

Large-scale movement patterns in a social vulture are influenced by seasonality, sex, and breeding region

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Abstract

Quantifying space use and segregation, as well as the extrinsic and intrinsic factors affecting them, is crucial to increase our knowledge of species-specific movement ecology and to design effective management and conservation measures. This is particularly relevant in the case of species that are highly mobile and dependent on sparse and unpredictable trophic resources, such as vultures. Here, we used the GPS-tagged data of 127 adult Griffon Vultures *Gyps fulvus* captured at five different breeding regions in Spain to describe the movement patterns (home-range size and fidelity, and monthly cumulative distance). We also examined how individual sex, season and breeding region determined the cumulative distance travelled and the size and overlap between consecutive monthly home-ranges. Overall, Griffon Vultures exhibited very large annual home-range sizes of $5,027 \pm 2,123$ km², mean monthly cumulative distances of $1,776 \pm 1,497$ km, and showed a monthly home-range fidelity of 67.8 ± 25.5 %. However, individuals from northern breeding regions showed smaller home-ranges and travelled shorter monthly distances than those from southern ones. In all cases, home-ranges were larger in spring and summer than in winter and autumn. Moreover, females showed larger home-ranges and less monthly fidelity than males, indicating that the latter tended to use the similar areas throughout the year. Overall, our results indicate that both extrinsic and intrinsic factors modulate the home-range the social Griffon Vulture and that spatial segregation depend on sex and season at the individual level, without relevant differences between breeding regions in individual site fidelity.

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ABSTRACT

Quantifying space use and segregation, as well as the extrinsic and intrinsic factors affecting them, is crucial to increase our knowledge of species-specific movement ecology and to design effective management and conservation measures. This is particularly relevant in the case of species that are highly mobile and dependent on sparse and unpredictable trophic resources, such as vultures. Here, we used the GPS-tagged data of 127 adult Griffon Vultures *Gyps fulvus* captured at five different breeding regions in Spain to describe the movement patterns (home-range size and fidelity, and monthly cumulative distance). We also examined how individual sex, season and breeding region determined the cumulative distance travelled and the size and overlap between consecutive monthly home-ranges. Overall, Griffon Vultures exhibited very large annual home-range sizes of $5,027 \pm 2,123 \text{ km}^2$, mean monthly cumulative distances of $1,776 \pm 1,497 \text{ km}$, and showed a monthly home-range fidelity of $67.8 \pm 25.5 \%$. However, individuals from northern breeding regions showed smaller home-ranges and travelled shorter monthly distances than those from southern ones. In all cases, home-ranges were larger in spring and summer than in winter and autumn. Moreover, females showed larger home-ranges and less monthly fidelity than males, indicating that the latter tended to use the similar areas throughout the year. Overall, our results indicate that both extrinsic and intrinsic factors modulate the home-range the social Griffon Vulture and that spatial segregation depend on sex and season at the individual level, without relevant differences between breeding regions in individual site fidelity.

Keywords: Griffon Vulture, home-range, scavenger, spatial segregation, site fidelity.

1.INTRODUCTION

Animal movements are a consequence of an organism’s internal state (e.g., sex, age, breeding stage) and environmental factors (e.g., food availability or weather), and can affect individual fitness and ecological processes at local and global scales (Hansson & Akesson, 2014). Individual movements are also influenced by inter and intraspecific relationships (e.g., competition), which may lead to spatial compartmentalization and the maintenance of population-specific movement patterns over time (Nathan et al., 2008). Deciphering how these factors modulate individual movements and how the latter are compartmentalized in space and time is essential to understanding population dynamics (Costa-Pereira et al., 2022) and identifying priority areas for conservation and management (Katzner & Arlettaz, 2020).

