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Article

Home-range Size and Space Use of Territorial Bonelli's Eagles (*Aquila Fasciata*) Tracked by High Resolution GPS/GSM Telemetry.

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Abstract: The current advent of GPS/GSM technology, with high resolution GPS dataloggers available, provides information of the highest quality, which is certainly better than previous tracking methods such as ARGOS telemetry or conventional VHF ground-tracking. As a result, this has improved our knowledge of home-range behavior and spatial ecology of many species, including large raptors. In this paper, we use satellite telemetry information to assess the home-range size and the role of individual, year, sex and season (breeding or non-breeding season) in space use of the Bonelli's eagle (*Aquila fasciata*). To this end, 51 territorial individuals (25 females and 26 males) were equipped with GPS/GSM transmitters and were tracked over a 7-year period (2015-2021) in eastern Spain. Overall, we recorded 4,791,080 fixes that were analyzed through kernel density methods (50%, 75% and 95% fixed kernels). Average home-range size according to the 95% kernel, 75% kernel and 50% kernel were 54.84 ± 20.78 km^2, 24.30 ± 10.18 km^2 and 11.17 ± 4.90 km^2, respectively. The home-range size of individuals occupying the same territory was similar, mainly due to the cooperative hunting behavior exhibited by the species. No interannual differences in the home-range of the same territory were found, showing a strong territorial fidelity of the breeding pairs. Overall, females' home-range size were smaller than males' ones due to the decrease of activity in the breeding season due to laying, incubation and chicks attendance at nests. No seasonal variation in the general home-range size was found. Moreover, we found low neighbor overlap among territories (4,18% ± 3.06%) that evidences a high level of intraspecific competition in Bonelli's eagles. Finally, this study highlights the advantages of the use of accurate telemetry information to improve our understanding of the spatial ecology of the endangered Bonelli's eagle, which ultimately will serve to better inform management actions for its conservation.

Keywords: animal ecology; conservation; raptors; telemetry; spatial ecology; management; Spain; behaviour; competition

Introduction

The home-range knowledge of the predatory species is of great interest to explain their behavior, the impact on the territory and their prey and for conservation. In the case of Bonelli's eagle (*Aquila fasciata*) is a species classified as "Near Threatened" (NT) in Europe (BirdLife International, 2015) and "Vulnerable" (VU) in Spain (RD 139/2011). This raptor has a large worldwide distribution, from the Iberian peninsula to Southeast Asian. In Spain occupies Mediterranean habitats with evergreen forest and an abrupt orography. The Bonelli's eagle is strongly territorial and defends its territory in pairs, where both individuals remain usually together for hunting, resting and flying.

Previous research about the home-range structure and space use of Bonelli's eagle were mostly based on radio-tracking technology (Bosch et al., 2010) or grounded on GPS-Argos telemetry (Pérez-García et al., 2013; Martínez-Miranzo et al., 2016). Recently, the use of GPS/GSM technology and dataloggers is allowing a large number of precise locations per day, thus favoring the advance of our understanding of the species' ecology.

This study provides a detailed assessment of space use and home-range size of territorial Bonelli's eagle in addition to the interannual, sex and seasonal variations, and the neighbor competitive pressure, which were also analyzed. This is the first time that this information has been assessed with GPS/GSM technology using dataloggers, with the highest precision and more than four million locations from 51 territorial Bonelli's eagles. Thus, this investigation provides new information on the spatial ecology of the species taking advantage of a larger sample size in terms of individuals and number of locations. We also compare our results with those obtained in previous studies and we further discuss them in relation to the quality of the information and the tracking technology employed. Hence, the main goals of this study are (i) to describe the home-range size and space use of territorial Bonelli's eagles; (ii) to evaluate the differences in home-range size between individuals of the same territory; (iii) to examine the influence of sex, year, season (breeding/non-breeding season) in spatial ecology; and (iv) to assess the territorial interaction between neighboring individuals.

