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ARTICLE

Breeding spatial behavior of an Iberian dimorphic raptor (*Circus cyaneus*) based on GPS tracking

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Abstract

The Hen Harrier (*Circus cyaneus*) is a medium-sized, dimorphic raptor from Eurasia which usually hunts birds and small mammals. Studies on the spatial behavior of the species based on GPS-tracking devices are extremely scarce at the global level. Thus, here we GPS-tracked 24 adult Hen Harriers (*Circus cyaneus*) to study the overall patterns of the breeding spatial ecology of the species in Iberia, including home range sizes, cumulated distances, temporary variability, and the effect of latitude. The breeding season period of the tagged Hen Harriers started on 21 March ± 25 days (mean ± SD) and ended on 04 July ± 21 days, with a duration of 104 ± 18 days. We found an effect of latitude on the phenology, with northern individuals breeding later than southern individuals. Breeding home ranges (95% KDE as *kernel density estimation*) averaged 53.7 ± 68.2 km^2, while core areas (50% KDE) averaged 6.2 ± 11 km^2. Home ranges were smaller during the central weeks of the breeding period, when females were arguably incubating, and progressively increased as chick-rearing progressed. Regarding fidelity to breeding areas, of the four females analyzed over 2 consecutive years, all returned to the same area to breed in the second year, with a measured overlap in home ranges of 51 ± 22 %, and core areas in 34 ± 40%. Future studies combining comprehensive field monitoring with remote tracking are necessary to further explore the behaviour of the species. Nonetheless, given that there are not GPS-based studies of Hen Harrier breeding ecology worldwide, our work provides a basic overview of the species that can be used as starting point for further studies.

Keywords Movement ecology · Reproduction · Raptors · Movement ecology · GPS telemetry · Birds of prey · Hen Harrier

Introduction

The Hen Harrier (*Circus cyaneus*) is a medium-sized raptor from Eurasia (Cramp and Simmons 1980) which usually hunts birds and small mammals (Clarke et al. 1997; García and Arroyo 2005). The species displays a significant sexual dimorphism, in both plumage pigmentation and size: females have more cryptic, brownish colors, and are on average 11% larger and 54% heavier than males (Cramps and Simmons 1980; Orta et al. 2020). Breeding populations from eastern Europe and northern Asia are fully migratory and usually perform long-distance migrations to overwinter in template areas, such as the Mediterranean basin or middle Asia (Cramp and Simmons 1980; Ferguson-Lees and Christie 2001; Panuccio et al. 2021). Conversely, breeding populations from western Europe are partial or short-distance migrants, with individuals performing short-range movements from northern to southern Europe (Del Hoyo et al. 1994). Iberia forms the southern limit of the breeding range of Hen Harriers in Western Palearctic. In this region, the species shows different spatial strategies, from sedentarism to itinerant movements or intra-peninsular migrations (Morollón et al. 2024), similar to other raptors breeding in Iberia (García-Macía et al. 2022a).

The breeding period of the Hen Harrier in Iberia typically takes place from March to July, and occasionally extends into August (García and Arroyo 2002; Arroyo 2022). The species usually nests on the ground among low semi-natural vegetation or cereal crops (Millon et al. 2002; Irwin et al. 2011; Maeso

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et al. 2024). Variability in nesting site habitat has been reported with the region: nests in northern areas typically occur in natural vegetation but the proportion of nests in cereal crops increases towards the south in the Iberian Peninsula (Arroyo 2022; Maeso et al. 2024).

Clutch size often ranges between 5 and 6 eggs (García and Arroyo 2001; Millón et al. 2002; Irwin et al. 2011). Small mammals (common voles and lagomorphs) and small birds are the main preys of the Hen Harrier during the breeding period in Spain (García and Arroyo 2005). The species generally nests some distance from conspecifics but may occasionally breed in small groups, although communal breeding is more likely to occur with Montagu's harriers (Panuccio et al. 2021). Polygyny has been reported in the species, often involving a male and two females, but rarely males have been observed provisioning up to seven females (Del Hoyo et al. 1994).

In 1994, the breeding population of Hen Harriers in Spain was estimated to be between 837 and 999 pairs, most breeders occurred in northern Iberia with a sparse distribution across the Iberian plateau (centre of Spain). The most recent census (2017) estimated the Iberian population at 500–800 breeding pairs, a decrease of about 35% compared to the previous census (2006) (Arroyo et al. 2017). This census showed a general decrease in the population sizes within northern Iberia and an increase within populations from central Iberia. It is currently listed as 'Endangered' in Spain due to habitat change and loss (López-Jiménez and Arroyo 2021).

Some remote tracking studies on habitat use (Maeso et al. 2024) and short-distance migration patterns (Morollón et al. 2024) have been performed in Iberia, but the spatial ecology of the species based on GPS is extremely scarce at the global level. Thus, basic studies on the spatial behavior of the species are essential. Here we GPS-tracked 24 adult Hen Harriers to study the spatial ecology of the species during the breeding period in Iberia, its southernmost reproductive range. Our specific objectives were (1) to estimate the phenology (onset, end and duration) of the breeding period of the Hen Harriers based on the observation of GPS data; (2) to analyze the influence of latitude on phenology; (3) to calculate movement and spatial-related metrics during the breeding period, such as home ranges (95% KDE as *Kernel Density Estimation*), core areas (50% KDE) and cumulated distances traveled; (4) to analyze sex differences in the previous metrics; and (5) to study shifts within the reproductive period in the previous metrics.

