

Article

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

Sara Morollón ¹, Vicente Urios ¹ and Pascual López-López ^{2,*}

¹ Grupo de Investigación Zoología de Vertebrados, Campus San Vicente del Raspeig, Universidad de Alicante, Edificio Ciencias III, 03080 Alicante, Spain; sara.morollon@ua.es (S.M.); vicenteuriuos@yahoo.es (V.U.)

² Movement Ecology Lab., Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia. C/Catedrático José Beltrán 2, 46980 Paterna, Valencia, Spain;

* Correspondence: Pascual.Lopez@uv.es

Abstract: High-resolution GPS/GSM dataloggers provide spatial information of the highest quality, which outperform 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 high-resolution GPS/GSM dataloggers to assess the home-range size and the role of sex, season (breeding or non-breeding season), and breeding status (reproductive or non-reproductive individuals) on the space use of 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 7 years (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). The average individual home-range size according to the 95%, 75%, and 50% kernels was $54.84 \pm 20.78 \text{ km}^2$, $24.30 \pm 10.18 \text{ km}^2$, and $11.17 \pm 4.90 \text{ km}^2$, respectively. Overall, the home-range size of individuals occupying the same territory was similar, mainly due to the cooperative hunting behavior exhibited by the species. We did not find interannual differences in the home-range size (95% fixed kernel) of the majority of individuals, showing a strong territorial fidelity of the breeding pairs. In general, females' home-range size was slightly smaller than males' size due to the decrease in activity in the breeding season as a result of laying, incubation, and chick attendance at nests. No seasonal variation in the 95% kernel was found, but it was found in the 75% and 50% kernels. In regard to the breeding status, higher home-range size was recorded in the non-reproductive individuals. Moreover, we found a low neighbor overlap among the territories ($4.18\% \pm 3.06\%$), which evidences a high level of intraspecific competition in the Bonelli's eagle. 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 behavior; birds of prey; datalogger; kernel density estimators; movement ecology; Spain

1. Introduction

The estimation of the home-range size and ranging behavior of predators is of great interest for their conservation, particularly endangered species. This is the case of the Bonelli's eagle (*Aquila fasciata*), a long-lived medium-sized raptor classified as "Near Threatened" (NT) in Europe [1] and "Vulnerable" (VU) in Spain (RD 139/2011). This raptor has a large worldwide distribution, from the Iberian peninsula to Southeast Asia [2]. In Spain, this species usually occupies Mediterranean habitats with evergreen forests and an abrupt orography where it found adequate places for nesting in cliffs and occasionally

on trees. The Bonelli's eagle shows a strongly territorial behavior, defending its territory in pairs, where both individuals usually remain together [3–6].

Previous research works in regard to the home-range size and ranging behavior of the Bonelli's eagle were mostly based on radio-tracking technology [7] or based on GPS-Argos telemetry [8,9]. Recently, the use of GPS/GSM dataloggers allows for 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 the territorial Bonelli's eagle in Mediterranean landscapes. In addition, we further explored the role of sex, seasonal variations, breeding status, and the neighbor competitive pressure on home-range size. This is the first time that this information has been assessed with high-resolution GPS/GSM technology incorporating the highest accuracy. Therefore, this investigation provides new information on the spatial ecology of the species while taking advantage of a larger sample size in terms of individuals and number of locations in comparison to previous works. As a result, the main goals of this study are to (i) describe the home-range size and ranging behavior of territorial Bonelli's eagles; (ii) examine the influence of sex, season (breeding/non-breeding season), and breeding status (reproductive/non-reproductive individuals) in spatial ecology; and (iii) assess the territorial interaction between neighboring individuals.

2. Materials and Methods

2.1. Study Area

The study area is located in eastern Spain, including Albacete, Alicante, Castellón, Cuenca, and Valencia provinces. The area covers approximately 7600 km² with an average altitude ranging between the coastline and 1200 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 of 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*).

2.2. Tracking

A total of 51 territorial adult and subadult Bonelli's eagles, 26 males and 25 females, were trapped in 22 different territories (Figure 1) by means of a remotely activated folding net between 2015 and 2021 (see Table S1, in Supplementary Materials). The trap was always under surveillance by the researchers which were hidden nearby. The trap was only activated once it was checked that the target individuals were inside. Both pair members of each territory, male and female, were trapped together in most cases. When a turnover in one of the pair members was detected (usually after the death of the former member), we trapped and marked the new member. 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, which is 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 [10,11]. The duty cycle of the transmitters was programmed to record a GPS location at 5-min intervals [4,5], from 1 h before sunrise to 1 h after sunset, year-round. Moreover, transmitters recorded one fix per hour during nighttime. Transmitters' data were retrieved, stored, and managed by means of the Movebank online repository (<http://www.movebank.org/> (accessed on 07/12/22)).