Materials and Methods

Study area

The study area is located in eastern Spain including Albacete, Alicante, Castellón, Cuenca and Valencia provinces. The area covers approximately 7,600 km^2 with an average altitude ranging between the coastline and 1,200 m asl. The climate is Mediterranean with an average annual temperature that varies between 17°C in the coastal areas and 8°C in the inner mountains. The dominant landscape is composed by Mediterranean scrublands (*Pistacia lentiscus, Rosmarinus officinalis, Thymus vulgaris, Stipa tenacissima*), oak forests (*Quercus ilex, Q. faginea, Q. suber*) and Mediterranean evergreen forests (*Pinus halepensis, P. pinaster, P. nigra*).

Tracking

A total of 51 territorial adult and subadult Bonelli's eagles, 26 males and 25 females, were trapped in 22 different territories between 2015 and 2021 (see Table S1, in Supplementary Material). All individuals were tagged with GPS/GSM solar energy dataloggers manufactured by e-obs GmbH (Munich, Germany) and Ornitela (Vilnius, Lithuania) using a backpack configuration by means of a Teflon tubular harness designed to ensure that the harness fell off at the end of the tag's life. The weight of the transmitters was 48 and 50 g, respectively, and represented 1.66 to 2.86% (average = 2.25%, SD = 0.38%) of the body mass of eagles, below the 3% threshold established to avoid negative effects on behavior (Kenward, 2001; García et al. 2021). The duty cycle of the transmitters was programmed to record a GPS location at five-minute intervals (López-López et al., 2021), from 1 h before sunrise to 1 h after sunset, year-round. Transmitters' data was retrieved, stored and managed by means of the Movebank online repository (http://www.movebank.org/).

Ethic statement

Trapping and marking activities were authorized and conducted under permissions issued by regional authorities (Conselleria de Agricultura, Medio Ambiente, Cambio Climático y Desarrollo Rural, Generalitat Valenciana, Spain) and all efforts were made to minimize handling time to avoid any suffering to eagles.

Home-range analysis

We computed kernel density estimation (KDE) (Worton, 1989) to calculate home-range indicators using the "reproducible home-range" (*rhr*) R package for statistical computing (Signer and Balkenhol, 2015; R Core Team, 2020). We considered three kernel levels: the 50% kernel (K50% isopleth) that is the nuclear area of the home-range, where the nest is also located; the 75% kernel (K75% isopleth) which was considered as the intermediate area of active use, which includes the feeding and resting areas; and the 95% kernel (K95% isopleth) that was considered as the total area of the home-range (Samuel et al., 1985; Kie et al., 2010). We used the daily individual K50%, K75% and K95% isopleths computed with the whole tracked period from the following day after tagging to the end day of data transmission (e.g. animal’s death, end of transmission), knowing that 15 days is the minimum tracking period to obtain a complete home-range (Morollón et al. 2022).

Data analysis

Overall, we recorded 4,791,080 high precision GPS location of the 51 adult Bonelli's eagles (26 males and 25 females) tracked during the period 2015-2021.

We used Generalized Linear Mixed Models (GLMM; following the study of Zuur et al., 2009) to analyze the variation of the monthly average of daily home-range size within each territory, considering “Territory” and “Individual” as random factors. “Individual” was nested into “Territory” to account for the hierarchical structure (i.e., non-independence) of data (Harrison et al., 2018). The variation was examined in relation to three fixed binary factors: “Sex”, “Breeding” and “Season”. We consider “Breeding” as the annual breeding status of the pairs, taking into account the years in which each pair did reproduce (“Yes”) and those in which they did not (“No”). “Season” was determined by using individuals' data combining fieldwork observations and detailed tracking information. The “Breeding” season was considered from January to June and the “Non-breeding” season from July to December. The monthly average of daily home-range sizes according to the three different spatial estimators (K95%, K75% and K50%) were logarithmically transformed and were used as the response variable in the GLMMs. The R package used for the analyses was “*lme4*” (Bates et al., 2015).

Finally, we calculated the annual territorial overlap between the individuals who occupy simultaneously (i.e., in the same year) neighboring territories. The annual percentage of overlap between neighboring territories was compared using the 95% kernel under the “*raster*” R package (Hijmans, 2020).