Methods

Study area

Hen Harriers were tagged across the distribution of the species in Spain, from the Atlantic strip to central Iberia (Fig. 1). The climate in northern Iberia is continental-oceanic with mild temperatures and moderate precipitations all year round, while the climate is typically Mediterranean in central and southern Iberia, with summer droughts and strong seasonal differences.

Heterogeneous landscapes including pseudo-steppes (crops), natural shrubs and open forests predominate within the range of the species in Iberia. Specifically, for the individuals used in our study, heterogeneous landscapes with predominance of cereal crops were the most frequent habitats during breeding, followed by areas of scrubland and natural vegetation (see Maeso et al. 2024).

Dataset and tagging process

Twenty iur adult Hen Harriers (16 females and 8 males; Table 1) were trapped and GPS-tagged in Spain during the breeding period (May–June) from 2019–2021. Hen Harriers were lured with a Eurasian Eagle-Owl (*Bubo bubo)* and captured with dho-gaza nets (similarly to Morollón et al. 2024 or García-Macía et al. 2022b).

A GPS transmitter was attached to each individual by a back-pack harness made of Teflon ribbon (Garcelon 1985, García et al. 2021). The transmitter models were OrniTrack-E10 3G (Ornitela, Vilnius, Lithuania) and Milsar U9 3G (Milsar, Nicosia, Cyprus), with total weights of devices (including harnesses) being less than 3% of the individual mass (transmitter weights = 12.71 ± 4.1 g, range = 12.4–19.3; bird weights = 506 ± 273 g, range = 315–540; $n = 24$), thus complying with the recommended range (Bodey et al. 2018).

GPS transmitters were set to provide 1 fix/15 minutes, creating a dataset with 113,571 GPS fixes. We selected this interval by technical constraints, considering that shorter intervals could have led to problems with transmitters battery and tracking duration. Recent studies have used higher resolution frequencies (up to a few seconds; López-López et al. 2021), but this may lead to temporal autocorrelation problems when calculating home ranges. Nonetheless, intervals from 5 minutes to 1 hour are very common in spatial ecology studies, which allows comparisons among species and populations (i.e., Damiani et al. 2022; García-Macía et al. 2022b; Zvidzai et al. 2022; Meyburg et al. 2023)

Individuals were ringed and biometric measurements were taken, with sex and age determined by established morphologic characteristics (Ferguson-Less and Christie 2001).

The capture and tagging of the individuals were carried out by expert ringers from the Spanish Ornithological Society (SEO/BirdLife) and Natural England, complying with ethical standards.