Home-range size and cumulative distance travelled are key elements in the study of animal movement ecology (Kie et al., 2010; Tucker et al., 2018; Thaker et al., 2019; Shaw et al., 2020), defining foraging patterns at the individual and population-level, and assessing their stability over time (e.g., Shaffer et al., 2017). For example, investigating variation in home-range size and cumulative distance travelled may reveal that certain individuals behave as central-place foragers during only a specific period of their life cycle (e.g., the breeding season; Carrete & Donazar, 2005; Delgado-Gonzalez et al., 2022). Similarly, the study of home-range overlap allows the analysis of attraction or repulsion relationships that may affect space use, for example, to avoid competition for resources (Cecere et al., 2018; Winner et al., 2018; Bolnick et al., 2003). This information could be used to explicitly map intra and interspecific meeting sites and prioritise high-quality habitats for communal roost or feeding hotspots (Kane et al., 2015; Cortes-Avizanda et al., 2014).

Vultures from the *Gyps* genus (which include seven species) are among the largest flying birds, showing high sociality and covering large areas in search of ephemeral and unpredictable resources such as carrion (e.g., 162,824 km² on average in case of Cape Vultures, *Gyps coprotheres* ; Jobson et al., 2021). The Eurasian Griffon Vulture *Gyps fulvus* is a monomorphic social species that breeds colonially (Donazar, 1993; Harel et al., 2017; Zuberogoitia et al., 2018; Almaraz et al., 2022). Individuals forage over vast areas to satisfy their energetic requirements (e.g., ranging from 140 to 4,233 km², Nathan et al., 2012; Montsarrat et al., 2013; Fluhr et al., 2021; Xirouchakis et al., 2021), frequently congregating around both wild and domestic ungulate carcasses (Cortes-Avizanda et al., 2010; 2012 but see also Delgado-Gonzalez et al., 2022). Although information exists on Griffon vulture movement ranges (Xirouchakis & Mylonas, 2007; Garcia-Ripolles et al., 2011; Zuberogoitia et al., 2013; Spiegel et al., 2013; 2015; Harel et al. 2017; Arrondo et al. 2018, 2020; Arkumarev et al., 2021; Xirouchakis et al., 2021; Fhlur et al., 2021), virtually nothing is known about the spatio-temporal variation in the movement patterns of adult individuals, as well as, on the factors (e.g., sex, breeding region) governing the spatial ecology and home range fidelity of this species from a mechanistic perspective.

In this paper, we gather movement data from 127 GPS-tagged adult Griffon Vultures captured in five breeding regions of peninsular Spain, the largest vulture population in Western Palearctic encompassing up to 37,000 breeding pairs (90% of all European populations) (Del Moral & Molina, 2018). Our main aim is to assess the effect of individual and environmental factors on movements and spatial use indicators. Specifically, our objectives are: 1) to estimate annual and monthly home-range sizes, monthly cumulative distances travelled, and monthly home-range site fidelity; and 2) to investigate the effect of season, sex and breeding regions on individual monthly home-range size, site fidelity, and cumulative distance. We hypothesize that adult Griffon Vultures, being a large monomorphic colonial species, will exhibit large home-ranges and will travel long distances to fulfil their requirements (mainly food), especially during the autumn and winter, when food availability is the lowest (Spiegel et al., 2013). We also predict that the fidelity of monthly home-ranges should be similar between sexes due to the lack of dimorphism, but would differ between seasons, as foraging constraints are more likely during the breeding period (see Carrete & Donazar, 2005). Finally, we expect differences between breeding regions due to difference in resources availability (Morant et al., 2022).

2. METHODS

2.1 Capture and tagging of vultures

From 2014 to 2022, we captured 127 adult Griffon Vultures (43 males and 84 females) in 5 breeding regions

distributed across northern (Alto Ebro: 49 individuals, Pyrenees: 21 individuals), central (Segovia: 15 individuals), and southern Spain (Cadiz: 12 individuals and Cazorla: 30 individuals) (see Fig 1). Breeding regions were delimited according to the proximity between nesting sites and the biogeographic characteristics of each area where nests are located. Birds were trapped using remotely activated cannon nets and cage traps baited with livestock carcasses. Individuals were tagged with yellow or blue plastic alphanumeric and metal rings and equipped with solar-powered GPS/GSM transmitters (Ecotone <https://ecotone-telemetry.com/en>, Ornitela <https://www.ornitela.com/>, and e-Obs <https://e-obs.de/>). The total weight of the transmitters and rings did not exceed 64g, which represented less than 3% of the body weight of the individuals (Bodey et al., 2018). The age of individuals was estimated from plumage moult (Donazar, 1993; Zuberogoitia et al., 2013), while sex was determined using molecular sexing techniques (Fridolfsson *et al.*, 1999).

