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Interannual home range variation, territoriality and overlap in breeding Bonelli's Eagles (*Aquila fasciata*) tracked by GPS satellite telemetry

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Abstract Animal movement patterns and use of space depend upon environmental resources (i.e., food availability), and on conspecific and interspecific interactions. We studied the home range of seven territorial Bonelli's Eagles (*Aquila fasciata*) tracked by GPS satellite telemetry over a period of 4–5 years to determine home range characteristics and annual and individual variations. Bonelli's Eagles hold an annual home range of Minimum Convex Polygon (MCP) = 205.6 km^2 (range 44.7–704.8 km^2) and Kernel 95 % = 44.4 km^2 (range 31.8–91.9 km^2). Eagles showed slight temporal variation in home range sizes, but a wide variation in use of space. Only 27.3 % of the accumulated home range was used during all seasons, while 30.3 % was used only during a single season. Areas around the nest, main hunting areas and roosting sites were utilised regularly every year in both breeding and non-breeding seasons. Accumulated home ranges were stabilised in year 3 of monitoring. Individuals displayed strong territoriality, even in non-breeding seasons, although eagles also made long trips (>15 km) well beyond their territorial boundaries, as assessed for the first time by GPS satellite telemetry. The overlap was slight for two adjacent pairs. In addition, we noticed a strong relationship between topographical landmarks and home range segregation. This study reinforces the idea that combining information on season patterns, conspecific distribution and topography can help define both the shape and size of home ranges more realistically.

Zusammenfassung

Jährliche Schwankungen von Aktionsraum, Territorialität und Raumüberlappung bei brütenden Habichtsadlern (*Aquila fasciata*), die mit Hilfe von GPS-Satelliten-Telemetrie verfolgt wurden

Bewegungsmuster und Raumnutzung von Tieren hängen von Ressourcen in ihrer Umwelt (d.h. Nahrungsverfügbarkeit) und inner- und zwischenartlichen Interaktionen ab. Wir haben die Aktionsräume von sieben territorialen Habichtsadlern (*Aquila fasciata*) untersucht, die mit Hilfe von GPS-Satelliten-Telemetrie vier bis fünf Jahre lang verfolgt wurden, um die Eigenschaften der Aktionsräume sowie jährliche und individuelle Variation zu ermitteln. Habichtsadler besitzen einen jährlichen Aktionsraum von 205.6 km^2 (Spannweite: 44.7–704.8 km^2) nach der Minimum-Konvex-Polygon(MCP)-Methode und von 44.4 km^2 (Spannweite: 31.8–91.9 km^2) nach der Kerndichteschätzungs-Methode. Die Adler wiesen nur geringe zeitliche Schwankungen in der Größe ihrer Aktionsräume auf, unterschieden sich jedoch deutlich in ihrer Raumnutzung. Lediglich 27.3 % des akkumulierten Aktionsraumes wurden in allen Jahreszeiten genutzt, 30.3

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% nur in einer einzigen Jahreszeit. Die Gebiete in Nestnähe, die Hauptjagdgebiete und die Schlafplätze wurden jedes Jahr sowohl innerhalb als auch außerhalb der Brutsaison genutzt. Die akkumulierten Aktionsräume wurden im dritten Beobachtungsjahr stabilisiert. Individuen zeigten ausgeprägte Territorialität, selbst außerhalb der Brutsaison, obwohl sie auch lange Flüge (>15 km) außerhalb ihrer Reviergrenzen unternahmen, wie erstmalig mit Hilfe von GPS-Satelliten-Telemetrie festgestellt werden konnte. Die Aktionsräume benachbarter Paare überlappten nur wenig. Zudem haben wir eine starke Beziehung zwischen topographischen Landmarken und Untergliederung des Aktionsraumes festgestellt. Diese Studie bekräftigt die Idee, dass das Kombinieren von Informationen über saisonale Muster, Verteilung von Artgenossen und Topographie dabei helfen kann, sowohl die Form als auch die Größe von Aktionsräumen realistischer zu definieren.

Introduction

Animal home ranges are defined by Burt (1943) as the area traversed by the individual in its normal activities of food gathering, mating and caring for young. Such area-restricted space use behaviour is determined by spatial, temporal and individual-level processes, and has fundamental consequences for many ecological processes (Börger et al. 2008). Many studies have focused on the factors determining home range (HR) size and shape (see the review in Adams 2001), and have highlighted the importance of factors like food availability (Grigione et al. 2002; Herfindal et al. 2005), habitat configuration (Whitfield et al. 2001) or conspecific and interspecific competitors (Newton 1979; Gargett 1990; Ottaviani et al. 2006). In contrast, knowledge about spatio-temporal variations in the size and shape of HRs has scarcely been documented (Börger et al. 2008).

Here, we focus on the endangered Bonelli's Eagle (*Aquila fasciata*), a territorial raptor that usually nests on cliffs (Cheylan 1973; Carrete et al. 2005; Larrey et al. 2007) and feeds preferably on common rabbits (*Oryctolagus cuniculus*), but also on other medium-sized preys such as Red-legged Partridges (*Alectoris rufa*) or Rock Pigeons (*Columba livia*) (Moleón et al. 2009). The importance of basic knowledge on its ecology could prove fundamental in conservation because this species has declined in the last three decades by about 20–50 % (Real and Mañosa 1997; Real 2004). Currently, the species is considered endangered in Spain (Real 2004) and is regarded as a Species of European Conservation Concern and Endangered in Europe by BirdLife International (2004).