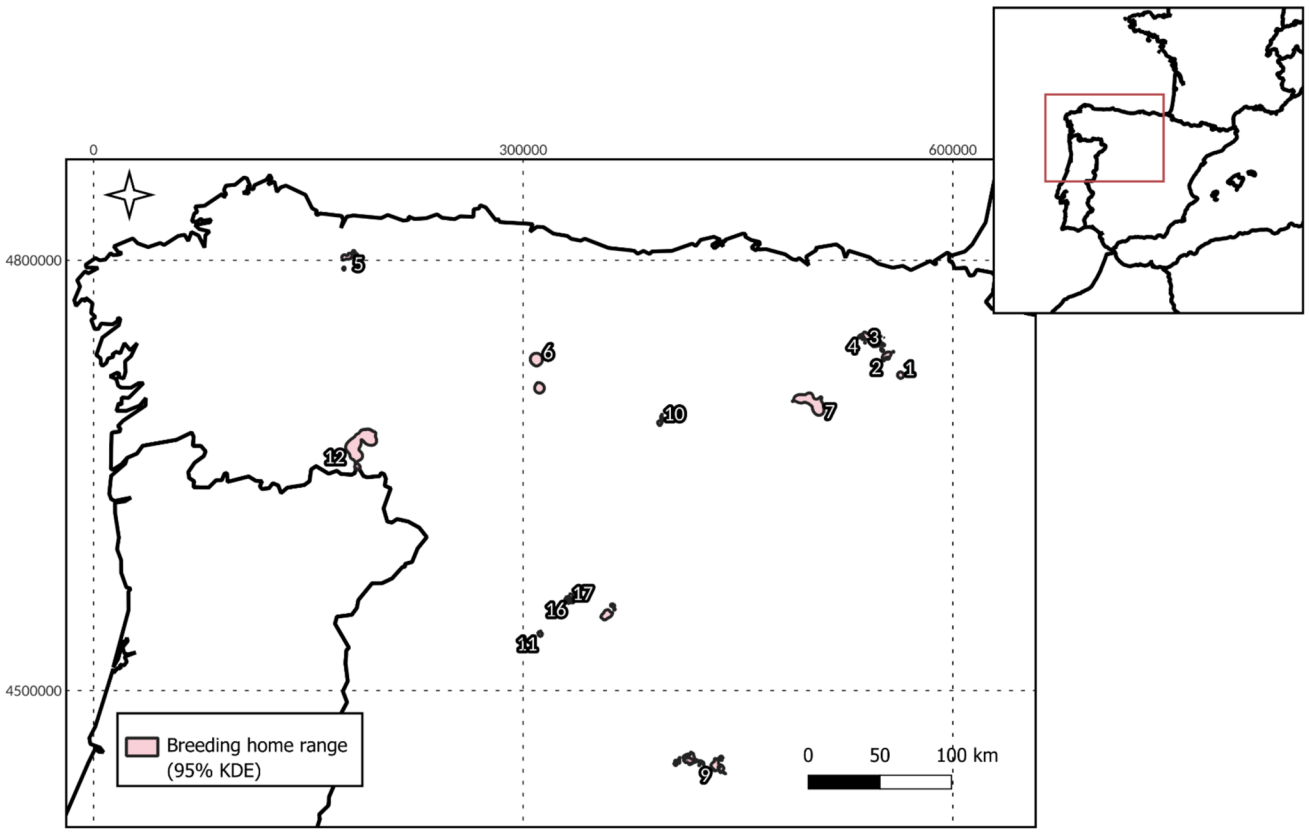


Fig. 1 Breeding home ranges (95% KDE) of the 17 GPS-tagged Hen Harriers during the reproductive period in Spain. Each individual home range is indicated with a number. Due to overlap between consecutive years (see Fig. 5), individuals with home ranges calculated for different years are represented by a single polygona)

Table 1 Home range sizes (95% KDE), core areas (50% KDE), and accumulated distances of the Hen Harriers breeding in Spain. Values are shown as mean ± SD (minimum–maximum); median

Sex	Home range size for the entire breeding period (95% KDE, km^2)	Weekly home range size (95% KDE, km^2)	Core area for the entire breeding period (50% KDE, km^2)	Weekly core areas (50% KDE, km^2)	Accumulated distance for the entire breeding period (km)
Female ($n = 16$ breeding periods)	54.3 ± 75.7 (0.7–264.8); 15.3	31.2 ± 75.4 (0.001–486); 2.98	6.6 ± 12.5 (0.05–49.4); 1.11	5.4 ± 14.4 (0.0002–95.2); 0.29	1,789 ± 1,338 (242–5,209); 1,497
Male ($n = 5$ breeding periods)	51.2 ± 21.4 (30.7–80.5); 46.7	51.3 ± 72.0 (1.18–445.42); 22.3	4.5 ± 2.4 (2.3–7.3); 4.24	8.0 ± 11.9 (0.08–62.3); 3.35	5,108 ± 1,522 (4,047–7,361); 4,512

Indirect selection of breeding individuals and calculation of phenological parameters

As field corroborations of successful breeding were not available (i.e., eggs laid, chicks hatched, or chicks fledged), we performed an indirect selection of breeding individuals using remote GPS data. Sophisticated studies have been performed to extract reproductive parameters from GPS-tracking data in nesting raptors (Oppel et al. 2024); however, considering the aims of our work and the particularities of the study species, we performed a simpler and conservative selection approach based on GPS data. Hen Harriers usually perform dispersal or nomadic-like movements before and after the breeding period in Spain (typically from March to July; García and Arroyo 2001), that is, movements of 10s or 100s of km outside breeding areas are carried out once chicks become independent, often extending this behavior until the next breading season (Fig. S1). Thus, we considered

that harriers were breeding (or, at least, attempting to breed) if they spend at least 2 consecutive months between February and August in an area of less than 200 km^2, without carrying out any directional long-distance movements outside (>50 km per day), and/or without spending nights outside this area. We established onset and end of breeding when tagged harriers stopped their dispersal behaviour and settled in an area, dramatically reducing their daily distances traveled or the home range sizes, and the end of breeding when individuals abandoned the breeding area and performed longer distance movements.

Calculation of movement-related variables and home ranges

We measured the Euclidian distance between GPS-locations using the '*amt*' R library (Signer et al. 2019), expressed as the sum of all weekly distances traveled. Weekly home ranges (95% KDE) and core areas (50% KDE) during breeding period were calculated using the 'adeHabitat' R library (Calenge 2006). We determined the year-to-year overlap of annual breeding home ranges (Kernohan et al. 2001) for four individuals using the function ''kerneloverlap' from 'adehabitatHR' R library.

Statistical analyses

Statistical analyses were performed with generalized linear mixed models (GLMMs) using the *lme4* package (Bates et al. 2015) in R (R Core Team 2023). First, a set of GLMMs was performed to explore sex differences. Cumulated distances, home ranges (95% KDE), and core areas (50% KDE) were fitted as response variables, while the "sex" was fitted as explanatory variable. All models were run including individual identification as a random effect.

Second, a set of GLMMs was performed to explore the influence of latitude on phenological metrics. Onset, end and duration of breeding were fitted as response variables, while the "latitude" (continuous variable) was fitted as explanatory variable. All models were run including individual identification as a random effect.

We used an AIC approach to determine which error distribution (Gamma or Gaussian) was better for GLMMs. We performed a model selection analysis using the function 'model.sel' from MuMin R package (Barton 2020). Models were compared using the Akaike Information Criterion (AIC). The selected models were those with the lowest AIC value (Burnham and Anderson 2002). Gamma distributions (link = "inverse") were selected for all response variables, with weights close to 1.

Significance levels for statistical analysis were set to 0.05. Maps were created with QGIS 3.16.6 (QGIS.org 2023). Figures were drawn with 'ggplot2' R package (Wickham 2016).

Results

We identified 21 complete breeding periods from 17 individuals compatible with reproductive behaviors (16 periods of females and 5 periods of males) from the original database (Fig. 1 and Fig. S2). Seven breeding periods from six individuals (3 of males and 4 of females) were discarded because their behavior was incompatible with breeding, i.e., they do not spend at least 2 consecutive months between February and August in an area of less than 200 km^2, carried out directional long-distance movements outside (>50 km per day), and/or spent nights outside this area during the breeding period.

