlled bow-net trap developed by V. G. Matarranz (Subdirección General para la Biodiversidad – Ministerio de Medio Ambiente). After being captured, each bird was equipped with a backpack transmitter with an activity switch (TW-3 32–40 g; Biotrack Ltd, Wareham, Dorset, UK), fitted with Teflon harness with a rupture point (Garcelon 1985) and powered for 2–3 years.

Each Eagle was individually radiotracked from sunrise to dusk in three non-consecutive daily sessions during each month of the year. Radiotracking sessions were conducted by an observer in a 4 × 4 vehicle using an Icom R10 receiver (Icom Inc., Osaka, Japan), 10× binoculars and a 20–60× telescope.

During the tracking period, the observer tried to stay in continuous radio contact with the Eagle to establish its location and behaviour. Transmitters with activity sensors revealed whether the bird was perched or flying. On the hour (± 10 min) the observer recorded the location of the bird. Locations were classified into four types: visual-perched, radio-perched, visual-flying and radio-flying. When the bird was observed perched, its position was recorded on a map on the basis of topographical and environmental features. When the bird could not be seen but radio signals indicated it was perched, the observer moved to calculate the bird's position by triangulation. If the activity sensor indicated that the bird had moved during triangulation, this location was not used. When the bird was seen in flight, locations were only recorded if the bird was within 3 km of the observer. When the bird was flying but not observed, locations were not recorded. If the bird changed the type of location within ± 10 min, the new location was recorded. Locations were marked *in situ* on 1 : 50 000 topographical maps (Institut de Cartografia de Catalunya). This procedure was made possible by the extensive network of roads in the areas frequented by the Eagles.

Home-range and spatial parameter analysis

Eagles' home-ranges were studied using MCP (minimum convex polygon 100%; Mohr 1947), which indicates the maximum area used including the outliers, and fixed kernel density contours (Worton 1989), which allows different levels of spatial use to be assessed. We used RANGES VII software (South *et al.* 2005) to analyse the 95%, 80% and 50% kernels as isolines with a smoothing factor of 1 (default), often used to describe different probabilities of use in home-ranges (Seaman & Powell 1996, Kenward 2001, Ratcliffe & Crowe 2001, Laver & Kelly 2008).

Home-range sizes were constructed using only hourly locations that were considered independent (Swihard & Slade 1985, Seaman & Powell 1996, Kenward 2001). To avoid a bias towards roosting areas, consecutively repeated locations in the early morning and late evening of inactive Eagles were excluded because they were considered to be non-independent.

To calculate the number of locations required to build the area of each home-range, we used the incremental area analysis method, applied with kernel and to sort independent locations at random (South *et al.* 2005). This method produces a plot of percentage of area vs. number of locations that tends towards an asymptote, and provides an approximate estimation of the number of locations required. The degree of stability shown by these graphs indicated that 150 locations for each individual were required to build the different annual kernel areas. When we studied possible intra-annual differences (breeding and non-breeding season), we equated the number of locations to the season that had the fewest locations and used at least 40 independent locations at random in each season, as recommended by Seaman *et al.* (1999). We considered the breeding season to last from February to June inclusively and the non-breeding season all other months (Arroyo *et al.* 1995).

Several spatial parameters were estimated from the data, including average distance covered (ADC) by the Eagles, the eccentricity of home-ranges and their overlap. ADC was a linear indicator of the home-range size and was calculated as the average distance from the arithmetic centre of all locations (ACL) to each particular location. The eccentricity of home-ranges was calculated as the distance from the centre of the breeding area (defined as a radius of 750 m from the arithmetical centre of the different nests used during the study period) to the ACL and was used to assess the extent to which the breeding area was centred on the home-range. The 750-m radius was chosen because the histogram of the hourly locations showed a sharp decrease at this distance and because it encompassed all the nests and habitual roosts in each territory.

Home-range overlap was estimated at two levels: between sexes holding a territory and between individuals from neighbouring territories. In the first case, the overlap was calculated as the greatest proportion of overlapping area during the whole of the tracking period for both sexes. In the latter case, the overlap was calculated for each individual as the area overlapping with any of their neighbours during the study period, excluding individuals of the same pair and isolated territories. We considered isolated territories to be those that were separated by at least a distance equivalent to the extent of a typical territory. Calculation of overlaps was performed using MIRAMON software (Pons 2002), a geographical information system developed by the Centre for Ecological Research and Forestry Applications (CREAF) that permits analysis of combinations of vector layers.