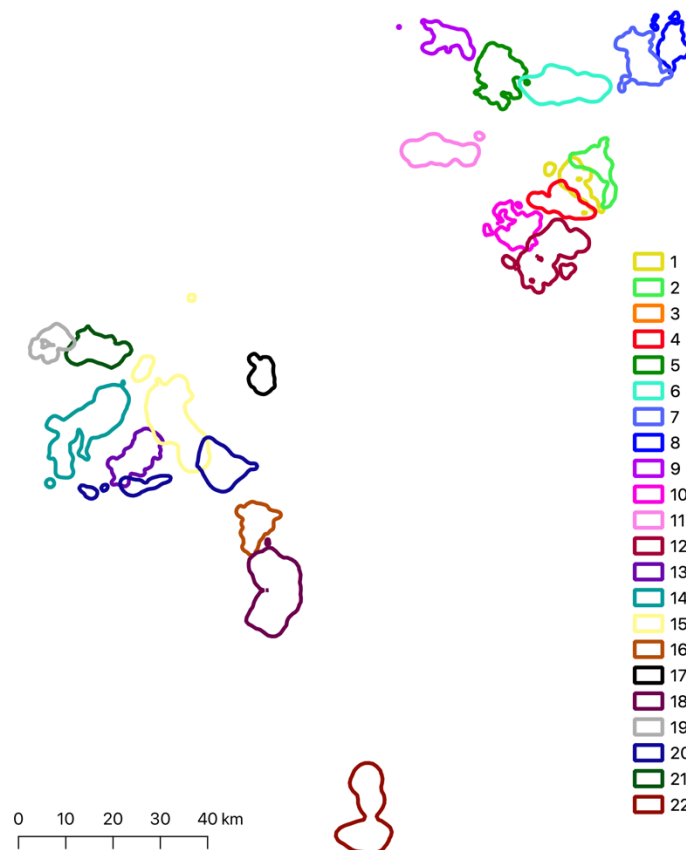


Figure 1. Spatial arrangement of 22 Bonelli's eagle territories in the study area. Due to conservation reasons, the map is hidden to avoid the exact location of each territory.

2.3. Ethical Statement

Trapping and marking activities were authorized and conducted under permissions issued by regional authorities (Generalitat Valenciana and Junta de Comunidades de Castilla-La Mancha, Spain) and all efforts were made to minimize handling time to avoid any suffering to the eagles.

2.4. Home-Range Analysis

We used kernel density estimation (KDE) methods [12] to compute home-range size using the “reproducible home-range” (rhr) R package [13,14]. The KDE methods are widely used to calculate home-range size in different taxonomic groups, such as in fishes (e.g., [15]), reptiles (e.g., [16]), mammals (e.g., [17–22]), and birds (e.g., [4,5,23–28]). We preferably used KDE rather than autocorrelated KDE (AKDE) methods since in our experience, computations based on AKDE methods resulted in an unrealistic larger home-range size (debated in Ref. [29]).

We considered three kernel levels: The 50% kernel (K50% isopleth) which is the nuclear area of the home-range, where the nest is usually located; the 75% kernel (K75% isopleth) which is considered as the intermediate area of active use, and includes the feeding and resting areas; and the 95% kernel (K95% isopleth) which is considered as the total area of the home-range [30,31]). 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), with the knowledge that 15 days is the minimum tracking period to obtain a complete home-range [5].

2.5. Data Modeling

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

We used generalized linear mixed models (GLMM; [32]) 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 [33]. The variation in home-range size was examined in relation to three fixed binary factors: “Sex”, “Breeding”, and “Season”. We considered “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 using individuals’ data combining field-work observations and detailed tracking information, and was divided into two different periods: Breeding season and non-breeding season. The “Breeding season” was considered from January to June (since all pairs breed within these months) 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” [34].

We used a one-way ANOVA test to analyze the interannual differences in the monthly average of daily home ranges (95% kernel) of the individuals occupying the same territory in different years (i.e., individuals tracked for at least 2 years).