The breeding period of the tagged Hen Harriers started on 21 March ± 25 days (range = 7 February–26 April) and ended on 04 July ± 21 days (range = 23 May–22 August), with total duration being 104 ± 18 days (range = 69–125). We found an effect of latitude on the phenology, whereby northern individuals tended to breed later (onset estimate = − 0.000012 ± 0.00003, p value < 0.002; End estimate = − 0.00008 ± 0.00003, p value = 0.01), although there was no evidence of any difference in duration (Fig. 2, Tables S1 and S2).

For females, home ranges averaged 54.2 ± 75.71 km^2 (n = 16), with a range of 0.7–264.8 km^2, while core area averaged 6.6 ± 12.5 km^2 (n = 16), with a range of 0.05–95.24 km^2. Females traveled 1789 ± 1338 km (range = 242–5209) during the entire breeding period, while males traveled 5108 ± 1522 (range = 4047–7361). For males, home range averaged 51.2 ± 21.4 km^2 (n = 5), with a range of 30.7–80.5 km^2, while core areas averaged 4.5 ± 2.4 km^2 (n = 5), with a range of 2.3–7.3 km^2.

Weekly home ranges and core areas for females averaged 31.15 ± 75.41 km^2 (range = 0.002–486.02 km^2) and 5.39 ± 14.42 km^2 (range = 0.00002–95.24), respectively. For males, weekly home ranges and core areas averaged 51.33 ± 72.03 km^2 (range = 1.18–445.42) and 7.99 ± 11.85 km^2 (range = 0.08–62.29 km^2), respectively. Weekly cumulated distance averaged 124 ± 143 km (range = 1–634) for females, and 295 ± 141 km (range = 69–686 km) for males (Table 1).

We found no significant differences between females and males in home range sizes (estimate= 0.09 ± 2.83, p value = 0.97) or core areas (estimate= − 0.037 ± 0.134, p value = 0.737), but we find a week but significant difference in cumulated distances (estimate= − 0.006 ± 0.002, p value = 0.004) (Table S3). However, data suggested that males (n = 5) tended to have larger home ranges, core areas and cumulated distances (Fig. 3).

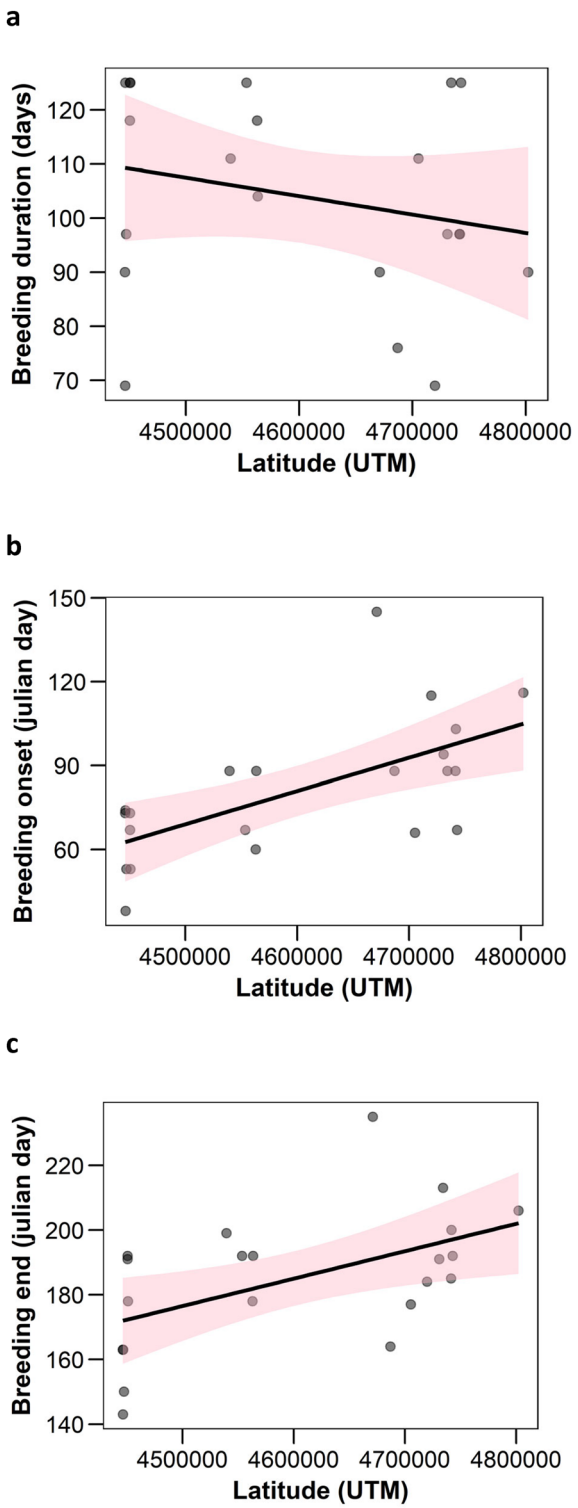


Fig. 2 Linear predicted effects of latitude (UTM) in breeding phenological parameters: **a** duration, **b** onset, **c** end. 95% confidence intervals are shown