We assessed the influence of sex, breeding status, season, geographical areas and intraspecific competition on Eagles' home-ranges and spatial parameters. To analyse the influence of sex we compared individuals of five territories where both sexes were tracked during the same period. Because some pairs did not lay eggs despite having mated and occupied a territory, we assessed the influence of breeding status, comparing breeding and non-breeding birds with pooled data for both sexes and for males separately. Females were not compared because of the small sample size.

To assess differences in patterns of spatial use during the annual life cycle of the Eagles and whether they were related to breeding season, we pooled data for all individuals sorted by their breeding status and sex.

Comparisons of three areas with different densities of Bonelli's Eagles and Golden Eagles assessed whether environmental or population patterns influenced the spatial parameters shown by eagles.

We studied the nearest neighbour distance (NND) as an indicator of the density of conspecifics and to analyse its influence on spatial parameters.

NND was estimated as the distance between the centres of neighbouring breeding areas (the arithmetical centre of the nest-sites) of simultaneously occupied neighbouring Bonelli's Eagle territories. The NND was studied both globally and by area using all territories within the study area. NNDs were also calculated for Golden Eagles. To correlate NND and spatial parameters, we only used radio-tracked birds from non-isolated territories.

The fidelity of Eagles to their breeding area was assessed in terms of the frequency with which they roosted (perched without activity during the night) in the breeding area and the average distance from the hourly locations to the arithmetical centre of the nests (DLN).

Data analysis

For analysis of data from independent samples, the medians and the interquartile range (IQR) and Kruskal–Wallis and Mann–Whitney *U*-tests were used. The Wilcoxon test was used for comparing paired data. Spearman rank correlation coefficients were used to assess relationships between different spatial parameters. To compare the proportional data for roosting sites in the breeding area for each season, the Wilcoxon test for paired data was used.

Differences were considered significant when $P < 0.05$ (Zar 1984). All statistical tests were performed using SPSS v15.0.

RESULTS

Home-ranges and spatial patterns

The median MCP for the 18 Bonelli's Eagles tracked was 50.3 km^2 (IQR: 42.1–82.6 km^2): for the 95% and 50% kernels, medians were 36.1 km^2 (IQR: 30.8–42.9 km^2) and 8.3 km^2 (IQR: 5.5–9.6 km^2), respectively. The median ADC was 2062 m (IQR: 1806–2191m) (Table 1).

The median breeding area eccentricity was 1477 m (IQR: 1147–1952 m, $n = 18$) (Table 1), which was positively correlated with the size of the 95% and 50% kernels and the ADC ($r_s = 0.616$, $P = 0.006$; $r_s = 0.756$, $P < 0.001$ and $r_s = 0.837$, $P < 0.001$, respectively). Non-significant correlation was found with MCP ($r_s = 0.063$, $P = 0.804$).

There were no significant differences in home-ranges (MCP, 95% and 50% kernels and ADC) between sexes ($n = 5$, Wilcoxon paired-data test). Similarly, there were no differences in home-range among breeding and non-breeding

Table 1. Home-range sizes and spatial territorial parameters of Bonelli's Eagles in Catalonia. Individual: code territory and sex (F: female, or M: male).

Individual	Bred	Area	Radiotracked period	100% MCP (km^2)	95% kernel (km^2)	50% kernel (km^2)	ADC (m)	Eccentricity (m)
3M1	Yes	NPR	July 2–June 3	129.9	110.7	27.6	3561	4009
3M2[a]	No	NPR	July 4–June 5	85.2	86.5	23.6	3883	5398
6F	Yes	NPR	July 2–June 4	97.0	24.5	4.6	1477	659
6M	Yes	NPR	July 3–June 4	100.6	26.9	5.2	1715	366
8F	Yes	NPR	July 3–June 4	35.2	35.9	8.9	2158	1999
8M	Yes	NPR	July 3–June 4	46.3	33.4	6.1	2029	1622
9M	Yes	CR	July 3–June 4	31.6	20.7	6.7	1697	1521
10M	Yes	CR	July 3–June 4	53.1	42.2	5.1	2074	1274
12F	No	CR	July 3–June 4	37.1	36.1	9.5	2202	2744
19F	Yes	CR	February 5–August 5[b]	36.5	29.9	3.6	1805	1252
19M	Yes	CR	January 5–December 5	115.0	36.1	9.1	2050	1571
53F	No	SPR	February 5–January 6	67.8	62.0	12.1	2832	1810
53M	No	SPR	February 5–October 5[b]	47.5	43.1	8.0	2114	1433
56F	No	SPR	February 5–January 6	42.7	22.8	5.2	1488	768
56M	No	SPR	February 5–October 5[c]	43.4	33.4	9.6	1809	1268
57F	Yes	SPR	February 5–November 5[b]	41.9	38.0	8.3	1923	1112
102M	Yes	SPR	July 3–June 4	74.6	64.3	15.4	2840	2002
123M	Yes	SPR	April 5–March 6	54.7	40.5	8.4	2078	1081