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 [35].

3. Results

3.1. Individual Home-Range Size

The average K95%, K75%, and K50% were $54.86 \pm 20.57 \text{ km}^2$ (range: 22.44–116.11 km^2), $23.91 \pm 10.47 \text{ km}^2$ (range: 10.14–56.42 km^2), and $11.17 \pm 4.86 \text{ km}^2$ (range: 4.59–27.32 km^2), respectively (Figure S1 and Table S2 in Supplementary Materials).

3.2. 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 were 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 (GLMM) 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	<0.001
	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

K75%	Breeding (No) × Season (Breeding)	0.094	0.018	5.373	1232.930	<0.001
	Sex (Female) × Breeding (No) * Season (Breeding)	0.011	0.017	0.616	1226.767	0.538
	(Intercept)	2.974	0.076	39.063	20.855	<0.001
	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	<0.001
K50%	Sex (Female) × Breeding (No) × Season (Breeding)	0.017	0.018	0.957	1227.514	0.339
	(Intercept)	2.180	0.078	28.047	20.908	<0.001
	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	<0.001
	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 (K95%, K75%, and K50%) was larger in males than in females ($p < 0.001$ in all cases). Moreover, it was larger during the non-breeding season (only K75% with $p = 0.012$ and K50% with $p = 0.001$) and in the years that the pair did not breed ($p = 0.030$; $p = 0.004$; and $p = 0.001$, respectively) (Table 1).

Taking into account the Season and the Sex, females showed a smaller monthly average daily home-range size than males during the breeding season (Tables 1 and 2; Figure 2). In contrast, there were no differences in home-range size during the non-breeding season (Tables 1 and 2; Figure 2).

Table 2. Monthly average (\pm standard deviation) daily home-range size (km^2) of the three levels (K95%, K75%, and K50%) taking into account “Season”, “Sex”, and “Breeding Status”.

Season	Sex	Breeding Status	n	K95%	K75%	K50%
Breeding	Females	-	283	48.30 \pm 30.60	20.60 \pm 14.40	9.21 \pm 6.65
Breeding	Males	-	319	62.80 \pm 46.70	27.40 \pm 22.60	12.40 \pm 10.80
Non-Breeding	Females	-	318	56.20 \pm 35.30	25.30 \pm 17.30	11.70 \pm 8.30
Non-Breeding	Males	-	337	57.20 \pm 29.80	25.60 \pm 13.90	11.80 \pm 6.62
Breeding	-	No	270	61.50 \pm 35.60	26.90 \pm 17.00	12.30 \pm 8.13
Breeding	-	Yes	332	51.60 \pm 43.70	22.10 \pm 21.10	9.77 \pm 9.90
Non-Breeding	-	No	288	51.40 \pm 32.10	23.20 \pm 15.30	10.70 \pm 7.28
Non-Breeding	-	Yes	367	60.80 \pm 32.40	27.20 \pm 15.60	12.50 \pm 7.54