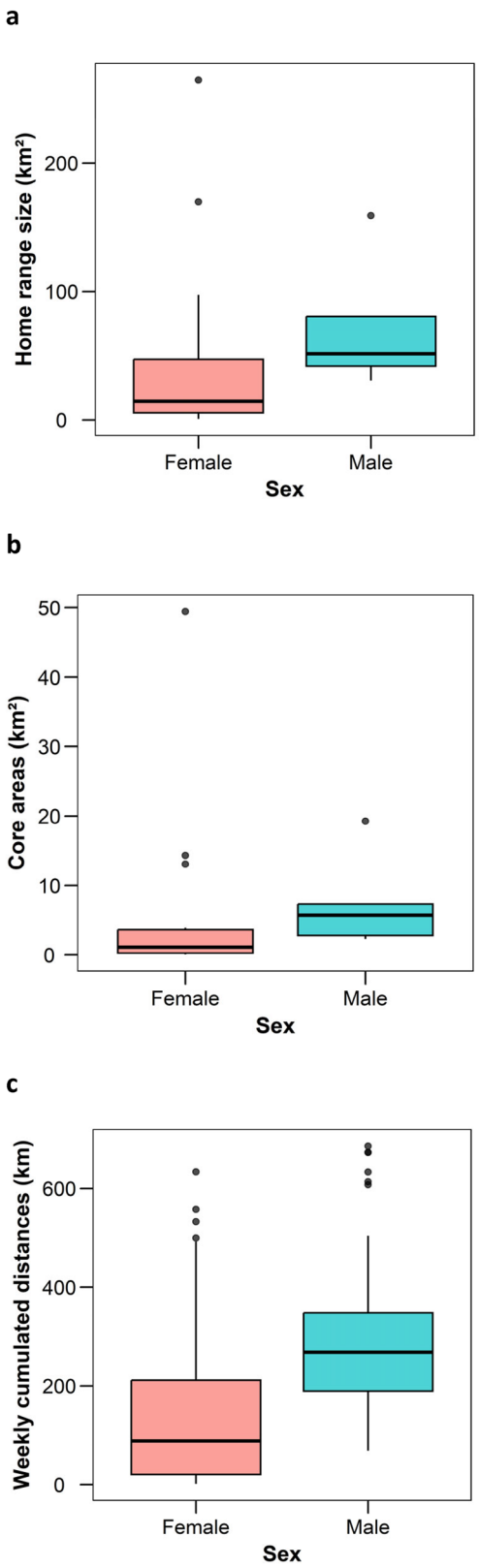


Fig. 3 Differences between sexes in home range sizes **a**, core areas **b** and weekly cumulated distances **c** during the breeding period in Spain

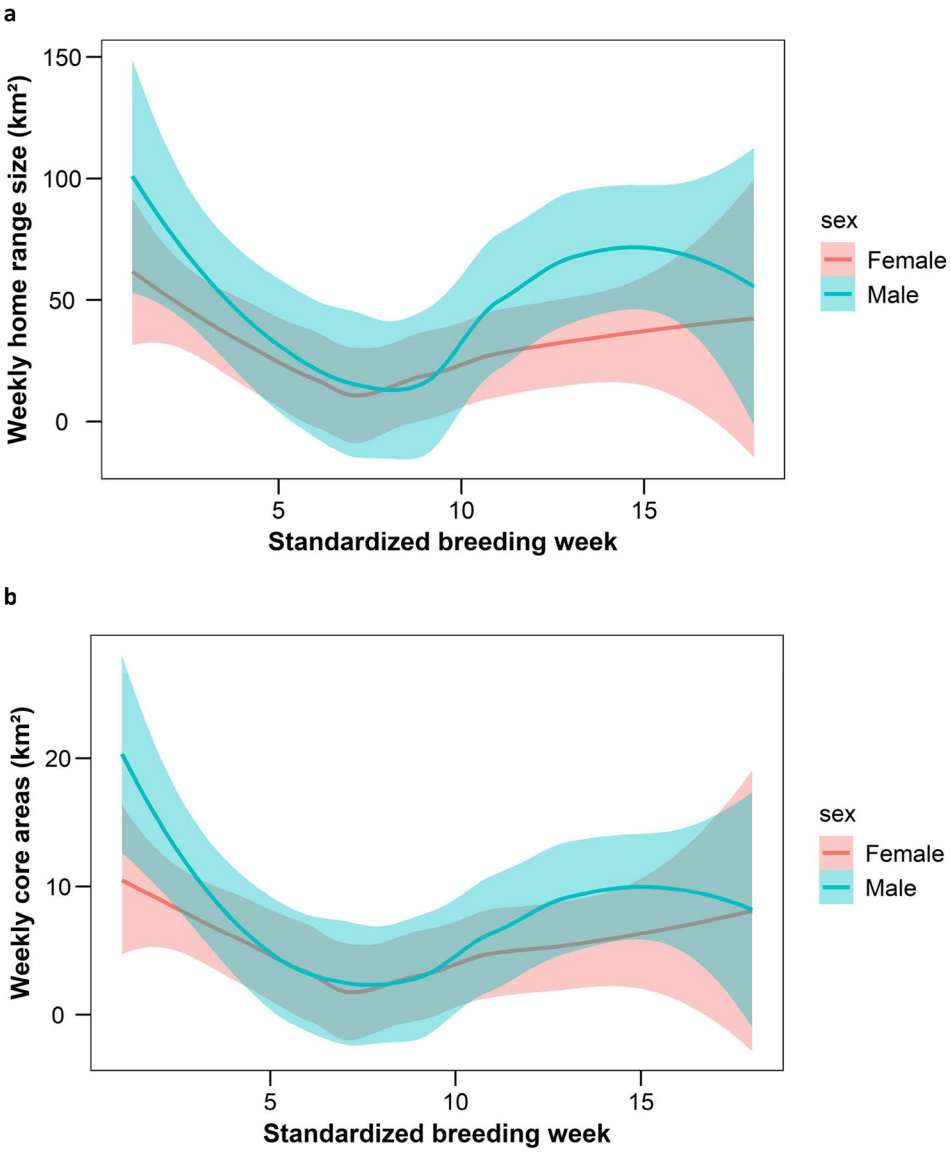


Fig. 4 Weekly evolution of home range sizes **a** and core areas **b** during the breeding period. Female are shown in pink and males in light green, with 95% confidence intervals

Weekly home range sizes changed during the breeding period. On average, individuals had smaller home ranges during the central weeks of the breeding period, and larger ranges during the last weeks of the breeding period. This tendency was more pronounced in males (Fig. 4).