[a]Subadult individual who replaced the 3M1 that died after a year.
[b]Death.
[c]Tag loss.

individuals, either in the pooled data for all birds or among males only (Mann–Whitney *U*-test). With data from all individuals pooled (*n* = 18), home-range parameters outside the breeding season were significantly higher than in the breeding season; similar relationships were found using only breeding individuals, or comparing males and females separately (Table 2). In contrast, when using data from non-breeding individuals only, no significant differences in spatial parameters between seasons were found (Table 2).

No significant differences were found in either home-range size or spatial parameters between different geographical areas, although in the Coastal Range these areas tended to be smaller (Table 3).

Within-pair overlap in home-range in five pairs had a median of 76.0% for the MCP (IQR: 72.2–88.0%) and 98.6% for the 95% kernel (IQR: 97.2–99.9%).

Of the 15 individuals studied whose home-range could possibly overlap with that of a neighbouring individual, 11 cases of overlap by MCP and eight by 95% kernel were found. The median proportion of the overlap area for MCP was 14.8% (IQR: 0.4–31.2%), and for 95% kernel it was 4.1% (IQR: 0.0–17.5%) (*n* = 15). Overlap between neighbouring individuals was greater in the SPR area than in NPR and CR (Table 3).

The global median of NND between the territories was 7098 m (IQR: 5492–10 305 m, *n* = 25), and 5455 m (IQR: 3438–9532, *n* = 30) when Golden Eagle nests were included (Fig. 1). Differences in NND between geographical areas were found and post-hoc tests showed that they were attributable to higher NND in the NPR (Table 3). Moreover, when Golden Eagle nests were included in the SPR (median: 3580 m, IQR: 2667–5630 m, *n* = 30), differences were observed between the three areas (Kruskal–Wallis test, H = 15.920, P < 0.001).

No significant correlations were found between NND and home-range sizes (MCP: r_s = 0.129, P = 0.647, and 95% kernel: r_s = −0.038, P = 0.893, *n* = 15) and between home-range sizes

Table 2. Comparison of home-range sizes between breeding season (February–June) and non-breeding season (July–January).

|	*n*	Breeding season Median (IQR)	*n*	Non-breeding season Median (IQR)	*Z*	*P*
All individuals						
MCP 100% (km^2)	18	32.0 (25.0–47.1)	18	39.4 (33.1–85.0)	−2.112	0.035
Kernel 95% (km^2)	18	28.6 (22.6–37.1)	18	39.8 (34.9–50.8)	−3.157	0.002
Kernel 50% (km^2)	18	5.1 (4.0–7.8)	18	8.9 (7.0–15.7)	−3.027	0.002
ADC (m)	18	1926 (1670–2130)	18	2208 (2002–2626)	−3.288	0.001
Breeding individuals						
MCP 100% (km^2)	12	31.4 (20.5–47.1)	12	44.8 (33.1–109.1)	−2.275	0.023
Kernel 95% (km^2)	12	24.5 (19.8–35.7)	12	39.8 (36.6–50.8)	−3.059	0.002
Kernel 50% (km^2)	12	4.2 (3.5–5.3)	12	8.4 (6.7–15.7)	−3.059	0.002
ADC (m)	12	1858 (1643–2039)	12	2208 (2002–2626)	−3.059	0.002
Non-breeding individuals						
MCP 100% (km^2)	6	36.6 (30.7–51.2)	6	36.9 (30.2–44.7)	−0.314	0.753
Kernel 95% (km^2)	6	35.0 (29.8–53.1)	6	39.3 (29.3–56.7)	−0.734	0.463
Kernel 50% (km^2)	6	9.9 (8.0–11.8)	6	11.4 (8.3–25.1)	−0.524	0.600
ADC (m)	6	2120 (1878–2503)	6	2168 (1881–2943)	−0.946	0.344
Males						
MCP 100% (km^2)	11	42.9 (28.6–52.7)	11	50.3 (36.1–114.6)	−2.045	0.041
Kernel 95% (km^2)	11	35.2 (22.4–38.7)	11	44.4 (39.1–67.4)	−2.667	0.008
Kernel 50% (km^2)	11	4.9 (3.6–7.6)	11	8.8 (7.5–28.9)	−2.845	0.004
ADC (m)	11	1980 (1804–2335)	11	2183 (2042–3144)	−2.668	0.008
Females						
MCP 100% (km^2)	7	31.3 (15.4–41.8)	7	34.3 (22.3–46.5)	−0.676	0.499
Kernel 95% (km^2)	7	25.8 (21.2–29.3)	7	36.6 (29.7–48.6)	−1.690	0.091
Kernel 50% (km^2)	7	5.4 (4.0–11.7)	7	9.0 (6.2–13.8)	−1.183	0.237
ADC (m)	7	1724 (1607–2101)	7	2232 (1690–2683)	−2.028	0.043