Results

Individual home-range size

The average K95%, K75% and K50% were 54.86 ± 20.57 km^2 (range: 22.44 - 116.11 km^2), 23.91 ± 10.47 km^2 (range: 10.14 - 56.42 km^2), and 11.17 ± 4.86 km^2 (range: 4.59 - 27.32 km^2), respectively (Figure S1 and Table S2 in Supp. Mat.).

Differences in home-range size

Our results showed that home range size can be explained by the additive effects of “Sex”, “Breeding” and “Season” as well as the interactions between “Sex” and “Season” and “Breeding” and “Season”. The interaction between “Sex” and “Breeding” was not significant across the three different spatial estimators. The multiple interactions between the three effects was not significant across the three spatial estimators (K95%, K75% and K50%) (Table 1). Results of $R^2_{\text{conditional}}$ corresponding to the effect of combined fixed and random factors were 0.259, 0.282 and 0.295 according to K95%, K75% and K50%, respectively. The variance explained by random factors (obtained as $R^2_{\text{conditional}} - R^2_{\text{marginal}}$) was 0.217, 0.226 and 0.228 according to K95%, K75% and K50%, respectively.

Table 1: Generalized Linear Mixed Model (GLMMs) results of variation in home-range size using three different spatial estimators. Significant variables are highlighted in bold.

Dep. Variable	Indep. Variable	Estimate	Std. Error	t	d.f	p-Value
K95%	(Intercept)	3,817	0,071	53,729	20,727	**0,000**
	Sex (Female)	-0,084	0,023	-3,608	24,589	**0,001**
	Breeding (No)	0,042	0,019	2,179	1234,838	**0,030**
	Season (Breeding)	-0,016	0,017	-0,899	1221,358	0,369
	Sex (Female)*Breeding (No)	0,017	0,018	0,948	707,351	0,343
	Sex (Female)*Season (Breeding)	-0,048	0,017	-2,761	1222,184	**0,006**
	Breeding (No)*Season (Breeding)	0,094	0,018	5,373	1232,930	**0,000**
	Sex (Female)*Breeding (No)*Season (Breeding)	0,011	0,017	0,616	1226,767	0,538
K75%	**(Intercept)**	2,974	0,076	39,063	20,855	**0,000**
	Sex (Female)	-0,100	0,025	-3,906	24,274	**0,001**
	Breeding (No)	0,057	0,020	2,851	1237,418	**0,004**
	Season (Breeding)	-0,045	0,018	-2,513	1220,620	**0,012**
	Sex (Female)*Breeding (No)	0,026	0,019	1,349	753,480	0,178
	Sex (Female)*Season (Breeding)	-0,059	0,018	-3,274	1221,557	**0,001**
	Breeding (No)*Season (Breeding)	0,107	0,018	5,823	1232,456	**0,000**
	Sex (Female)*Breeding (No)*Season (Breeding)	0,017	0,018	0,957	1227,514	0,339
K50%	**(Intercept)**	2,180	0,078	28,047	20,908	**0,000**
	Sex (Female)	-0,106	0,027	-4,012	24,016	**0,001**
	Breeding (No)	0,067	0,020	3,313	1238,865	**0,001**
	Season (Breeding)	-0,063	0,018	-3,422	1220,088	**0,001**
	Sex (Female)*Breeding (No)	0,028	0,019	1,467	781,441	0,143
	Sex (Female)*Season (Breeding)	-0,063	0,018	-3,440	1221,091	**0,001**
	Breeding (No)*Season (Breeding)	0,116	0,019	6,252	1232,181	**0,000**
	Sex (Female)*Breeding (No)*Season (Breeding)	0,019	0,018	1,055	1227,970	0,292

In general, taking into account all individuals, the home range size was larger in males than in females, also larger during the non-breeding season and in the years that the pair did not bred.