Tracking devices were programmed to record fixes (i.e. GPS positions) at 5-10 min intervals from 1 h before sunrise to 1 h after sunset (see Table 1 for details of the tracking devices and sampling frequency). GPS data were incorporated into the Movebank online data repository (www.movebank.org). Data were standardised by resampling the GPS fixes to 15 min for each individual to homogenising our dataset. Vultures were tracked on average 1,040 \pm 809 days with a mean number of fixes per individual of 41,335 \pm 40,493.

2.2 Estimation of home range, cumulative distance travelled and site fidelity

We estimated annual and monthly home-ranges using the 95% kernel density estimator contours (KDE) and the cumulative distance travelled for each tagged individual using the “amt” package (Signer et al., 2019). Cumulative distance travelled per month were measured as the total length of each track (in km) (Edelhoff et al., 2016). Individuals with less than ten fixes per day were discarded (n=4 cases).

We measured the individual home-range fidelity by calculating the percentage of overlap between consecutive monthly home-range (Fieberg & Kochanny, 2005). We selected the 95% KDE as an estimator of home-range to evaluate differences in foraging areas. The percentage of overlap was quantified using the Bhattacharyya coefficient, which ranges between 0 (complete segregation) and 1 (perfect overlapping; Fieberg & Kochanny, 2005; Winner et al., 2018).

2.3 Data analysis

We analyse the effect of sex, season and breeding regions on the monthly home-range sizes, cumulative monthly distances travelled (normal error distribution, identity link function), and percentage of monthly overlap (beta error distribution, identity link function) using generalized linear mixed models (GLMMs; glmmTMB package, Brooks et al., 2017). Sex, season and breeding region were included as fixed factors, while individual identity and year were included as random terms in the models to avoid pseudoreplication.

Models were compared using the Akaike Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). The best model was the one with the lowest AICc value. All models with a difference of $\Delta\text{AICc} < 2$ were considered alternatives (Burnham & Anderson, 2002). For the best model, homogeneity of variance and normality of residuals was inspected by using the “ggresid” package to check the goodness-of-fit of our best models (Goode and Rey 2019). We estimated the variance explained by the fixed and random factors by using the “performance” package (Lüdtke et al., 2021), while differences between their levels were assessed through Tukey posthoc tests using the “emmeans” package (Lenth, 2022). All tests were two-tailed, statistical significance was set at $p < 0.05$, and all results were shown as mean \pm standard deviation. Results of the Tukey post hoc tests included the marginal means and its standard error. Spatial and statistical analyses were done in R version 4.0.3 (R Core Team 2020).

3. RESULTS

Griffon Vultures exploited very large annual home-range sizes (*ca.* 5,000 km²), showing average monthly cumulative distances travelled of 1,776 km (Table 1), and a monthly home-range fidelity of $67.77 \pm 25.05\%$. Monthly home-ranges differed between sexes, seasons and breeding regions (Tables 2 and 3; Fig 2). Males showed a smaller monthly home-range size than females (Table 3). Birds also showed larger home-ranges during spring and summer compared to autumn and winter (Table S2; Fig 2). Individuals from southern

breeding regions (Cazorla, Cadiz), and central Pyrenees showed, on average, larger home-ranges than those of central (Segovia) and northern breeding regions (Alto Ebro) (Table S2 and Fig 2).

Monthly cumulative distance travelled were similar for both females and males (Table 2 and 3; Fig 3). However, birds travelled longer distances during spring and summer than during autumn and winter (Table S2). Individuals from Alto Ebro, Segovia and Pyrenees travelled larger monthly distances than those of Cazorla and Cadiz (Table S2; Fig 3).

The monthly home-range fidelity was slightly higher for males than females, and during spring and summer, being the lowest in autumn and winter. Likewise, there were differences in fidelity between breeding regions. Individuals from Central Spain (Segovia) showed higher fidelity over time than those from the north (Alto Ebro, Pyrenees) and southern Spain (Cádiz, Cazorla) (Table 2, 3 and S2; Fig 4).