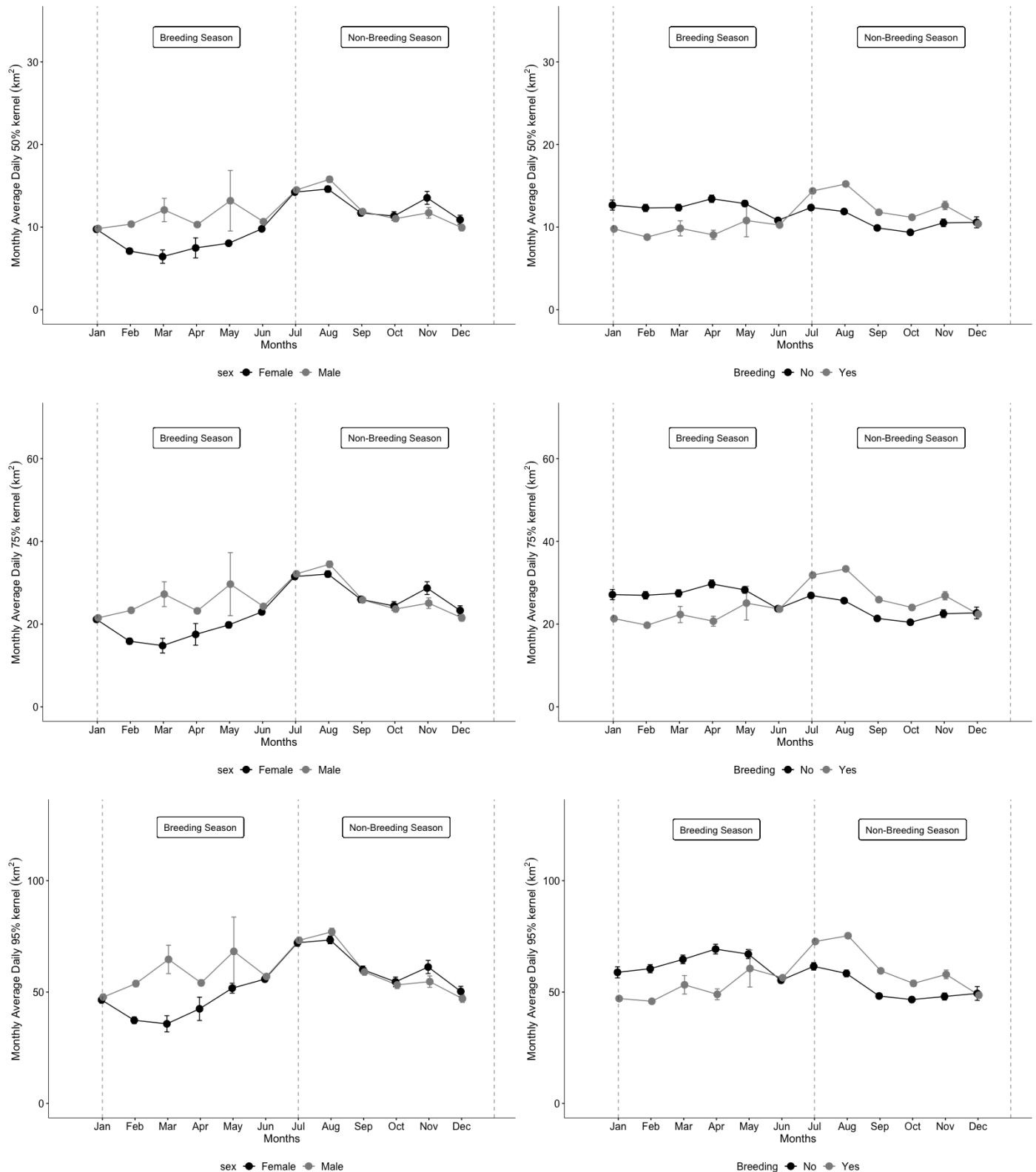


Figure 2. Seasonal differences between sexes (left) and breeding status (right) in the monthly average of daily home-range size (K95%, K75%, and K50%) over the year. Vertical dashed black lines delimitate the different seasons.

Taking into account the Season and the Breeding Status, non-reproductive individuals showed a larger monthly average daily home-range size than reproductive individuals during the breeding season (Tables 1 and 2; Figure 2). During the non-breeding season, the reproductive individuals showed a larger monthly average daily home-range size

than non-reproductive individuals (Tables 1 and 2; Figure 2). More detailed comparisons are available in Supplementary Material (Figures S2–S12).

Our results show an inflection point in the monthly home-range size pattern in June and December, both when comparing sexes and breeding status. Females increase their home-range in June, which is similar to males until December, then it decreases again. In regard to the breeding status, breeding individuals increase their home-range in June and decrease in December, while the opposite occurs for non-breeding individuals (Figure 2).

There were no interannual differences in the monthly average of daily home-range size according to the 95% kernel in the majority of the individuals who were tracked for 2 years or more (68.18%, $n = 44$) (Table S3 in Supplementary Materials).

3.3. Overlapping between Neighboring Territories

The overlap between neighbor home-ranges (K95%) of all individuals ($n = 38$) showed an average value of $4.18\% \pm 5.53\%$ (Table 3). Five territories (numbers 9, 11, 14, 17, and 22) were not used in this analysis since they had no neighboring territories occupied in the same year or since there were isolated.

Table 3. Average and standard deviations (SD) of overlap percentages between simultaneous neighboring territories.