Recent studies using terrestrial telemetry have described the annual HR of Bonelli's Eagle in different regions of Spain (Sanz et al. 2005; Bosch et al. 2009; Cabeza Arroyo and de la Cruz Solís 2011). However, as far as we know, no study has focused on the interannual and temporal variation in size and shape, and fidelity to these areas. In addition, this is the first time that movements of territorial adults have been assessed by means of GPS satellite telemetry. Previously, this technique has been successfully used to study juvenile dispersal patterns in this raptor (Cadahia et al. 2005, 2007; Gardiazábal et al. 2010).

The aims of this study are to: (1) describe the HR and core areas of territorial Bonelli's Eagles; (2) analyse their interannual variations; (3) and assess the territorial interactions between neighbouring eagles.

Methods

Study area

The study was conducted in the provinces of Valencia (Central-Eastern Spain) and Tarragona (Catalonia, North-Eastern Spain). The Valencia area is a mountainous zone with several river canyons along the Jucar River and its tributaries. Land cover consists mainly in Mediterranean forests of *Pinus halepensis* and *Quercus ilex* with secondary scrub, scattered with non-irrigated plantations with remains of riparian vegetation. Human presence is low, but several windfarms are being built or are planned for this area. Here, two neighbouring Bonelli's Eagle territories were studied, whose nests were spaced from each other by between 1.9 and 3.7 km. This distance is shorter than the mean nearest neighbouring distance (NND) described for Bonelli's Eagle in this area (8.2 km; Rico-Alcázar et al. 1999). The distance to the nearest nest of Golden Eagles (*Aquila chrysaetos*), a possible competitor species, is 5.7 km (own data). The Tarragona area is very similar to the aforementioned area, and is characterised by steep mountain ranges (from 400 to 1,100 m). Land cover consists mainly in secondary pinewoods and scrub. Human presence is low. The density of Bonelli's Eagle in this area is also very high (see Bosch et al. 2009).

Trapping and monitoring

We trapped seven territorial Bonelli's Eagles, two neighbouring adult males in Valencia, and three adult males and two adult females in Tarragona (Table 1). We used a radio-controlled bow-net trap lured with pigeons. Trapped birds were ringed with metal (the eagles from Valencia also had PVC rings) and they were equipped with a 45-g Argos/GPS PTTs (Microwave Telemetry, MD, USA). Transmitters were powered with solar panels and were fixed to birds as backpacks by a Teflon harness with a central ventral

Table 1 Characteristics of Bonelli's Eagle (*Aquila fasciata*) individuals tracked by territory, province, tracked period, total days (days) and total number of locations (*N Loc*)

Individual	Sex	Territory	Province	Tracking period		Days	N Loc
M1	♂	1	Valencia	23 May 06	9 Apr 10	1,396	2,952
M2	♂	2	Valencia	17 Aug 06	30 Jun10	1,393	4,414
M3	♂	3	Tarragona	18 Oct 05	13 Apr 06	175	289
M4	♂	4	Tarragona	5 Jul 07	29 Jan 11	1,284	4,892
F1	♀	5	Tarragona	27 Sep 06	27 Oct 06	30	60
M5	♂	5	Tarragona	29 Jun 07	17 Dec 10	1,248	4,002
F2	♀	5	Tarragona	13 Dec 07	26 Jun 08	193	476

rupture point (Garcelon 1985). PTTs were programmed to work between 6.00 h and 21.00 h. Individuals were sexed by biometric data such as body weight and length, and age (they were all determined as adults) by plumage characteristics (García Matarranz and Fernández 2011). Eagles were trapped and handled with all the necessary government permits.

Data analysis

Annual home range and core areas of territorial Bonelli's Eagles

Home ranges were estimated using Hawth's tools in ArcGIS 9.0 (Beyer 2004). We used Fixed Kernel methods (FK; Worton 1989). Moreover, 90 % Isopleths (FK90) were taken as an estimate of the total home range and 50 % isopleths (FK50) as core areas (Börger et al. 2006; Cardador et al. 2009). Minimum Convex Polygon MCP and 95 % Isopleths (FK95) were also calculated to make comparisons with previous studies. For comparative purposes, the selection of localisations for Fixed Kernel construction followed the same method as in Bosch et al. (2009).The smoothing factor was calculated by least-squared cross-validation LSCV (Gitzen and Millspaugh 2003; Gitzen et al. 2006; Horne and Garton 2006; Cardador et al. 2009). To evaluate seasonal variations, we defined two study periods: breeding season (BS) from January to July and non-breeding season (NBS) from August to December for Valencian eagles, and 1 month later for Catalonian eagles (del Hoyo et al. 1994; López-López et al. 2007; own data).We assessed the influence of breeding success in the home range size by comparing successful and non-successful individuals first for both sexes and after for males separately because of the small female sample size.

Satellite tracking also allowed us to assess long trips, defined as movements longer than 15 km from the nest or the central point of the nests most used.