Regarding fidelity to breeding areas, of the four females analyzed over 2 consecutive years, all returned to the same area to breed in the second year, with a measured overlap in home ranges of 51 ± 22 %, and core areas in 34 ± 40% (Fig. 5, Table S4).

Discussion

In this study, we analyzed the breeding behavior of the Hen Harrier (*Circus cyaneus*) based on remote tracking data for the first time. We provided a basic overview of the breeding ecology of the species by estimating home range sizes, core areas, and cumulated distances. Furthermore, we provided some insights on the influence of latitude on breeding phenology, temporary evolution of spatial and movement-related metrics within the reproductive period, as well as sex differences and year-on-year repeatability of breeding areas.

The size of breeding areas of Iberian Hen Harriers (estimated as 95% Kernel Density Estimarion) was coincident with those of other Iberian raptors, including territorial species such as Bonelli's eagle (*Aquila fasciata*) (Pérez-García et al. 2013) and imperial eagle (*Aquila adalberti*) (Fernández et al. 2009), as well as facultative scavengers like the red kite (*Milvus milvus*) (García-Macía et al. 2022b). Hen Harrier home range sizes were also comparable to those of Northern Harrier (*Circus hudsonius*, formerly *Circus cyaneus hudsonius*), a very similar species found in North America (Slater and Rock 2005). For this species, MacWhirter and Bildstein

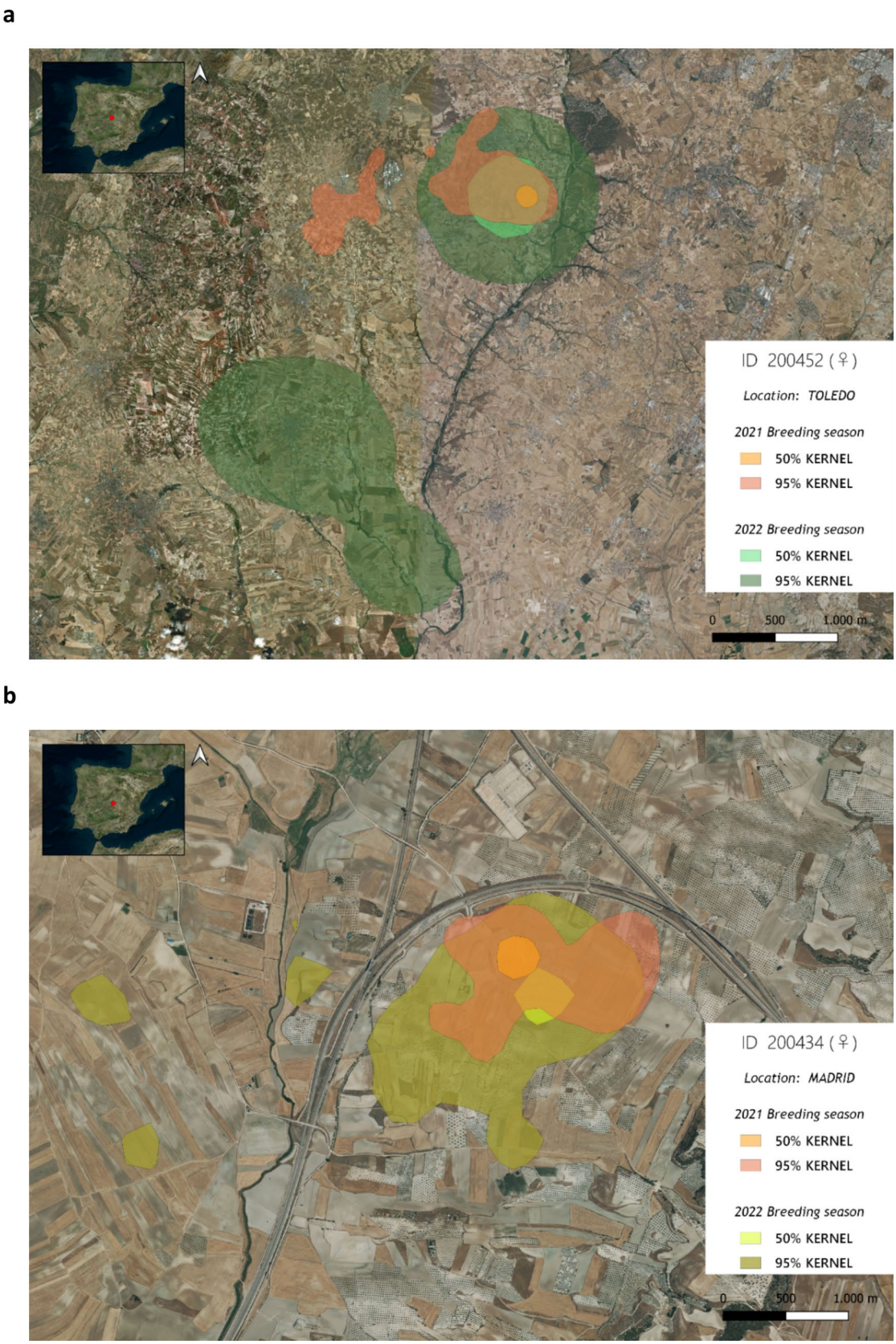
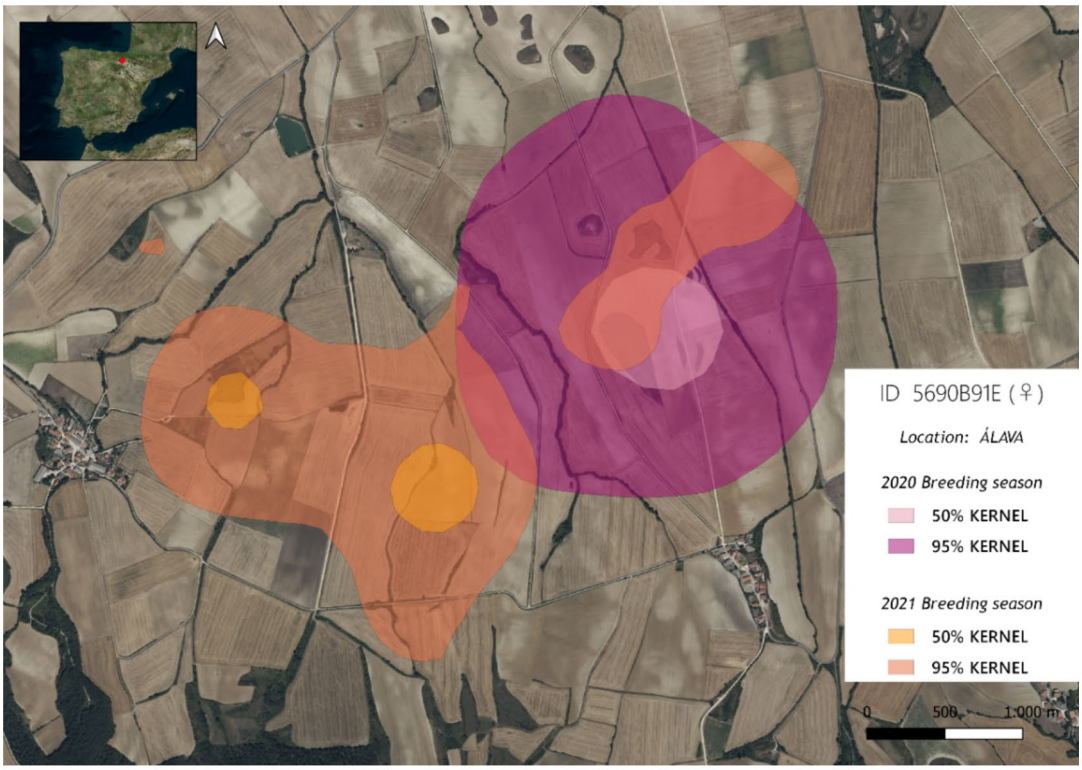