Wilcoxon paired-data test (IQR, interquartile range).

Table 3. Annual home-range sizes and ADC by geographical areas (*n* = 18).

		NPR		CR		SPR			
	n	Median (IQR)	*n*	Median (IQR)	*n*	Median (IQR)	*H*	*P*
MCP 100% (km^2)	6	45.5 (41.3–72.2)	5	37.1 (34.0–84.0)	7	47.5 (42.7–67.8)	2.655	0.265
Kernel 95% (km^2)	6	39.6 (30.8–68.1)	5	36.1 (25.3–39.2)	7	40.5 (33.4–62.0)	1.192	0.551
Kernel 50% (km^2)	6	9.5 (7.3–15.0)	5	6.7 (4.4–9.3)	7	8.4 (8.0–12.1)	1.487	0.476
ADC (m)	6	2158 (1729–3095)	5	2050 (1751–2138)	7	2078 (1809–2832)	0.421	0.810
Overlap MCP[a] (%)	4	0.7 (0.0–1.6)	5	0.9 (0.0–1.5)	6	33.4 (20.6–37.3)	8.270	0.016
Overlap 95% kernel[a] (%)	4	0.0 (0.0–0.0)	5	0.0 (0.0–9.1)	6	17.6 (6.7–24.3)	8.437	0.015
Average NND[b] (m)	4	12 662 (10 305–17 139)	6	9275 (6416–9643)	15	6979 (4610–8601)	8.019	0.018

[a]Individuals in isolated territories were excluded (*n* = 15).
[b]All territories of the geographical areas were included (*n* = 25).
Kruskal–Wallis test (IQR, interquartile range).
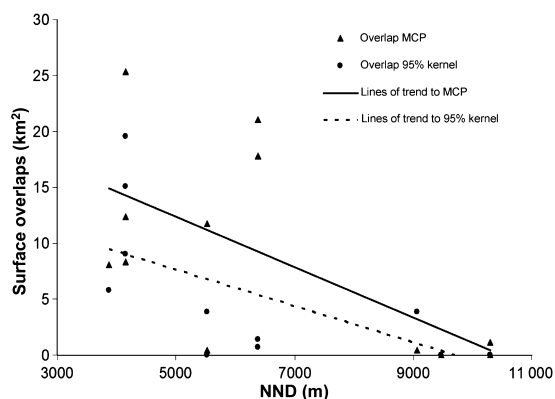
Figure 2. Relationship between NND and overlapping area with neighbouring individuals for MCP (*n* = 15, r_s = −0.641, *P* = 0.010) and 95% kernel (*n* = 15, r_s = −0.843, *P* < 0.001), and lines of trend.

and overlap with neighbouring individuals (MCP: r_s = −0.032, *P* = 0.908, *n* = 15, and 95% kernel: r_s = 0.181, *P* = 0.519). In contrast, we found a significant negative correlation between NND and the proportion of overlap with neighbouring individuals (MCP: r_s = −0.641, *P* = 0.010, *n* = 15; 95% kernel: r_s = −0.843, *P* < 0.001) (Fig. 2).

Breeding area fidelity

Roosting frequency in the breeding area in the 18 Bonelli's Eagles during the year was 53.2% (IQR: 46.4–68.9%, *n* = 18) and was higher in the breeding season than in the non-breeding season (Table 4). Both males and females roosted more frequently in the breeding area during the breeding season than during the non-breeding season, although only males showed significant differences.