Inter-annual variations in the home range

We calculated the accumulated home range, defined as the total area used by tracked eagles during the whole

monitoring period. We considered that this value was stable when the annual home range increased by less than 10 % and reached the asymptote (McLoughlin and Ferguson 2000). We also calculated home range fidelity, defined as the percentage of the total accumulated home range used during each year or study period (Laver and Kelly 2008; Börger et al. 2008).

Territoriality and interactions between neighbours

To assess territorial interactions, we used the satellite tracking data of the two neighbouring adult male eagles from Valencia (Table 1). Although recent studies indicate that at least 10 locations per month could estimate HR (Börger et al. 2006), our interest in studying the fine-level selection and interactions between the two neighbouring individuals involved maximising the number of locations for each individual, so we included all available localisations. A HR overlap was defined as the proportion of territory shared by neighbours during the whole tracking period for both individuals (5 years).

To study the effect of topography on spatial segregation, we evaluated the percentage of locations included in predefined geographical boundaries. These limits were drawn from the barriers and geographical landmarks of the territory (i.e., the maximum slope line, the peaks line and the different valleys) (Eason et al. 1999). We also evaluated the number and the distance of intrusions of each individual into the neighbouring territory. Intrusions were measured as the perpendicular distance in relation to the previously defined territorial boundary line. Due to precision errors of locations made by the GPS device, we only considered values above 36 m (double GPS minimum precision).

Statistical procedures

To evaluate the differences between HR and core area sizes, and between interannual differences and fidelity to HR, we used Kruskal-Wallis tests (Zar 1999). To analyse the differences in FK levels, sex, breeding season periods and overlap, we used Wilcoxon tests (Zar 1999). All the tests were conducted in a R-project, with statistical

Table 2 Home range size per year (km^2), maximum distance to nest (km) and number of locations (*N Loc*) per year

Individual	Year	MCP	FK 95 %	FK 90 %	FK 50 %	Max nest	N Loc
M1	2006	236.5	48.6	34.8	7.4	21.5	199
	2007	79.0	42.6	31.4	4.7	13.3	296
	2008	160.4	48.3	32.8	6.4	19.5	802
	2009	274.5	41.4	32.1	8.9	23.2	1,140
	2010	205.6	44.4	34.1	7.5	16.1	515
	Subtotal	205.6 ± 75.4	44.4 ± 3.3	32.8 ± 1.4	7.4 ± 1.6	19.5 ± 4	
M2	2006	124.6	46.9	35.7	9.6	13.6	775
	2007	162.7	37.1	28.9	8.0	28.4	458
	2008	242.9	45.2	34.7	7.5	31.4	1,184
	2009	215.6	47.6	36.6	10.4	17.1	1,727
	2010	68.4	41.6	29.6	6.7	8.3	270
	Subtotal	162.7 ± 70	45.2 ± 4.4	34.7 ± 3.6	8.0 ± 1.5	17.1 ± 9.8	
Median Valencia		184.2 ± 30.3	44.8 ± 0.6	33.8 ± 1.3	7.7 ± 0.4	18.3 ± 1.7	
M3	2005	44.7	36.9	27.9	6.9	6.4	130
	2006	78.0	54.1	42.1	11.7	9.4	159
	Subtotal	61.4 ± 23.5	45.5 ± 12.1	35 ± 10.1	9.3 ± 3.5	7.9 ± 2.1	
M4	2007	88.6	52.0	40.1	8.2	12.5	390
	2008	182.5	75.6	55.1	10.4	13.8	1,551
	2009	323.2	91.9	68.0	11.9	24.1	1,613
	2010	215.1	87.1	60.1	8.0	22.2	1,338
	Subtotal	198.8 ± 96.8	81.4 ± 17.8	57.6 ± 11.8	9.3 ± 1.9	18.0 ± 5.8	
F1	2006	704.8	44.4	35.3	8.9	50.9	60
M5	2007	345.9	31.8	23.9	4.4	40.7	354
	2008	343.3	43.1	31.3	6.5	21.9	1,152
	2009	140.0	36.4	27.3	5.5	18.0	1,253
	2010	151.4	33.2	24.0	4.8	13.7	1,243
	Subtotal	247.4 ± 115.0	34.8 ± 5.0	25.7 ± 3.5	5.2 ± 0.9	20.0 ± 11.9	
F2	2008	560.1	38.5	28.1	5.0	75.4	460
Median Tarragona		247.4 ± 267.7	44.4 ± 18.7	35.0 ± 12.6	8.9 ± 2.2	20.0 ± 28.0	
Total median		205.6 ± 234.2	44.4 ± 15.4	34.7 ± 10.4	8.0 ± 1.8	19.5 ± 24.2	

significance based upon two-tailed tests and $p < 0.05$. All the measurements are given with their average standard deviation.

Results

Annual home range and core areas of territorial Bonelli's Eagles

The HRs of all individuals were 205.6 ± 234.2 km^2 at MCP, 44.4 ± 15.4 km^2 at FK 95; 34.7 ± 10.4 km^2 at FK 90, and 8.0 ± 1.8 km^2 at FK 50 (Table 2). Significant differences were found between individuals (Kruskal–Wallis FK 50 $H_6 = 21.63$, $p < 0.005$; FK 90 $H_6 = 21.60$, $p = 0.001$). However, these differences disappeared when we excluded

male M4 (Kruskal-Wallis $H_5 = 8.04$, $p = 0.15$). We did not find any significant difference in HR size between sexes (Wilcoxon test FK 50 $W = 66$, $p = 0.067$; FK 90 $W = 42$, $p = 0.35$) or between years (Kruskal–Wallis test, FK 90 $H_5 = 4.83$, $p = 0.43$; FK 50 $H_5 = 6.35$, $p = 0.27$).