Fig. 5 Year-to-year overlap between breeding areas (95% and 50% KDE) of four individuals (panels **a**–**d**). The panel d also show the overlap between the breeding areas of two females during the same period

c



d

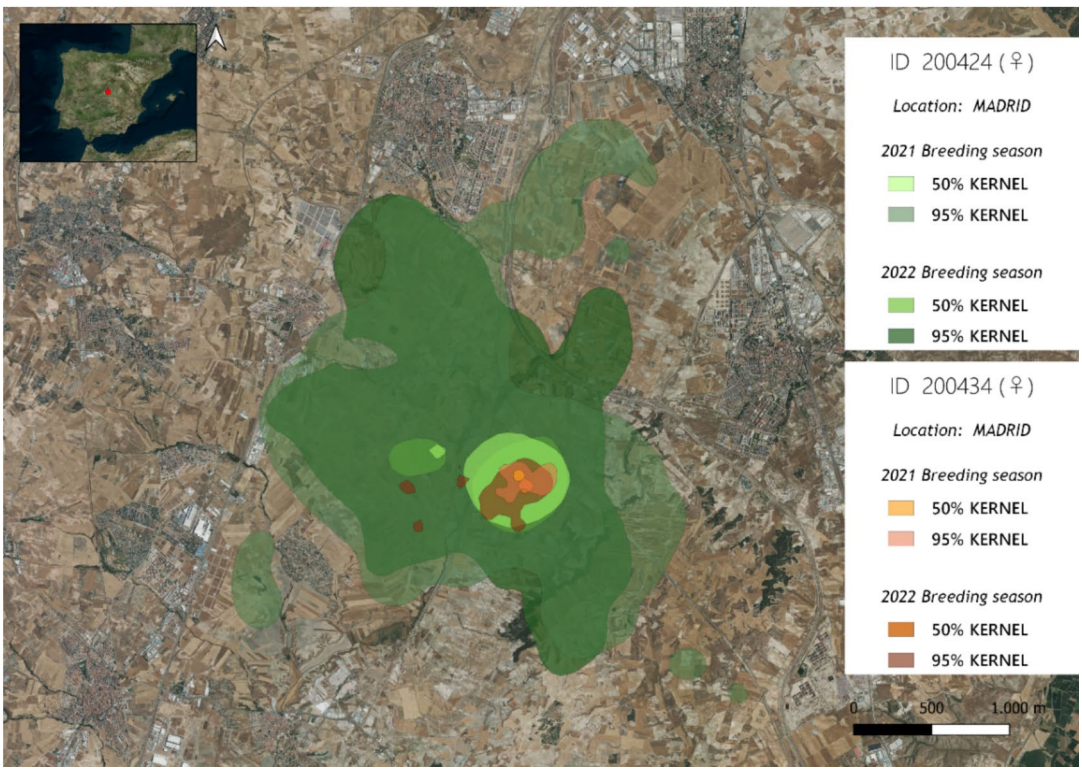


Fig. 5 (continued)