The seasonal trend was the opposite in non-breeding birds, although no significant differences were detected (Table 4).

The median distance from locations to the arithmetical centre of the nests (DLN) was 2061 m (IQR: 1916–2785 m, *n* = 18), with greater distances (Wilcoxon paired-data test) of up to 18 km from the nest being observed outside the breeding season. Similar trends were observed in both breeding males and females. However, non-breeding individuals were observed at similar distances from nests in both seasons (Table 4).

When breeding (*n* = 12) and non-breeding individuals (*n* = 6) were compared, differences in the median of the DLN were found in the breeding season (Mann–Whitney *U*-test, *U* = 8.0, *P* = 0.009) but not outside the breeding season (Mann–Whitney *U*-test, *U* = 30.0, *P* = 0.779).

DISCUSSION

The home-ranges derived from the tracked Bonelli's Eagles varied from 32 to 130 km^2 in the MCP and from 21 to 111 km^2 in the 95% kernel. These results are similar to those described by Cheylan and Ravayrol (1996) and Mure (1999) from the northernmost part of the species' range in France (MCP: 50–115 km^2, *n* = 3). This is also the case in Valencia (eastern Spain), (MCP: 55–84 km^2, *n* = 3 and 95% kernel 16–45 km^2) (Sanz *et al*. 2005) and Extremadura (southwest Spain) (MPC: 22–109 km^2, *n* = 3) (Cabeza & de la Cruz pers. comm.).

Each home-range estimator (MCP and probability kernel) can be interpreted as an indicator of various behaviours within the home-range. In all territories, breeding sites were within the
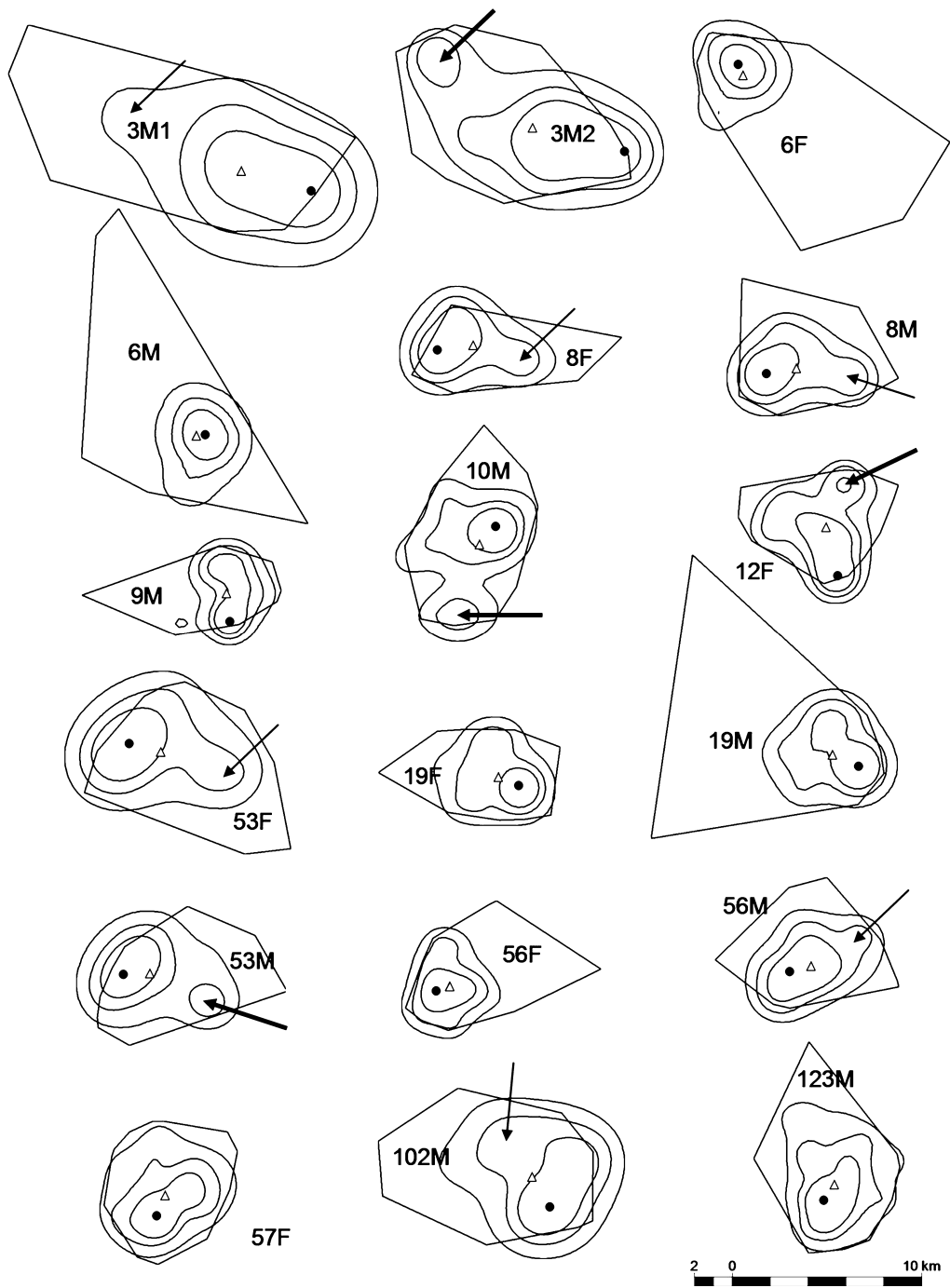
Figure 3. Shapes of 100% MCP, 95% kernel, 80% kernel and 50% kernel (●: centre of breeding area. △: arithmetical centre of locations. ——▶: intensively used areas. ———▶: main elongation areas). [Correction added after online publication 23 November 2009: 'main elongation areas' and 'intensively used areas' swapped to correct legend].