During the breeding season, females showed a monthly average daily home range size (n = 283) of 48.3 ± 30.6 km^2, 20.6 ± 14.4 km^2 and 9.21 ± 6.65 km^2, according to K95%, K75% and K50%, respectively. On the other hand, the monthly average daily home range size of males (n = 319) were 62.8 ± 46.7 km^2, 27.4 ± 22.6 km^2 and 12.4 ± 10.8 km^2 according to K95%, K75% and K50%, respectively. In the same period, breeding individuals showed a monthly average daily home range size (n = 332) of 51.6 ± 43.7 km^2, 22.1 ± 21.1km^2 and 9.77 ± 9.90 km^2, according to K95%, K75% and K50%, respectively. In contrast, the monthly average daily home range size of non-breeding individuals (n = 270) were 61.5 ± 35.6 km^2, 26.9 ± 17.0 km^2 and 12.3 ± 8.13 km^2 according to K95%, K75% and K50%, respectively.

During the non-breeding season, females showed a monthly average daily home range size (n = 318) of 56.2 ± 35.3 km^2, 25.3 ± 17.3 km^2 and 11.7 ± 8.30 km^2, according to K95%, K75% and K50%, respectively. The monthly average daily home range size of males (n = 337) were 57.2 ± 29.8 km^2, 25.6 ± 13.9 km^2 and 11.8 ± 6.62 km^2 according to K95%, K75% and K50%, respectively. In this period, breeding individuals showed a monthly average daily home range size (n = 367) of 60.8 ± 32.4 km^2, 27.2 ± 15.6 km^2 and 12.5 ± 7.54 km^2, according to K95%, K75% and K50%, respectively. Moreover, the monthly average daily home range size of non-breeding individuals (n = 288) were 51.4 ± 32.1 km^2, 23.2 ± 15.3 km^2 and 10.7 ± 7.28 km^2 according to K95%, K75% and K50%, respectively. More detailed comparisons are available in Supplementary Material (Figures S2-S12).

An inflection point in the monthly home range pattern is observed in the months of June and December, both when comparing sexes and breeding status. Our results show that females increase their home range in June and it is similar to that of males until December, when it decreases again. Regarding the breeding status, breeding individuals increase their home range in June and decrease in December, while the opposite happens for non-breeding individuals (Figure 1).