Home ranges were slightly larger during the breeding season (FK 50 = 7.2 ± 2.5 km^2; FK 90 = 36.0 ± 11.7 km^2; $n = 19$) than during the non-breeding season (FK 50 = 6.5 ± 2.1 km^2; FK 90 = 30.2 ± 10.3 km^2; $n = 19$), but only after excluding male M4 (FK 90 $W = 65$, $p = 0.003$). When comparing HR sizes between successful breeding individuals versus unsuccessful ones, we found that their core areas were similar and that HR FK 90 was slightly bigger in successful birds for both all individuals and males only (FK90 Kruskal–Wallis $H_1 = 3.60$, $p = 0.06$; FK50 $H_1 = 0.01$, $p = 0.92$) (Table 3).

Table 3 Territorial size (km^2) and home range fidelity per year of tracking (% HR/year) in each breeding period studied [breeding season (*BS*) vs. non-breeding season (*NBS*)] and at both levels (FK50 core area vs. FK90 home range)

		Annual HR	% HR/year			
			1	2	3	4
FK 50	BS	6.9 ± 2.5	40.3 ± 17	18.7 ± 4.6	14.2 ± 5.8	28.4 ± 25.4
	NBS	6.8 ± 2.1	32.4 ± 7.3	18.6 ± 1.4	19.4 ± 12.9	29.6 ± 9.9
FK 90	BS	32.7 ± 11.7	23.0 ± 5.4	18.7 ± 5.1	22.7 ± 8.1	35.6 ± 15.5
	NBS	29.1 ± 10.4	27.4 ± 7.2	20.7 ± 3.3	20.2 ± 12.9	31.7 ± 8.8

Interannual spatial variations in the home range

HR fidelity was relatively low. Only 27.3 % of the accumulated HR was regularly used during all the monitored seasons (*n* = 4), while 30.3 % was used only during a single season (Fig. 1). We did not find any statistical differences in HR fidelity either between reproductive periods (Wilcoxon test, FK 50 *W* = 111, *p* = 0.54; FK 90 *W* = 118, *p* = 0.72) or among individuals (Kruskal–Wallis H_3 = 1.03, *p* = 0.79) and FK levels (Wilcoxon test, *W* = 460, *p* = 0.49).

The accumulated HR for three of the four individuals studied stabilised after the third monitoring year to 48.37 ± 6.0 km^2 (at FK 90 level), except for one individual M4 whose accumulated HR was estimated at 948.7 km^2 and did not stabilise. The accumulated core area (FK 50) varied vastly between individuals from 8.8 km^2 of M5 to 23.8 km^2 of M4 (Fig. 2).

Longer movements

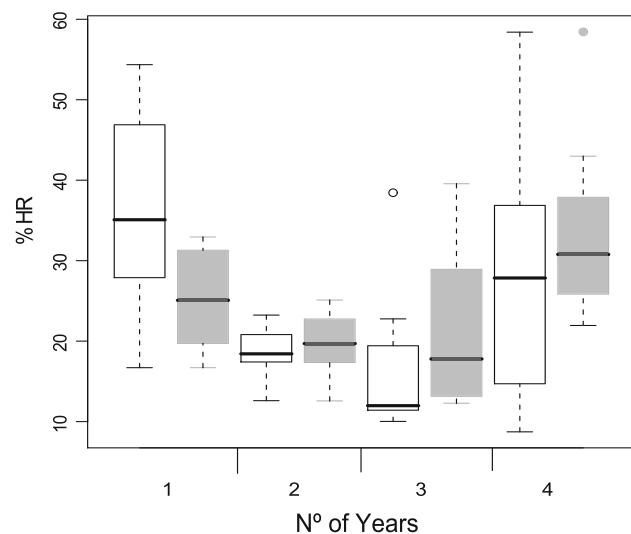We detected a total of 31 trips of >15 km, of which 74.2 % only lasted 1 day. The two longest trips, 5 and 6 days, were also the farthest ones, 74.5 and 50.9 km, and resulted in the specimens' death (F1 and F2, both poisoned). The maximum distance recorded from the nest was 74.5 km, but 61.3 % of long movements were made between 15 and 20 km (median = 19.5 ± 15.5 km). Excursions further away (>20 km) were recorded more frequently in autumn.