50% kernel, where the Eagles' main activity was concentrated throughout the year. The 80% kernel described the areas actively selected for foraging and roosting outside the breeding site

(Fig. 3), the 95% kernel revealed the whole area used by Eagles over the year and the MCP showed the total area including the outlier locations.

Table 4. Breeding area fidelity. Frequency of roosting in the breeding area and distance from the hourly locations to the arithmetic centre of the nests (DLN).

	n	Breeding season Median (IQR)	Non-breeding season Median (IQR)	*Z*	*P*
% Roosting in the breeding area					
All individuals	18	56.5 (50.0–70.0)	45.0 (30.7–64.7)	−1.988	0.047
Breeding individuals	12	60.0 (52.4–72.7)	33.3 (26.3–62.5)	−2.756	0.006
Breeding males	8	56.4 (50.6–61.4)	39.2 (27.4–60.4)	−2.240	0.025
Breeding females	4	72.7 (61.1–73.9)	31.6 (25.0–62.5)	−1.604	0.109
Non-breeding individuals	6	46.7 (35.1–65.7)	60.1 (41.5–73.2)	−1.095	0.273
Non-breeding males	3	51.7 (33.3–70.0)	65.8 (55.6–76.0)	−1.342	0.180
Non-breeding females	3	46.9 (40.5–52.9)	50.7 (36.8–64.7)	−0.447	0.655
DLN (m)					
All individuals	18	1884 (1689–2118)	2327 (2021–3178)	−3.027	0.002
Breeding individuals	12	1818 (1501–1984)	2327 (2151–3011)	−3.059	0.002
Breeding males	8	1843 (1747–1984)	2333 (2176–3011)	−2.521	0.012
Breeding females	4	1528 (939–1981)	2270 (1933–3146)	−1.826	0.068
Non-breeding individuals	6	2223 (1978–3576)	2446 (1633–4331)	−0.105	0.917
Non-breeding males	3	2130 (2057–4417)	1881 (1735–7029)	0.000	1.000
Non-breeding females	3	2316 (1740–3295)	3010 (1327–3431)	0.000	1.000

Wilcoxon paired-data test of the differences between breeding season and non-breeding season (IQR, interquartile range).

Significant variation between birds and territories was found in both the overall surface area foraged and in the form and proportion of the different kernels. Thus, in some individuals the 95% kernel coincided closely with the MCP, whereas in others the 95% kernel was a small and often eccentric part of the MCP (Fig. 3). This could indicate that whereas some Eagles regularly use the whole area of the home-range, others occasionally travel as far as 18 km from nests and beyond the boundaries of their home-ranges during excursions into areas without neighbours.

A significant eccentricity value for breeding areas in relation to global home-range was found, which indicates differential selection between breeding and foraging areas. In this sense, some territories had isolated intensively used areas far from nest-sites or elongated shapes (3M2, 10M, 12F, 53M, 3M1, 8F, 8M and 53F, Fig. 3). These areas were used primarily for foraging and roosting outside the breeding season and coincided with a larger home-range and larger distances to the nest (DLN) in this period. This differential use of the space could be a consequence of the heterogeneity of the territories and the irregular distribution of food resources (Sanz *et al.* 2005, Carrete *et al.* 2006).