Territory 1 (T1)	Territory 2 (T2)	Average Overlap %	SD Overlap %	T1-T2	Average Overlap %	SD Overlap %
		T1-T2	T2	lap %	T2-T1	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				4.18	5.53	

4. Discussion

Our results show that Bonelli’s eagles extend their home-range $54.84 \pm 20.78 \text{ km}^2$, which ranges between 22 and 116 km^2 according to the 95% kernel. These results are larger than those described by [36] in Valencia (30.5 km^2 ; range: $15.82\text{--}44.48 \text{ km}^2$) and [7] in Catalonia (36.1 km^2 ; range: $33.4\text{--}110.7 \text{ km}^2$), with both using radio-tracking techniques. In contrast, our results are similar to those reported by [8] in Valencia and Tarragona ($44.4 \pm 15.4 \text{ km}^2$; range: $31.8\text{--}91.9 \text{ km}^2$) and [9] in Aragón, with both using GPS-Argos telemetry (57.25 km^2 ; range: $23.48\text{--}152.24 \text{ km}^2$). The higher the accuracy of GPS locations in comparison to the VHF radio-tracking accounts for the differences observed between the methods [37].

The high variability in the home-range size across territories may be due to different factors, such as geographical differences [38], pressure from neighboring pairs, population density [3,39], interactions with humans [23], and/or different quality of territories [40]. This indicates that there might be territories with high availability of prey that allow pairs to survive for years, while others can be up to three or four times larger.

4.1. Differences in Home-Range Size between Sexes and Seasons

Overall, males showed larger home-range size than females. However, these sex differences were not previously described in the literature [7–9,36]. Sexual differences could be explained by the decrease in the home-range size of the females during the breeding season since they move less due to the fact that they are in charge of the incubation and chicks' attendance [4]. The 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 delivering the prey to the nest to feed the female and the chicks [4].

In contrast to previous studies, we found no differences in home-range size between the breeding and non-breeding season, at least according to K95%. For example, some studies reported larger home-range size in the breeding season [8], whereas others were reported in the non-breeding season [7,9]. These differences could be accounted for the 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' attendance. However, during the non-breeding season, no differences were found between males and females in their home-range. This could be explained by the fact that they spend most of their time together according to the GPS information and direct observation in the field (i.e., resting, cooperative hunting, flying, etc.).

4.2. Differences in Home-Range Size between Breeding Status and Seasons

The inflection point in territory size observed in June (Figure 2), where breeding individuals increase their home-range, coincides with the abandonment of the nest by juveniles. Once the juveniles are more independent, relaxation and less parental effort take place, and thus an increase in their home-range is observed. On the other hand, non-breeding individuals maintain constant territory throughout the year. Our results show that the home-range of breeding individuals increases, whereas those of non-breeding individuals decreases. This can be explained by the fact that breeding pairs are the ones that set the tone since they have more energy requirements and are presumably in better physical shape. In contrast, the non-breeding pairs are the ones that need to adjust to these requirements, occupying or ceding the territory, depending on the breeding pairs. Moreover, this inflection point is observed in December, where the opposite occurs, increasing the breeding area in non-breeding individuals and decreasing in the breeding ones.

4.3. 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 Bonelli's eagle. The consistency of our results (4.18%) with previous studies is remarkable (4.1% in [7]; 4.33% in [8]). Bonelli's eagles are territorial raptors that exhibit agonistic behavior in the case of territorial invasion and they even extend their territory in the case of disappearance of a neighboring pair (authors' pers. obs.).

4.4. Implications for Conservation

The information provided in this study on the home-range size and ranging behavior of the Bonelli's eagle throughout the annual cycle provides a useful tool for the management and conservation of this species. Bonelli's eagle is one of the key species used to delimitate protected areas in Mediterranean ecosystems. Therefore, a detailed knowledge of the home-range size and its variation throughout the annual cycle could be used for a significantly effective design. Moreover, this information will make it possible to assess the impacts of various anthropic activities and to mitigate or even eliminate them. In

contrast to the general pattern used decades ago, in which land planning was focused only on protecting nesting areas and the immediate nearby, our study shows that the continued presence of pairs throughout its territory year-round (see K95%, K75%, and K50%) requires a comprehensive protection or management of the entire home-range, including not only nesting areas, but also feeding and resting grounds.