Territoriality and interactions between neighbours

Tracked Bonelli's Eagles showed strong territorially. In the two adjacent territories in Valencia, the overlapping area was very small throughout the monitoring period; at FK, the 50 level mean was 0.12 ± 0.23 % (*n* = 8) and at FK 90 the mean was 4.33 ± 1.30 % (*n* = 8). No differences were found between BS and NBS (Wilcoxon test, FK 50 *W* = 10, *p* = 0.62; FK 90, *W* = 2, *p* = 0.11). The topographic barrier marking the line of peaks and the Júcar river valley separated 99.99 % of all the locations of M2 and 99.98 % of those of M1 (Fig. 3). Intrusions were scarce (M1 = 32 and M2 = 42; mean per ind/year = 7.4 ± 6.2). The distances travelled within an adjacent territory were variable for both individuals and ranged from 38 m (the limit of the device's precision) to 4,074 m, but the median distance was short (429.3 ± 593.6 m).
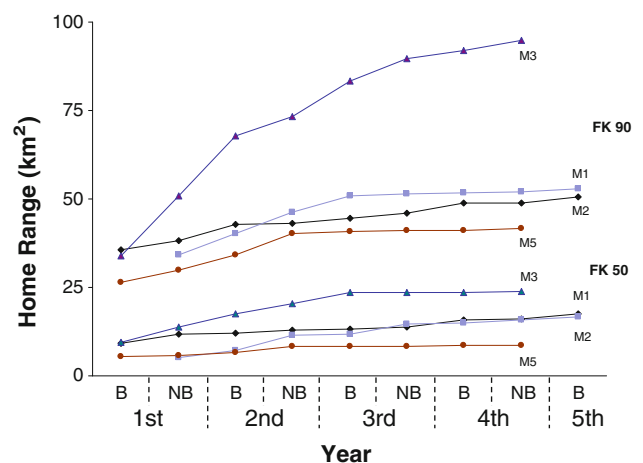

Fig. 1 Percentage of accumulated home range (%) used by Bonelli's Eagles (*Aquila fasciata*) during each study year (FK50, core area *white bars*; FK90, home range *grey bars*)

Fig. 2 Accumulated home range size throughout thel monitoring period. *B* breeding season; *NB* non breeding season; *FK50* corea area; *FK90* home range
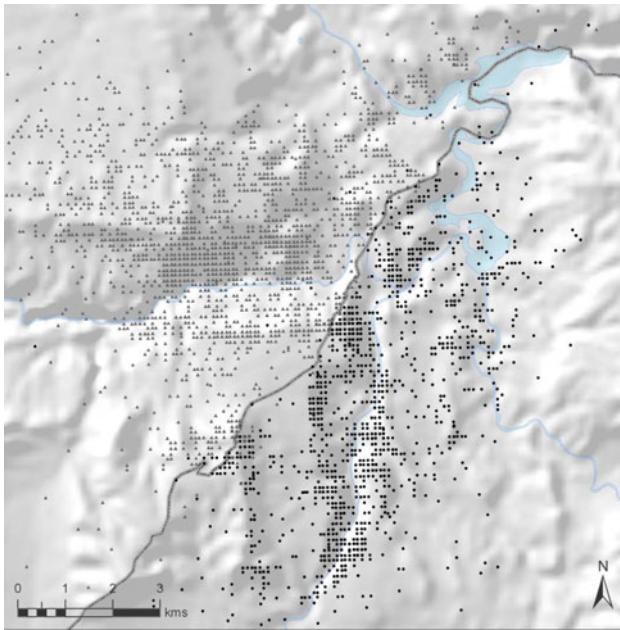
Fig. 3 Topographical boundaries and spatial localisation over the 4-year study for the Valencian satellite-tracked Bonelli's Eagles. *Grey triangles* M1, *black dots* M2

In addition, none of the eagles tracked in Tarragona was located inside another individual's HR. Moreover, two birds which took long exploratory trips avoided entering neighbouring territories.

Discussion

Bonelli's Eagles tracked by GPS satellite showed annual HR sizes, calculated by MCP, of 205.6 km^2 (range 44.7–704.8 km^2). This value is higher than those described in previous work using radio-tracked Bonelli's Eagles in Spain: Valencia (55–84 km^2; Sanz et al. 2005), Catalonia (50.3 km^2; Bosch et al. 2009) or Extremadura (22–109 km^2; Cabeza Arroyo and de la Cruz Solís 2011), and in southern France (50–115 km^2; Mure 1999). These differences are probably due to the increased ability of satellite trackers to detect the long-distance movements that eagles made outside their normal foraging areas. Although long trips are infrequent (0–4 per year), they remain unregistered by terrestrial radio tracking and may finally bias the MPC results, which is very sensitive to outliers (Börger et al. 2006). In contrast, the HR calculated at Kernel 95 % (44.4 km^2, range 31.8–91.9 km^2) was very similar to the results reported in previous works (see above). This confirms that kernel-based estimation methods produce more realistic HR results, irrespectively of sample size and outliers (Börger et al. 2006). Only male M4 had a much larger HR, probably because a wildfire burned part of its core area, including one

nest in a pine tree. In contrast, we did not find significant differences between territories of Valencia (where a wind-farm was under construction) and birds from Catalonia.