Several authors have highlighted the important pair bond existing between territorial Bonelli's Eagles that lasts throughout the year (Cheylan 1972, Real 1983). The lack of differences between sexes in home-range sizes, which overlap considerably (71–98%), revealed the very close bonds that exist in pairs even outside the breeding season; for example, birds roosted together. During incubation and the first weeks of chick-rearing, females spent most of their time on the nest. The negligible differences found between male and female home-range size at this time could be due to the fact that males guard the nest and hunt nearby (Pérez-Mellado *et al.* 1977, Real 1983, Morvan & Dobchies 1987) and because females forage in the same areas as males when they are helping to feed their young (Zozaya 2005). Comparable home-range sizes for both sexes have also been obtained in the similarly territorial and sedentary Golden Eagle (Marzluff *et al.* 1997).

Terrestrial tracking procedures may have led to some biases in our estimates of home-ranges and spatial parameters. Nevertheless, Bonelli's Eagles spend long periods of time perched and the study area had an extensive network of roads that permitted observers to be in contact with birds most of the time. In addition, when Eagles were flying, the probability of detecting them was high because the signal ranges given for 'above-ground' conditions were considerable (Kenward 2001). Thus, observers only failed to receive a signal when birds

were perched in a deep ravine and low bias is to be expected in the detection of birds. The accuracy of locations is thus not thought to have had any significant influence on the fixed kernel density estimates given the expected magnitude of the home-ranges (Moser & Garton 2007).

During the year, the behaviour of Bonelli's Eagles was strongly influenced by the species' breeding cycle, which begins in the middle of winter and ends in the summer (del Hoyo *et al.* 1994), and this pattern may influence the spatial use at individual (breeding status) and temporal levels (breeding season). Over the year as a whole, there were no quantitative differences between breeding and non-breeding individuals in the area of home-ranges; however, breeding individuals had smaller home-ranges during the breeding season and more extended territories outside this period, as has been observed in Golden Eagles (Marzluff *et al.* 1997, Haworth *et al.* 2006). Seasonal differences observed in the spatial use of the home-range could be explained by the fact that breeding Eagles are more tied to their nests as they are involved in reproductive behaviour. This was also demonstrated by the shorter distances covered from the breeding area, as well as by the high frequency of roosting there. Non-breeding Eagles maintained a consistent home-range size throughout the year, but concentrated their activity further from nests (DLN), which suggests that the areas foraged by these Eagles differed from those used by breeding birds during the breeding season. The large areas of the home-range of breeding Eagles outside the breeding season, which included locations far from the nests, correspond to the spatial parameters observed in non-breeding Eagles. This could indicate that outside the breeding season, breeding Eagles exploit similar areas to non-breeding Eagles. This change in the use of space with respect to the season coincides with the specific foraging patterns and different prey consumed outside the breeding season (Real 1991, Moleón *et al.* 2007). Seasonal change in range use seems to be common in raptors (Marzluff *et al.* 1997, Haworth *et al.* 2006) and it is likely to be related to the constraint of central place foraging when breeding. Moreover, while the breeding areas studied provide some of the requisites for nesting (e.g. cliffs for nest-building), it is unlikely that breeding areas in our region provide enough prey for the whole year. They may thus not be optimal for foraging and so when Eagles are not restricted to the nests (non-breeding individuals or in the non-breeding season), they prefer to move outside their breeding areas.

In general, individual Bonelli's Eagles showed great fidelity to their breeding areas during the breeding season, and outside the breeding season Eagles regularly used their breeding areas to roost. This year-round fidelity to the breeding area highlights the importance of defending this resource at both intra- and interspecific levels. Both Golden Eagles and Peregrine Falcons *Falco peregrinus* occupy Bonelli's Eagle breeding areas and nests during prolonged absences, particularly outside the breeding season or when one individual of the pair dies (Fernández & Insausti 1990, Gil-Sánchez *et al.* 1996, pers. obs.). However, a regular presence of Eagles in their breeding areas is likely to prevent them being usurped by competitors (Cheylan 1973, Gil-Sánchez 1999).