Supplementary Materials: The following supporting information can be downloaded at: www.mdpi.com/xxx/s1. Figure S1: Monthly average of the daily home-range size at three different levels (K95%, K75%, and K50%). Figure S2: Boxplot of the monthly average of the daily home-range size (K95%) per territory. Figure S3: Differences in daily home-range size (K95%) among years. Figure S4: Differences in daily home-range size (K95%) among years and territories. Figure S5: Differences in daily home-range size (K95%) among years per individual. Figure S6: Differences in daily home-range size (K95%) between sexes. Figure S7: Differences in daily home-range size (K95%) between sexes and territories. Figure S8: Differences in daily home-range size (K95%) between seasons. Figure S9: Differences in daily home-range size (K95%) between seasons and territories. Figure S10: Differences in daily home-range size (K95%) between sexes, seasons, and territories. Figure S11: Differences in daily home-range size (K95%) between the breeding status. Figure S12: Differences in daily home-range size (K95%) between the breeding status and individuals. Table S1: Summary information of the 51 Bonelli's eagles tracked by GPS/GSM satellite telemetry in eastern Spain. Table S2: Summary statistics of daily home-range size (km²) per individual according to three different spatial estimators (i.e., K95%, K75%, and K50%). Table S3: ANOVA results of interannual variation in monthly average daily home-range size according to the 95% kernel by individual. Significant variables are highlighted in bold.

Author Contributions: S.M., P.L.-L., and V.U. conceived the ideas, designed the methodology, collected the data, wrote the manuscript, and contributed critically to the drafts. S.M. and P.L.-L. analyzed the data. P.L.-L. and V.U. provided the final approval for publication. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by Red Eléctrica de España, ACCIONA Eólica de Levante, LafargeHolcim and the Wildlife Service of the Valencian Community regional government (Conselleria d'Agricultura, Desenvolupament Rural, Emergència Climàtica i Transició Ecològica, Generalitat Valenciana, Spain).

Institutional Review Board Statement: Ethical review and approval were waived for this study because it does not include animals used for experimentation (see Ethical Statement).

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 (accessed 07/12/22)). 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).

Acknowledgments: We would like to thank F. García, J. Giménez, V. García, J. De la Puente, A. Bermejo, M. Montesinos, J.M. Lozano, M. Aguilar, M.A. Monsalve, A. Perona, A. López, I. Estellés, O. Egea, F. Cervera, J. Crespo, M. Vilalta, M. Surroca, T. De Chiclana, S. Ferreras, C. García, E. Mondragón, T. Camps, M. Marco, and V. Agustí for their help in fieldwork and eagles trapping. Special thanks to J. Jiménez of the regional government (Generalitat Valenciana's Wildlife Service) for his help with this project. This paper takes part in Sara Morollón's doctoral thesis at the University of Alicante.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. BirdLife International. Species Factsheet: *Aquila Fasciata*. 2022. Available online: <http://www.birdlife.org> (accessed on 2 July 2022).
2. Del Hoyo, J.; Elliot, A.; Sargatal, J. *Handbook of the Birds of the World*; Linx Edicions: Barcelona, Spain, 1994; Volume II. New world vultures to guineafowl.
3. López-López, P.; García-Ripollés, C.; Urios, V. Population Size, Breeding Performance and Territory Quality of Bonelli's Eagle *Hieraetus Fasciatus* in Eastern Spain. *Bird Study* **2007**, *54*, 335–342.
4. López-López, P.; Perona, A.; Egea-Casas, O.; Morant, J.; Urios, V. Tri-Axial Accelerometry Shows Differences in Energy Expenditure and Parental Effort throughout the Breeding Season in Long-Lived Raptors. *Curr. Zool.* **2022**, *68*, 57–67.