4. DISCUSSION

Griffon Vulture movements varied between seasons, breeding regions and sexes. We found that movements were larger during spring and summer, which is similar to other soaring raptors such as Bearded Vulture or Bonelli's Eagle (see Margalida et al., 2016; Pérez-García et al., 2013). This could be related to the food requirements associated with reproduction, which may force vultures to prospect larger areas, seeking for dispersed and unpredictable carcasses to satisfy the food requirements of the offspring and themselves (Carrete & Donazar, 2005). However, seasonal differences could be also explained by longer days (and therefore more time to forage) and better atmospheric conditions particularly during summer, minimising energy expenditure during long-range movements (see Martín Díaz et al., 2020). Similarly, differences in monthly home-range size and cumulative distance travelled between regions could be explained by differences in both, the importance of predictable and non-predictable food availability and the ability to move due to better flight conditions due to the presence of thermal uplifts (Scacco et al., 2021). For instance, the southern populations may experience higher thermal uplift availability (mainly due to warmer climatic conditions in summer), thus minimizing the energy expenditure while increasing the movement capacity of birds (e.g., see Scacco et al., 2019).

Differences in foraging performance between sexes are common in mammals and birds, and are often due to differences in body size and parental duties (Lewis et al., 2002). In monomorphic species such as the Griffon Vulture, these differences might be associated with energetic and nutritional requirements for reproduction (Pinet et al., 2012; Bennison et al., 2022). Our results showed that females have larger home-ranges and travel farther than males. These findings align with other studies in which the same dataset was analysed and where females exhibited larger travelled distances than males during the reproduction (see Delgado-González et al., 2022; Gangoso et al., 2021), including other vulture species (see Bamford et al., 2007; Kruger et al., 2014; Kane et al., 2015, Margalida et al., 2016; García-Jiménez et al., 2018).

Contrary to our expectations, we also found sex differences in the monthly home-ranges fidelity. Males showed greater fidelity than females, indicating that the latter use different areas throughout the year. This gender variation in seasonal fidelity may respond to differences in foraging efficiency or, rather, to resource selectivity (Hertel et al., 2020; Delgado-González et al., 2022). In fact, according to Fernández-Gómez et al. (2022) males may be more prone to feed on predictable resources such as supplementary feeding stations or vulture restaurants, while females may rely on more ephemeral and less clumped food resources. Thus, there may be parallel strategies in the large-scale exploitation of space and, therefore, sexual spatial segregation (Perrig et al., 2021). Alternatively, the fact that males show a greater fidelity of their monthly home-ranges throughout the year and that it is higher during the spring-summer period could be related to their greater territoriality. Males may be more involved in nest guarding (Kokko & Morrell, 2005) in response to competence for nesting sites (see Taborsky, 2021). Interestingly, females not only showed higher extension of home-ranges than males, but also exhibited lower site fidelity. All this reinforces the argument that females might forage more in different locations throughout the year, therefore showing lesser home-range fidelity over time than males. These sex and seasonal differences in individual home range fidelity were similar between breeding regions except in the case of Cadiz and Segovia, where females exhibited lower

fidelity during spring/summer.

Differences (or lack of them) between breeding regions in individual movement patterns indicate that local effects not explored in this work may be affecting them. This is evidenced by the low variance explained by the fixed factors of the best models and the high variance explained by random factors (e.g., home range size fidelity models). The latter indicate that high inter-individual differences in home range area and fidelity exists. Moreover, there are variables such as distance to trophic resources, colony size or habitat type that perhaps could improve the results from our models and better explain breeding region level differences in the evaluated parameters (see Harel et al., 2017; Cecere et al., 2018; Delgado-González et al., 2022). Finally, it should be taken into account that the effect of differences in sampling duration of individuals of some breeding regions also affects the observed home range sizes which may have led to an underestimation of this and other parameters such as cumulative distance or home range fidelity.

5. CONCLUDING REMARKS

Our work adds evidence to the spatial requirements of large soaring birds such as vultures, and the importance of individual and regional differences in explaining their movement patterns. Contrary to our expectations, we found sex-dependent spatial segregation in this monomorphic species, maybe related to behavioural differences between males and females, particularly during the breeding period. Moreover, we observed that vultures showed larger home-ranges and cumulative distance travelled during the breeding period, when site-fidelity is higher, with females with females traveling further. Finally, despite high levels of variation in home range sizes between breeding regions, there were no clear differences in site fidelity between breeding regions over time, which may indicate stability in the home range.