(1996) estimated breeding home range sizes ranging from 1.7 to 150 km^2.

Hen Harriers occupying more northerly areas tended to breed later than southern ones, which is supported by the results of previous published data in Spain (Arroyo et al. 2017). This finding is also consistent with expected influence of environmental conditions such as ambient temperature, rainfall and resource availability on reproductive phenology (Burant et al. 2021), whereby northern Iberia is generally colder and wetter than central Iberia, which has a typically Mediterranean climate (summer droughts, higher temperatures, etc.). These differences have been shown at higher European latitudes too. For example, in France, Ireland and Scotland, egg-laying often occurs during the first week of May (Amar and Redpath 2002; Millon et al. 2002; Irwin et al. 2008), which is similar to timing of northern Iberian harriers. However, due to the low sample size in this study, future studies should explore the effect of latitude in more detail at different regional and national scales.

Males tended to occupy larger areas and travel further during the breeding period, although we did not find statistically significant differences in movement and spatial parameters because of the small and sex biased sample. However, these trends are supported by other studies on the spatial ecology of raptors during the breeding period (i.e., Kocina et al. 2021; López-López et al. 2021; García-Macía et al. 2022b). Breeding period range size is clearly related to role differentiation between sexes with females incubating eggs and brooding chicks, and the male provisioning the female at or near the nest (Keeley and Bechard 2017; Martínez et al. 2020). In line with these behavioral patterns, reversed size dimorphism is common in birds of prey, with females bigger and heavier than males (Newton 1979; Cramp and Simmons 1980). Specifically, female Hen Harriers are on average 11% larger and 54% heavier than males (Orta et al. 2020). The differences between sexes usually lead to behavioural contrasts, especially in terms of foraging patterns and prey size (McDonald et al. 2005; Slagsvold et al. 2007; Warkentin et al. 2016). Thus, raptors with high sexual dimorphism usually feed on different preys, while monomorphic species do not often display any sex-specific foraging pattern (Krüger et al. 2005). Insectivorous species are usually the least dimorphic, while those depending upon birds or mammals as prey, as Hen Harriers, are often dimorphic (Krüger et al. 2005; Panter and Amar 2022).

Furthermore, home ranges and core areas shifted over the breeding period: on average, individuals had smaller home ranges during the central weeks of the breeding period. Home ranges were minimum during the central weeks of the breeding period, when female is incubating, and progressively increase as chick-rearing progresses and nestlings need more supplies of food. These changes in home range sizes reflect changes in energy expenditure due to the different foraging effort. This trend was also supported by some works based on GPS telemetry and tri-axial accelerometery (López-López et al. 2021).

Despite the 'itinerant' and 'migratory' movements of the species during the post-reproductive period and winter (Morollón et al. 2024; and own data), the Hen Harriers in our study (four individuals with at least 2 years of tracking) showed fidelity to their breeding area. This repeatability of breeding areas has been found in many raptors (Battley 2006; Bell et al. 2009; Lourenço et al. 2011; García-Macía et al. 2022b), and may be a strategy to ensure favorable breeding conditions from 1 year to the next. The low sample size in our study do not allow to draw major conclusions about the entire Iberian population of the Hen Harrier, but the repeatability rates found in the individuals in our study (4 out of 4, 100%) point to a trend that is likely to apply to larger samples.

Some methodological weaknesses of our study should be highlighted. First, the sample size of males was significantly lower than that of females (5 breeding periods of males vs. 16 breeding periods of females), which does not allow us to draw any major conclusions on sex differences on the spatial behavior of Iberian Hen Harriers. This low sample size of males may be a consequence of the lower number of males compared to females in the Iberian population of the species, which is also relatively small (500–800 pairs; Arroyo et al. 2017) and probably organized into polygynous groups with one male and several females (Del Hoyo et al. 1994). Another weakness in our study is the qualitative and GPS-based classification of Hen Harriers as 'breeders' or 'non-breeders' due to the lack of field observations to confirm the reproduction of individuals. However, the distinctive spatial ecology of the species, with individuals performing long dispersal-like movements before and after the breeding period, reduces human error in the classification. However, future studies combining comprehensive field monitoring with remote tracking are needed to further explore the behavior of the species. Given that there are not GPS-based studies of Hen Harrier breeding ecology worldwide, our work provides a basic overview of the species that can be used as starting point for further studies.

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Author contributions JG-M designed the study, performed the analyses and wrote the original draft; SM compiled the data and performed the analyses; SL led fieldwork, supervised the project and rewieved the manuscript; VU supervised the project and reviewed the manuscript.

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Data availability GPS data are available in Movebank.org under author's permission.

Declarations

Competing interest The authors declare no conflicts of interest.

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