5. Morollón, S.; Urios, V.; López-López, P. Fifteen Days Are Enough to Estimate Home-Range Size in Some Long-Lived Resident Eagles. *J. Ornithol.* **2022**, *163*, 849–854.
6. Morollón, S.; López-López, P.; Urios, V. A New View of Territoriality in Large Eagles: The Territory Pre-Exists Regardless of Their Occupants. *Res. Sq.* **2022**. <https://doi.org/10.21203/rs.3.rs-1665218/v1>.
7. Bosch, R.; Real, J.; Tinto, A.; Zozaya, E.L.; Castell, C. Home-ranges and Patterns of Spatial Use in Territorial Bonelli's Eagles *Aquila Fasciata*. *IBIS* **2010**, *152*, 105–117.
8. Pérez-García, J.M.; Margalida, A.; Afonso, I.; Ferreira, E.; Gardiazábal, A.; Botella, F.; Sánchez-Zapata, J.A. Interannual Home Range Variation, Territoriality and Overlap in Breeding Bonelli's Eagles (*Aquila Fasciata*) Tracked by GPS Satellite Telemetry. *J. Ornithol.* **2013**, *154*, 63–71.
9. Martínez-Miranzo, B.; Banda, E.; Gardiazábal, A.; Ferreira, E.; Aguirre, J.I. Differential Spatial Use and Spatial Fidelity by Breeders in Bonelli's Eagle (*Aquila Fasciata*). *J. Ornithol.* **2016**, *157*, 971–979.
10. Kenward, R.E. *A Manual for Wildlife Radio Tagging*; Academic Press: Cambridge, MA, USA, 2000.
11. García, V.; Iglesias-Lebrija, J.J.; Moreno-Opo, R. Null Effects of the Garcelon Harnessing Method and Transmitter Type on Soaring Raptors. *IBIS* **2021**, *163*, 899–912.
12. Worton, B.J. Kernel Methods for Estimating the Utilization Distribution in Home-range Studies. *Ecology* **1989**, *70*, 164–168.
13. Signer, J.; Balkenhol, N. Reproducible Home Ranges (Rhr): A New, User-friendly R Package for Analyses of Wildlife Telemetry Data. *Wildl. Soc. Bull.* **2015**, *39*, 358–363.
14. R Core Team. *R: A Language and Environment for Statistical Computing*; R Core Team: Vienna, Austria, 2022.
15. Wells, R.; TinHan, T.C.; Dance, M.A.; Drymon, J.M.; Falterman, B.; Ajemian, M.J.; Stunz, G.W.; Mohan, J.A.; Hoffmayer, E.R.; Driggers, W.B., III. Movement, Behavior, and Habitat Use of a Marine Apex Predator, the Scalloped Hammerhead. *Front. Mar. Sci.* **2018**, *5*, 321.
16. Miller, K.J.; Erxleben, D.R.; Rains, N.D.; Martin, J.C.; Mathewson, H.A.; Meik, J.M. Spatial Use and Survivorship of Translocated Wild-caught Texas Horned Lizards. *J. Wildl. Manag.* **2020**, *84*, 118–126.
17. Osipova, L.; Okello, M.; Njumbi, S.; Ngene, S.; Western, D.; Hayward, M.; Balkenhol, N. Using Step-selection Functions to Model Landscape Connectivity for African Elephants: Accounting for Variability across Individuals and Seasons. *Anim. Conserv.* **2019**, *22*, 35–48.
18. Montalvo, V.H.; Fuller, T.K.; Saénz-Bolaños, C.; Cruz-Díaz, J.C.; Hagnauer, I.; Herrera, H.; Carrillo, E. Influence of Sea Turtle Nesting on Hunting Behavior and Movements of Jaguars in the Dry Forest of Northwest Costa Rica. *Biotropica* **2020**, *52*, 1076–1083. <https://doi.org/10.1111/btp.12803>.
19. Van Der Marel, A.; Waterman, J.M.; López-Darias, M. Social Organization in a North African Ground Squirrel. *J. Mammal.* **2020**, *101*, 670–683.
20. Wysong, M.L.; Hradsky, B.A.; Iacona, G.D.; Valentine, L.E.; Morris, K.; Ritchie, E.G. Space Use and Habitat Selection of an Invasive Mesopredator and Sympatric, Native Apex Predator. *Mov. Ecol.* **2020**, *8*, 18.
21. Rueda, C.; Jiménez, J.; Palacios, M.J.; Margalida, A. Exploratory and Territorial Behavior in a Reintroduced Population of Iberian Lynx. *Sci. Rep.* **2021**, *11*, 14148.
22. Shakeri, Y.N.; White, K.S.; Waite, J.N. Staying Close to Home: Ecological Constraints on Space Use and Range Fidelity in a Mountain Ungulate. *Ecol. Evol.* **2021**, *11*, 11051–11064.
23. Perona, A.M.; Urios, V.; López-López, P. Holidays? Not for All. Eagles Have Larger Home Ranges on Holidays as a Consequence of Human Disturbance. *Biol. Conserv.* **2019**, *231*, 59–66.
24. Williams, S.M.; Lindell, C.A. The Influence of a Single Species on the Space Use of Mixed-Species Flocks in Amazonian Peru. *Mov. Ecol.* **2019**, *7*, 37.
25. Liu, T.; Xu, Y.; Mo, B.; Shi, J.; Cheng, Y.; Zhang, W.; Lei, F. Home Range Size and Habitat Use of the Blue-Crowned Laughingthrush during the Breeding Season. *PeerJ* **2020**, *8*, e8785.
26. Morant, J.; Abad-Gómez, J.M.; Álvarez, T.; Sánchez, Á.; Zuberogoitia, I.; López-López, P. Winter Movement Patterns of a Globally Endangered Avian Scavenger in South-Western Europe. *Sci. Rep.* **2020**, *10*, 17690.
27. Abril-Colón, I.; Alonso, J.C.; Palacín, C.; Ucero, A.; Álvarez-Martínez, J.M. Factors Modulating Home Range and Resource Use: A Case Study with Canarian Houbara Bustards. *Mov. Ecol.* **2022**, *10*, 49.
28. Wang, C.; Yu, X.; Xia, S.; Liu, Y.; Huang, J.; Zhao, W. Potential Habitats and Their Conservation Status for Swan Geese (*Anser Cygnoides*) along the East Asian Flyway. *Remote Sens.* **2022**, *14*, 1899.
29. Noonan, M.J.; Tucker, M.A.; Fleming, C.H.; Akre, T.S.; Alberts, S.C.; Ali, A.H.; Altmann, J.; Antunes, P.C.; Belant, J.L.; Beyer, D. A Comprehensive Analysis of Autocorrelation and Bias in Home Range Estimation. *Ecol. Monogr.* **2019**, *89*, e01344.
30. Samuel, M.D.; Pierce, D.J.; Garton, E.O. Identifying Areas of Concentrated Use within the Home Range. *J. Anim. Ecol.* **1985**, *54*, 711–719. <https://doi.org/10.2307/4373>.
31. Kie, J.G.; Matthiopoulos, J.; Fieberg, J.; Powell, R.A.; Cagnacci, F.; Mitchell, M.S.; Gaillard, J.-M.; Moorcroft, P.R. The Home-Range Concept: Are Traditional Estimators Still Relevant with Modern Telemetry Technology? *Philos. Trans. R. Soc. B Biol. Sci.* **2010**, *365*, 2221–2231.
32. Zuur, A.F.; Ieno, E.N.; Walker, N.J.; Saveliev, A.A.; Smith, G.M. *Mixed Effects Models and Extensions in Ecology with R*; Springer: Berlin/Heidelberg, Germany, 2009; Volume 574.
33. Harrison, X.A.; Donaldson, L.; Correa-Cano, M.E.; Evans, J.; Fisher, D.N.; Goodwin, C.E.; Robinson, B.S.; Hodgson, D.J.; Inger, R. A Brief Introduction to Mixed Effects Modelling and Multi-Model Inference in Ecology. *PeerJ* **2018**, *6*, e4794.