In our study, Bonelli's Eagles used slightly larger HR during the breeding season than during the non-breeding season. This pattern has been documented in other territorial raptors, as well as in the Spanish Imperial Eagle (*Aquila adalberti*) (Fernández et al. 2009) and in the Golden Eagle (Haworth et al. 2006). In contrast, other authors have found the opposite pattern for this species elsewhere (Bosch et al. 2009; Cabeza Arroyo and de la Cruz Solís 2011) and for Golden Eagles (Marzluff et al. 1997). These findings can be explained because, during reproduction, Bonelli's Eagles need two essential requirements inside their HR: a suitable place for nesting (principally cliffs) and one or several hunting areas (Newton 1979). When the breeding season ends, the eagles might move from nesting areas and concentrate in high quality areas with abundant prey availability (Mañosa et al. 1998; Balbontín 2005; González et al. 2006a). As a result, the distance to these areas might influence the HR size in opposite ways. Moreover, the breeding status does not appear to be a decisive factor to determine the HR size. This result is similar to that described by Bosch et al. (2009) and can be explained by the fact that Bonelli's Eagles need to defend their territory from neighbours. In our case, the neighbouring eagles tracked in Valencia showed no differences in the number of intrusions over the years when both breed successfully, or in the years in which breeding failure took place. In contrast, in Lesser Spotted Eagles (*Aquila pomarina*), successful males were seen to be more territorial than unsuccessful ones (Meyburg et al. 2006).

Although the eagles used similar-sized areas over the years, only around 30 % of their areas was used throughout the study period. HR fidelity is not a frequently evaluated topic in birds of prey. The few works published in the literature suggest that, for example, in Spanish Imperial Eagles, fidelity in two successive breeding seasons came close to 75 % (Fernández et al. 2009) and it was close to 70 % in Golden Eagles (Marzluff et al. 1997). Regularly used areas seem to correspond to habitat patches rich in potential prey (Sanz et al. 2005; Bosch et al. 2009). Low HR fidelity can be determined by the spatial-temporal heterogeneity in prey abundance or availability (Lôhmus 2003; Carrete et al. 2006). We suggest this behaviour to be an alternative strategy for use of local resources. Individuals seemed to regularly explore new patches each year to find new hunting areas. In fact, the eagles often forage intensively in only a few patches within their HRs, and although they do not seem to be able to regulate their main prey populations on a territorial scale (Moleón et al. 2011), they might regulate them locally within their HR.

Switching foraging patches may allow their prey populations to recover and favour interannual variations in space use.

On the other hand, we determined that eagles reached a maximum accumulated HR over a 3-year period. Börger et al. (2006) highlighted that the timing of the sampling period over which location data are collected can have a marked effect on the ability to identify temporal patterns. Therefore, in light of our data, properly quantifying the maximum HR size of territorial species, including annual variations by means of longer term tracking, appears to be a necessity (McLoughlin and Ferguson 2000: Fig. 2). In addition, the low spatial fidelity of inter-annual HRs has important implications for the management and conservation actions for this species. Therefore, our results suggest the need for long-term follow-ups to identify the effective interannual area of use and to avoid default buffer assignments to each occupied nest to conduct impact assessments (Bosch et al. 2009).

Our results also show that the overlap between neighbours was very low, even outside the breeding season, in spite of the individual inter-annual variations in the HR. This result contradicts previous studies showing a high degree of overlap (Bosch et al. 2009). This could be due to smoothing parameter calculations, a critical component in kernel density estimations (Börger et al. 2006). We used a more accurate smoothing factor calculated by least-squared cross-validation (LSCV; Gitzen et al. 2006; Börger et al. 2006) than the smoothing factor selected by default, as used by Bosch et al. (2009). LSCV is currently recommended (Seaman and Powell 1996; Seaman et al. 1999) for large simple sizes because it does not overestimate the HR.

Bonelli's Eagles made long-distance journeys outside their occupied nest during both the breeding and the non-breeding seasons. Although long-distance flights have been described in this species (i.e., up to 18 km; Bosch et al. 2009), they have been more frequently detected, perhaps due to the use of radio tracking. In fact, recent studies with satellite transmitters have found long-distance movements during breeding periods in the Spanish Imperial Eagle (i.e., up to 61 km; Fernández et al. 2009) or in the Lesser Spotted Eagle (Meyburg et al. 2007). In this latter case, the authors found that females visited areas located 57 km from their territories (Meyburg et al. 2007), while males moved shorter distances. This agrees with our results in which female movement distances were longer (means of 63.5 km for females and 18.7 km for males). Yet, given the small sample size, and that in both cases females died while making these excursions, we cannot draw more robust conclusions. In contrast, Spanish Imperial Eagle males made longer movements than females (Fernández et al. 2009). According to these authors, their results highlight that sighting adult individuals outside known breeding areas does not imply the existence of new territorial pairs (Fernández et al. 2009), which could also be applied to Bonelli's Eagle.

The reasons we suggest to explain these long-distance flights include their roles as an exploratory surveillance of the HR (Marzluff et al. 1997; McGrady et al. 2002), the search for food-rich patches (Fernández et al. 2009), exploring neighboring territories and potential partners (Meyburg et al. 2007) and, finally, human disturbances (González et al. 2006b; Fernández et al. 2009). Indeed, in our study, one of these long trips could be related to post-capture stress. The M5 bird was released after its capture and marking, and the following fix was registered 1 h later at 40.1 km from the capture point, revealing that the bird was flying very fast (near 80 km/h). During a 2-day period, we obtained no fix from him and the next fix was close to the nest.