In birds of prey, it is well known that intra- and interspecific competition can strongly influence the distribution of birds' breeding areas and their home-range sizes (Newton 1979, Gargett 1990, Ottaviani *et al.* 2006). At intraspecific level, home-ranges did not differ between geographical areas, although they did have significantly different conspecific densities. The highest degree of overlap was found in the area with the greatest density of Eagle pairs (SPR). There was also a negative correlation between NND and the percentage overlap. This could be a consequence of the fact that the closer an Eagle is to its neighbour, the more likely it is to overlap with it, although it may also indicate that Eagles sometimes share parts of their home-ranges. Nevertheless, when this occurred it was usually in the least frequently foraged areas. In this respect, the low percentage of overlapping territories and their spatial adjustment – almost without any free foraging space between them – indicates that some degree of intraspecific competition occurs, as has been demonstrated in other raptors (Newton 1979, Gargett 1990). Furthermore, in the SPR – the only area with nesting Golden Eagles – the NND was halved and we found the highest degree of overlap between neighbouring Bonelli's Eagle territories.

The use of MCP and kernels to analyse overlap can lead to different biases. Both techniques can incorporate areas not actually used by the Eagles, in the case of the MCP due to the presence of outliers and in the kernels depending on the smoothing factor used. Thus, in near neighbouring territories (low NNDs) an overestimation of the overlap may

be expected. Nevertheless, locations of Eagles within the home-range of neighbouring territories indicated that overlap may be frequent in this species.

A general pattern in home-range size was observed, which suggests that phylogenetic and behavioural factors are influential in spatial territorial use (Ottaviani *et al.* 2006). Bonelli's Eagle has specific morphological features such as high wing loading and a low aspect ratio (Parellada *et al.* 1984) that may influence its foraging behaviour, selection of breeding sites (Cheylan 1972, Real 1991, Ontiveros 1999) and distribution throughout the Mediterranean and sub-tropical region (Ferguson-Lees & Christie 2001). Thus, although individual and environmental factors influence the use of space patterns shown by Bonelli's Eagles, these birds are also apparently limited by their own morphological and phylogenetic characteristics.

Implications for management and conservation

Traditionally, conservation efforts for birds of prey have focused on breeding areas and the breeding season, largely because it has always been considered that breeding success can be maximized in this way (Meyburg & Chancellor 1994). Our study indicates that breeding areas are used all year round by Bonelli's Eagles, even outside the breeding season, during which time the birds rest, roost and prepare for the following breeding season. Thus, it would be expedient to regulate disturbing leisure activities (climbing, hiking and mountain biking) all year round, given that there are indications that these may be detrimental for the species outside the breeding period. Indeed, one of the pairs tracked in this study moved to a new and less suitable site after climbing in the area was permitted outside the breeding season. These areas should be even better protected from the irreversible damage caused by major infrastructures and urban development, which force birds to abandon territories and render them useless as breeding sites.

Our results show that some birds make extensive use of areas distant from nest-sites (between 2 and 14 km away), which are used for foraging and roosting. Some of these areas, which are located in more modified landscapes, are potentially dangerous due to the presence of power lines and intensive pressure (e.g. hunting). Mortality rates rise in these areas (Real & Mañosa 1997, Real *et al.* 2001) and are the main factors behind the decline in Bonelli's Eagle populations (Carrete *et al.* 2002b, 2005). Thus, the identification and protection of these key areas are crucial to maintain the quality of Eagles' territories.

The levels of eccentricity observed in the breeding area compared with home-ranges suggest that important bias may occur when studies treat the breeding area as the centre of the home-range. Extrapolating from a radius around a nest is not always an accurate way of defining sensitive areas (Kochert *et al.* 1999, Whitfield *et al.* 2001, 2007). Moreover, individual variation in spatial use by Bonelli's Eagles may limit the validity of the use of average values of home-range size in management decisions. The generally heterogeneous spatial-temporal use of home-ranges by Eagles, in which some patches are used much more than others, should stimulate further investigation into the ecological, physical and biological patterns of these selected areas. Thus, we recommend research into the modelling of potential patterns as a means of defining the use of space by Bonelli's Eagles.

Bonelli's Eagle is considered a charismatic umbrella species in European Mediterranean ecosystems (Carrete *et al.* 2002b, Moleón *et al.* 2009), where it is well distributed or where there are known abandoned territories. These Mediterranean areas now suffer from serious human impact that has led to irreversible transformations of landscapes and the loss of valuable habitats. Knowledge of spatial patterns and home-ranges in Bonelli's Eagle is a useful tool on which to base *in situ* conservation measures and for implementing sustainable regional planning.

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