-
34. Bates, D.; Mächler, M.; Bolker, B.; Walker, S. Fitting Linear Mixed-Effects Models Using Lme4. *J. Stat. Softw.* **2015**, *67*, 1–48. <https://doi.org/10.18637/jss.v067.i01>.
 35. Hijmans, R.J.; van Etten, J. *raster: Geographic Data Analysis and Modeling*; R Package Version 3.4-5; 2020. <https://cran.r-project.org/web/packages/raster/raster.pdf>.
 36. Sanz, A.; Minguez, E.; Anadon, J.; Hernandez, V. Heterogeneous use of space in three breeding territories of Bonelli's eagle (*Hieraetus fasciatus*). *Ardeola* **2005**, *52*, 347–350.
 37. López-López, P. Individual-Based Tracking Systems in Ornithology: Welcome to the Era of Big Data. *Ardeola* **2016**, *63*, 5–34.
 38. Carrascal, L.M.; Seoane, J. Factors Affecting Large-Scale Distribution of the Bonelli's Eagle *Aquila Fasciata* in Spain. *Ecol. Res.* **2009**, *24*, 565–573. <https://doi.org/10.1007/s11284-008-0527-8>.
 39. Ferrer, M.; Morandini, V.; Newton, I. Floater Interference Reflects Territory Quality in the Spanish Imperial Eagle *Aquila Adalberti*: A Test of a Density-Dependent Mechanism. *IBIS* **2015**, *157*, 849–859. <https://doi.org/10.1111/ibi.12289>.
 40. Martínez-Miranzo, B.; Banda, E.; Aguirre, J.I. Home Range Requirements in Bonelli's Eagle (*Aquila Fasciata*): Prey Abundance or Trophic Stability? *Eur. J. Wildl. Res.* **2019**, *65*, 85.