The analysis of localisations in relation to topographic frontiers allowed us to test the low overlap and the small number of intrusions between neighbouring territories. Establishing boundaries might benefit from natural landmarks, thus minimising antagonist neighbour conflicts (Eason et al. 1999; Adams 2001; Mesterton-Gibbons and Adams 2003: Fig. 3). Our results also show, for the first time, that territory boundaries were extremely stable over the years.

In conclusion, our results provide interesting information about the spatio-temporal variations of the HR and the interactions between neighbouring Bonelli's Eagles for the first time using the unbiased method of GPS satellite telemetry. Our results reinforce the idea that HR use is dependent on dynamic interactions among multiple factors (Börger et al. 2008); therefore, combined information on territorial size, topography and conspecific interactions may help define territorial sizes more realistically.

References

Adams ES (2001) Approaches to the study of territory size and shape. Annu Rev Ecol Syst 32:277–303

Balbontín J (2005) Identifying suitable habitat for dispersal in Bonelli's eagle: an important issue in halting its decline in Europe. Biol Conserv 126:74–83

Beyer HL (2004) Hawth's analysis tools for ArcGIS. Available online at http://www.spatialecology.com/htools

BirdLife International (2009) Hieraaetus fasciatus. In: IUCN red list of threatened species. On line: http://www.iucnredlist.org. Accessed 15 May 2010

Börger L, Franconi N, De Michele G, Gantz A, Meschi F, Manica A, Lovari S, Coulson T (2006) Effects of sampling regime on the mean and variance of home range size estimates. J Anim Ecol 75:1393–1405

Börger L, Dalziel BD, Fryxell J (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. Ecol Lett 11:637–650

Bosch R, Real J, Tintó A, Zozaya E, Castell C (2009) Home-ranges and patterns of spatial use in territorial Bonelli's eagles Aquila fasciata. Ibis 152:105–117

Burt WH (1943) Territoriality and home range as applied to mammals. J Mammal 24:346–352

Cabeza Arroyo A, de la Cruz Solís C (2011) Individual and seasonal variability in territory size of three adult Bonelli's eagles Aquila fasciata in Extremadura (SW Spain). Ardeola 58:165–173

Cadahia L, Urios V, Negro JJ (2005) Survival and movements of satellite-tracked Bonelli's eagle Hieraetus fasciatus during their first winter. Ibis 147:415–419

Cadahia L, Urios V, Negro JJ (2007) Bonelli's eagle Hieraaetus fasciatus juvenile dispersal: hourly and daily movements tracked by GPS. Bird Study 54:271–274

Cardador L, Mañosa S, Varea A, Bertolero A (2009) Ranging behaviour of Marsh Harriers Circus aeruginosus in agricultural landscapes. Ibis 151:766–770

Carrete M, Sánchez-Zapata JA, Calvo JF, Lande R (2005) Demography and habitat availability in territorial occupancy of two competing species. Oikos 108:125–136

Carrete M, Sánchez-Zapata JA, Tella JL, Gil-Sánchez JM, Moleón M (2006) Components of breeding performance in two competing species: habitat heterogeneity, individual quality and density-dependence. Oikos 112:680–690

Cheylan G (1973) Notes sur la compétition entre l'aigle royal Aquila chrysaetoset l'aigle de Bonelli Hieraaetus fasciatus. Alauda 41:203–212

Del Hoyo J, Elliott A, Sargatal J (1994) Handbook of the birds of the world. Lynx, Barcelona

Eason PK, Cobbs GA, Trinca KG (1999) The use of landmarks to define territorial boundaries. Anim Behav 58:85–91

Fernández M, Oria J, Sánchez R, González LM, Margalida A (2009) Space use of adult Spanish imperial eagles Aquila adalberti. Acta Ornithol 44:17–26

Garcelon DK (1985) Mounting backpack telemetry packages on bald eagles. Institute for Wildlife Studies, Arcata

García Matarranz V, Fernández M (2011) In situ identification of male and female of Bonelli's eagle Aquila fasciata. In: Scher O, Lecacheur M (eds) La conservation de l'Aigle de Bonelli. Actes du colloque international. CEN LR, CEEP, CORA FS and DREAL LR. Montpellier, pp 38–42

Gardiazábal A, Ferreiro E, Alcántara M, Fernández A (2010) Dispersión juvenil y filopatría del Águila-azor perdicera (Hieraaetus fasciatus) en Aragón. Rev Anillamiento 25(26):41–49

Gargett V (1990) Black eagle, a study. Acorn, Johannesburg

Gitzen RA, Millspaugh JJ (2003) Comparison of least-squares cross-validation bandwidth options for kernel home range estimation. Wildl Soc Bull 31:823–831

Gitzen RA, Millspaugh JJ, Kernohan BJ (2006) Bandwidth selection for fixed-kernel analysis of animal utilization distributions. J Wildl Manag 70:1334–1344

González LM, Oria J, Margalida A, Sánchez R, Prada L, Caldera J, Aranda A, Molina JI (2006a) Effective natal dispersal and age of maturity in the threatened Spanish imperial eagle Aquila adalberti: conservation implications. Bird Study 53:285–293

González LM, Arroyo BE, Margalida A, Oria J, Sánchez R (2006b) Effect of human activities on behaviour and success of breeding Spanish imperial eagles Aquila adalberti. Anim Conserv 9:85–93