Our findings open new promising avenues for research on inter-individual differences in optimal foraging, and on the intrinsic and extrinsic factors operating at multiple levels (Williams & Safi 2020). Beyond this, increasing our knowledge of how these patterns translate into regional differences (or lack thereof) is crucial in predicting population dynamics through movement ecology (Shaw *et al.*, 2020). This information is crucial for the effective management and conservation of highly mobile species which require protective measures to be implemented at large spatial scales.

DATA AVAILABILITY STATEMENT

The data used on the analyses are publicly available at Zenodo data repository upon article acceptance.

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AUTHOR CONTRIBUTIONS

JMPG and JM conceived the initial idea and designed work schemes; JM performed all the analyses, figures, tables, and appendices, and led the writing, with significant contributions from EA, JASZ, JAD, ACA, MR, GB, FM, JO, MC, AM, POV, JMM and DS. All authors contributed to the literature review and reviewed manuscript drafts. All authors gave final approval for publication.

ETHIC STATEMENT

All procedures regarding animal manipulation and tagging were carried out strictly in accordance with the relevant guidelines and regulations of the “Patrimonio natural y de la biodiversidad” (Article 61, Law 42/2007, Ministerio para la Transición Ecológica y el Reto Demográfico, España) and complied with all regional permits (regional government of Castilla y León, Junta de Andalucía, Comunidad Foral de Navarra, Generalitat de Catalunya, Gobierno de Aragón and Diputación Foral de Gipuzkoa).

COMPETING INTERESTS

The authors declare no competing interests.

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Tables and Figures

Table 1. Annual and monthly home-range size (in km²; estimated at 95% KDE), and cumulative distance travelled (in km) of 127 adult Griffon vultures tagged with GPS in Spain. All values are shown with mean (+- SD) and their range (minimum and maximum values) in brackets.

	Home-range (km ²)	Cumulative distance travelled (km)
Annual	5,027 ± 2,123 (1,981- 9,863)	15,090 ± 11,256 (38 – 65,347)
Monthly	4,889 ± 1,753 (1,908-6,822)	1,776 ± 1,497 (20 – 16,745)

Table 2. Models obtained to assess the effects of individual sex, season and population on the movement and spatial segregation patterns of 127 GPS-tagged griffon vultures in Spain. The null model was included in our set of models. k: number of parameters; AICc: Akaike Information Criterion corrected for small sample sizes; ΔAICc: difference between the AICc of model i and that of the best model (i.e. the model with the lowest AICc); w: Akaike weight. For each best model, variability (as a percentage) explained by the fixed and random predictors (R²) are shown. The best models (ΔAICc<2) are highlighted in bold.

Movement patterns	Model	k	AIC _c	[?]AIC _c	AIC _{cw}	R ² fixed
Home range size (km ²)	Season + sex + breeding region	6	59582.1	0.00	0.993	28.18
	Breeding region + season	5	59612.7	30.56	0.007	
	Breeding region + Sex	5	59849.0	266.88	0.000	
	Season + Sex	5	59862.2	280.05	0.000	
	Season	4	59877.6	295.45	0.000	
	Breeding region	4	59877.7	295.58	0.000	
	Sex	4	60132.9	550.79	0.000	
	Null	3	60147.5	565.39	0.000	

Cumulative distance (km)	Season + sex + breeding region	6	67835.8	0.00	0.988	33.29
	Season + breeding region	5	67844.6	8.74	0.012	
	Season + sex	5	67941.3	105.48	0.000	
	Season	4	67952.4	116.59	0.000	
	Breeding region + sex	5	69656.5	1820.6	0.000	
	Breeding region	4	69665.9	1830.	0.000	
	Sex	4	69771.4	1935.6	0.000	
	Null	3	69784.4	1948.5	0.000	
	Spatial segregation	Model	k	AIC_c	[?]AIC_c	AIC_{cw}
Monthly home-range fidelity (%)	Season + sex + breeding region	6	-1415.9	0.00	0.998	0.842
	Season + breeding region	5	-1392.5	23.45	0.002	
	Season + sex	5	-1371.2	44.73	0.000	
	Season	4	-1353.0	62.90	0.000	
	Breeding region + sex	5	-1230.5	185.46	0.000	
	Breeding region	4	-1209.2	206.70	0.000	
	Sex	4	-1189.4	226.54	0.000	
	Null	3	-1171.3	244.57	0.000	