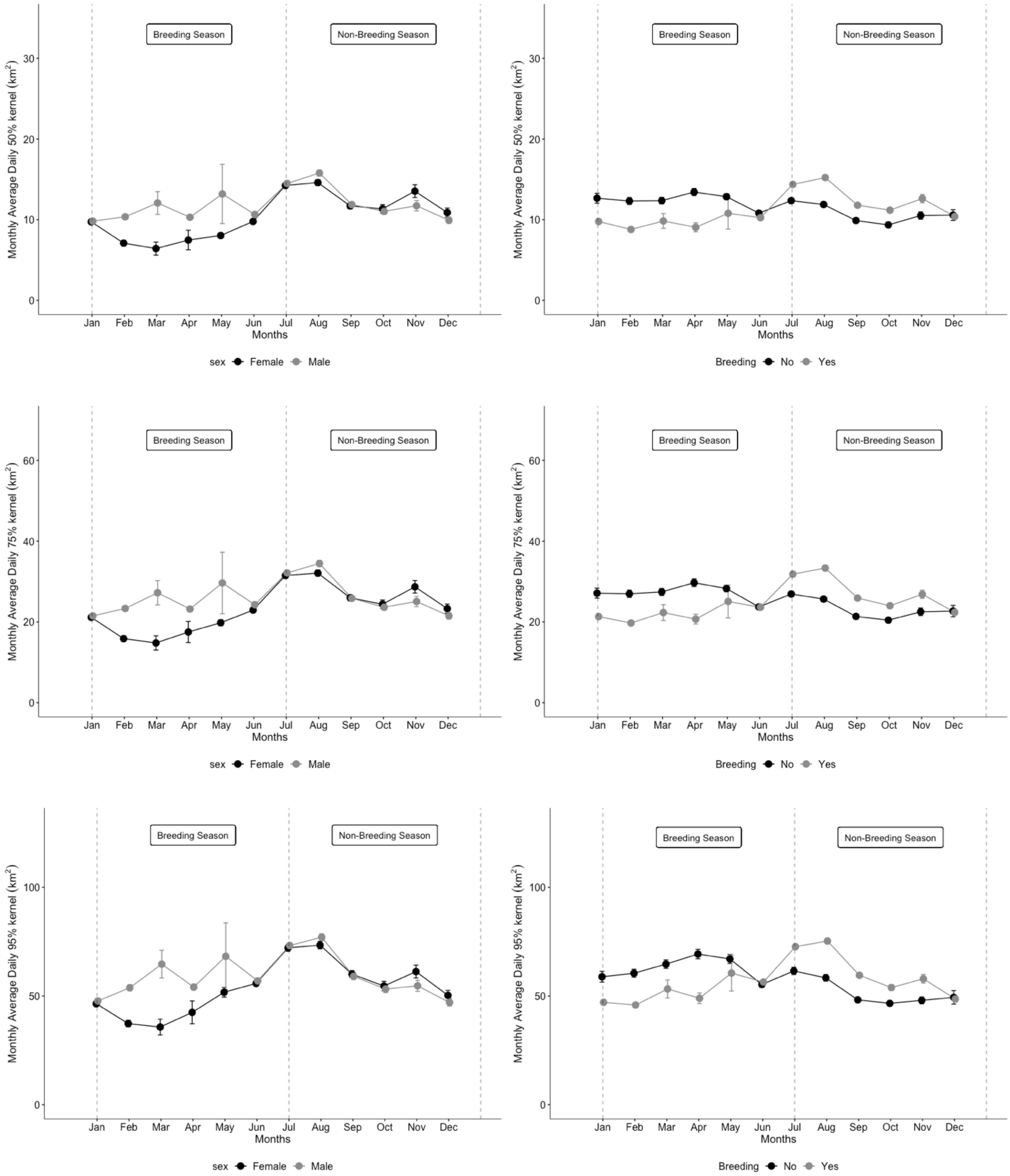

Figure 1. Seasonal differences between sexes (left) and breeding status (right) in monthly average of daily home range size (K95%, K75% and K50%) over the year. Vertical dashed black lines delimitate the different seasons.

Overlapping between neighboring territories

The overlap between neighbor home-ranges (K95%) of all individuals (n=38) showed an average value of 4.18 ± 5.53 % (Table 2). There were five territories (territories number 9, 11, 14, 17 and 22) that did not overlap (i.e., in the same year) with another neighboring territory or because there were isolated.

Table 2. Average and standard deviations of overlap percentages between simultaneous neighboring territories.

Territory 1 (T1)	Territory 2 (T2)	Average overlap % T1-T2	SD overlap % T1-T2	Average overlap % T2-T1	SD overlap % T2-T1
1	2	3.71	3.76	3.60	3.14
1	3	0.15	NA	0.07	NA
1	4	9.95	1.85	10.71	2.19
1	12	0.49	NA	0.30	NA
2	3	2.67	3.21	1.66	2.30
6	3	5.23	3.86	3.98	3.05
8	7	0.72	0.33	0.45	0.24
10	12	0.72	0.33	1.96	0.85
15	13	1.12	0.52	2.76	1.70
15	20	19.74	12.03	9.30	3.06
16	18	1.09	1.24	0.55	0.61
20	13	4.68	2.43	20.17	19.18
21	19	1.19	0.51	1.70	0.87
Total Average				**4.18**	**5.53**

Discussion

Our results show that Bonelli's eagles extend their home-range 54.84 ± 20.78 km^2 that ranges between 22 and 116 km^2 according to the 95% kernel. These results are larger than those described by Sanz et al. (2005) in Valencia (30.5 km^2, range: 15.82–44.48 km^2) using radio-tracking techniques, and those of Bosch et al. (2010) in Catalonia using radio-tracking techniques (36.1 km^2; range: 33.4–110.7 km^2). In contrast, our results are similar to those reported by Pérez-García et al. (2013) in Valencia and Tarragona (44.4 ± 15.4 km^2; range: 31.8–91.9 km^2) and Martínez-Miranzo et al. (2016) in Aragón that used GPS-Argos telemetry (57.25 km^2; range: 23.48–152.24 km^2). The higher accuracy of GPS locations in comparison to VHF radio-tracking accounts for the differences observed between methods (López-López, 2016).