Grigione M, Beier P, Hopkins RA, Neal D, Padley WD, Schonewald CM, Johnson ML (2002) Ecological and allometric determinants of home range size for mountain lions (Puma concolor). Anim Conserv 5:317–324

Haworth PF, Mcgrady MJ, Whitfield DP, Fielding AH, McLeod DRA (2006) Ranging distance of resident golden eagles Aquila chrysaetos in western Scotland according to season and breeding status. Bird Study 53:265–273

Herfindal I, Linnell JDC, Odden J, Nilsen EB, Andersen R (2005) Prey density, environmental productivity and home-range size in the Eurasian lynx (Lynx lynx). J Zool 265:63–71

Horne JS, Garton EO (2006) Selecting the best home range model: an information-theoretic approach. Ecology 87:1146–1152

Larrey F, Roger T, Morvan R, Girard C (2007) Aigle de Bonelli, méditerranéen méconnu. Regard du vivant, Castelnau le Lez

Laver PN, Kelly MJ (2008) A critical review of home range studies. J Wildl Manag 72:290–298

Lôhmus A (2003) Are certain habitats better every year? A review and a case study on birds of prey. Ecography 26:545–552

López-López P, García-Ripollés C, Urios V (2007) Population size, breeding performance and territory quality of Bonelli's eagle (Hieraaetus fasciatus) in eastern Iberian Peninsula. Bird Study 54:335–342

Mañosa S, Real J, Codina J (1998) Selection of settlement areas by juvenile Bonelli's eagle in Catalonia. J Raptor Res 32:208–214

Marzluff JM, Knick ST, Vekasy MS, Schueck LS, Zarriello TJ (1997) Spatial use and habitat selection of Golden eagles in southwestern Idaho. Auk 114:673–687

McGrady MJ, Grant JR, Bainbridge IP, McLeod DRA (2002) A model of golden eagle(Aquila chrysaetos) ranging behaviour. J Raptor Res 36(Suppl 1):62–69

McLoughlin PD, Ferguson SH (2000) A hierarchical pattern of limiting factors helps explain variation in home range size. Ecoscience 7:123–130

Mesterton-Gibbons M, Adams ES (2003) Landmarks in territory partitioning: a strategically stable convention? Am Nat 161:685–697

Meyburg B-U, Meyburg C, Matthes J, Matthes H (2006) GPS satellite tracking of lesser spotted eagles Aquila pomarina: home range and territorial behaviour in the breeding area. Vogelwelt 127:127–144

Meyburg B-U, Meyburg C, Franck-Neumann F (2007) Why do female lesser spotted eagles (Aquila pomarina) visit strange nests remote from their own? J Ornithol 148:157–166

Moleón M, Sánchez-Zapata JA, Real J, García-Charton JA, Gil-Sánchez JA, Palma L, Bautista J, Bayle P (2009) Large scale spatio-temporal shifts in the diet of a predator mediated by an emerging infectious disease of its main prey. J Biogeogr 36:1502–1515

Moleón M, Sánchez-Zapata JA, Gil-Sánchez JM, Barea-Azcón JA, Ballesteros-Duperón E, Virgós E (2011) Laying the foundations for a human-predator conflict solution: assessing the impact of Bonelli's eagle on rabbits and partridges. PLoS One 6(7): e22851. doi:10.1371/journal.pone.0022851

Mure M (1999) Détermination par suivi visuel des habitats utilisés par l'Aigle de Bonelli Hieraaetus fasciatus en Ardèche. Alauda 67:289–296

Newton I (1979) Population ecology of raptors. Poyser, London

Ottaviani D, Cairns SC, Oliverio M, Boitani L (2006) Body mass as a predictive variable of home-range size among Italian mammals and birds. J Zool 269:317–330

Real J (2004) Águila-azor perdicera. (*Hieraaetus fasciatus*). In: Madroño A, González C, Atienza JC (eds) Libro Rojo de las aves de España. SEO/Birdlife, pp 154–157

Real J, Mañosa S (1997) Demography and conservation of Western European Bonelli's eagle *Hieraaetus fasciatus* populations. Biol Conserv 79:59–66

Rico-Alcázar L, Sánchez-Zapata JA, Izquierdo A, García JR, Morán S, Rico D (1999) Tendencias recientes en las poblaciones del Águila Real (*Aquila chrysaetos*) y el Águila-Azor Perdicera (*Hieraaetus fasciatus*) en la provincia de Valencia. Ardeola 46:235–238

Sanz A, Mínguez E, Anadón JD, Hernández VJ (2005) Heterogeneous use of space in three breeding territories of Bonelli's eagle *Hieraaetus fasciatus*. Ardeola 52:347–350

Seaman DE, Powell RA (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77:2075–2085

Seaman DE, Millspaugh JJ, Kernohan BJ, Brundige GC, Raedeke KJ, Gitzen RA (1999) Effects of simple size on kernel home range estimates. J Wildl Manag 63:739–747

Whitfield DP, Mcleod DRA, Fielding AH, Broad RA, Richard J, Evan RJ, Haworth PF (2001) The effects of forestry on golden eagles on the island of Mull, western Scotland. J Appl Ecol 38:1208–1220

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168

Zar JH (1999) Biostatistical analysis, 4th edn. Prentice-Hall, Upper Saddle River