The high variability in the home range across territories according to the 95% kernel may be due to different factors, such as geographical differences (Carrascal and Seoane, 2009), the potential occupation of more than one territory, the pressure from neighboring pairs, population density (López-López et al. 2007; Ferrer et al., 2015), interactions with humans (Perona et al., 2019) and/or the different quality of territories (Martínez-Miranzo et al. 2019). This indicates that there may be territories with a high availability of prey that allow pairs to survive for years, while others can be up to three or four times larger.

Home-range size by individuals

As expected in a territorial raptor, we did not find differences in home-range size (K95%, K75% and K50%) between individuals that occupy the same territory. This could be explained by the hunting behavior of the Bonelli’s eagle, which is characterized by a cooperative hunting technique in which both members of the pair search for prey together.

Differences in home-range size between sexes and seasons

Overall, males had larger home-range size than females. However, these sex differences were not previously described in the literature (Bosch et al, 2010; Pérez-García et al., 2013; Martínez-Miranzo et al. 2016). Sexual differences could be explained by the decrease in the home-range size of the females during the breeding season because they move less since they are in charge of the incubation and feeding of the chicks. This decrease in this period affects the general size of females’ home-range. In contrast, during the breeding period, males are in charge of prospecting the home-range for hunting and take the prey to the nest to feed the female and the chicks.

In contrast to previous studies, we found no differences in home-range size between the breeding and non-breeding seasons. For example, some studies reported larger home-range in the breeding season (Pérez -García et al. 2013), whereas others in the non-breeding season (Bosch et al. 2010; Martínez-Miranzo et al. 2016). These differences could be accounted for different quality of information since our data are based on a larger sample size (n = 51) and higher accuracy (GPS/GSM technology versus radio-tracking or Argos-GPS information).

Furthermore, when “season” and “sex” were taken into account at the same time, we detected a smaller home-range size of females in the breeding season due to the lesser movement during the incubation and chicks feeding. However, outside the breeding season, no differences were found between males and females in their home-range, since they spend most of their time together according to GPS information and direct observation in the field (i.e., resting, hunting, flying, etc.)

Differences in home-range size between breeding status and seasons

The inflection point in territory size observed in June (Figure 1), where breeding individuals increase their home range, coincides with the abandonment of the nest by juveniles. Breeding pairs during the breeding season have a more restricted territory because they are concerned with incubating and protecting the eggs and feeding the chicks when the eggs hatch. Once the juveniles are more independent, relaxation and less parental effort take place, and thus an increase in their home range. On the other hand, adult non-breeding individuals keep their territory constant throughout the year. Our results show that home-range of breeding individuals' increase whereas those of non-breeding individuals decrease. This can be explained since breeding pairs are the ones that set the tone as they have more energy requirements and are presumably in better physical shape, and the non-breeding pairs are the ones that need to adjust to these requirements, occupying or ceding territory depending on the breeding pairs. This inflection point is also seen in December, where the opposite happens, increasing the breeding area in the non-breeding individuals and decreasing in the breeding ones.

Overlap between neighboring territories

We observed a low overlap of home-ranges between neighbors. This could be explained by the high level of intraspecific competition of the Bonelli's eagle. The consistency of our results (4.18%) with previous studies is remarkable (Bosch et al. 2010, 4.1%; Pérez-García et al 2013, 4.33%).

Implications for conservation

Our study shows how accurate telemetry information can improve our understanding of the spatial ecology of the endangered Bonelli’s eagle. This is crucial, particularly taking into account that a detailed knowledge of the home-range behavior will ultimately serve to better inform management actions for its conservation.

Conflict of interest

The authors declare that no conflict of interest exists.

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Data Availability Statement

All data used in this study are publicly available upon request to data managers in the online data repository Movebank (www.movebank.org). The projects are: "Bonelli's eagle University of Alicante Spain" (project ID = 58923588), "Bonelli's eagle Alicante Spain" (ID = 430140799), "Bonelli's eagle University of Valencia Spain" (ID = 193515984) and "Movement ecology of large raptors in Spain" (ID = 640908212).

Authors' contribution

S.M., P.L.L and V.U. conceived the ideas, designed methodology, collected the data, wrote the manuscript and contributed critically to the drafts. S.M. and P.L.L analysed the data. P.L.L and V.U. gave final approval for publication.

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