Table 3. Estimates for fixed terms of the best models of monthly home range size, cumulative distance travelled per month and monthly home-range fidelity for GPS-tracked Griffon Vultures in Spain. Season, Sex and Breeding region variables were coded as a factor, being “Winter”, “Female” and “Alto Ebro” the reference values for statistical comparisons. Significant values are highlighted in bold. Abbreviations: SE= Standard error.

Response variable	Predictors	Estimate ± SE	z value	P-value
Monthly home-range size	Season (Spring)	2250.6 ± 193	11.660	<0.001
	Season (Summer)	2195.7 ± 195.6	11.225	<0.001
	Season (Autumn)	204 ± 193.9	1.053	0.292
	Sex (Male)	-1294.5 ± 291	-4.449	<0.001
	Breeding region (Segovia)	-899.8 ± 586.8	-1.533	0.125
	Breeding region (Cádiz)	1670.7 ± 507.2	3.294	0.001
	Breeding region (Cazorla)	5750 ± 319.8	17.980	<0.001
	Breeding region (Pyrenees)	1920.3 ± 397.9	4.827	<0.001
Cumulative distance	Season (Spring)	1393.69 ± 47.05	29.622	<0.001
	Season (Summer)	1925.70 ± 48.43	39.763	<0.001
	Season (Autumn)	162.46 ± 49.79	3.263	0.001
	Sex (Male)	41.15 ± 73.88	0.557	0.577
	Breeding region (Segovia)	169.34 ± 174.01	0.973	0.331
	Breeding region (Cadiz)	950.40 ± 139.34	6.821	<0.001
	Breeding region (Cazorla)	419.20 ± 84.79	4.944	<0.001
	Breeding region (Pyrenees)	649.23 ± 108.33	5.993	<0.001
Monthly home-range fidelity	Season (Spring)	0.439 ± 0.046	9.502	<0.001
	Season (Summer)	0.629 ± 0.046	13.549	<0.001
	Season (Autumn)	0.315 ± 0.047	6.653	<0.001
	Sex (Male)	0.267 ± 0.058	4.543	<0.001
	Breeding region (Segovia)	0.691 ± 0.147	4.688	<0.001
	Breeding region (Cadiz)	-0.099 ± 0.135	-0.729	0.465
	Breeding region (Cazorla)	0.253 ± 0.096	2.635	0.008
	Breeding region (Pyrenees)	0.255 ± 0.112	2.279	0.022

FIGURE CAPTIONS

Fig 1. Movements and nest locations of 127 adult Griffon Vultures tagged with GPS in northern (Alto Ebro and Pyrenees), central (Segovia) and southern (Cádiz, and Cazorla) Spain. N represents the number of tagged vultures for each breeding region. Photo credit: Manuel de la Riva.

Fig 2. Mean monthly home-range size (in km², based on 95% KDE \pm SD) of 127 adult Griffon Vultures (43 females and 84 males) tagged in northern (Alto Ebro and Pyrenees), central (Segovia) and southern (Cadiz, and Cazorla) Spain. The standard deviation is shown as error bars.

Fig 3. Mean monthly cumulative distance travelled (in km) of 127 adult Griffon Vultures (43 females and 84 males) tagged in northern (Alto Ebro and Pyrenees), central (Segovia) and southern (Cádiz, and Cazorla) Spain. The standard deviation is shown as error bars.

Fig 4. Differences in the monthly home-range fidelity (in %) at individual level between females and males in different season of 127 adult Griffon Vultures (43 females and 84 males) tagged in northern (Alto Ebro and Pyrenees), central (Segovia) and southern (Cádiz, and Cazorla) Spain. The standard deviation is shown as error bars.

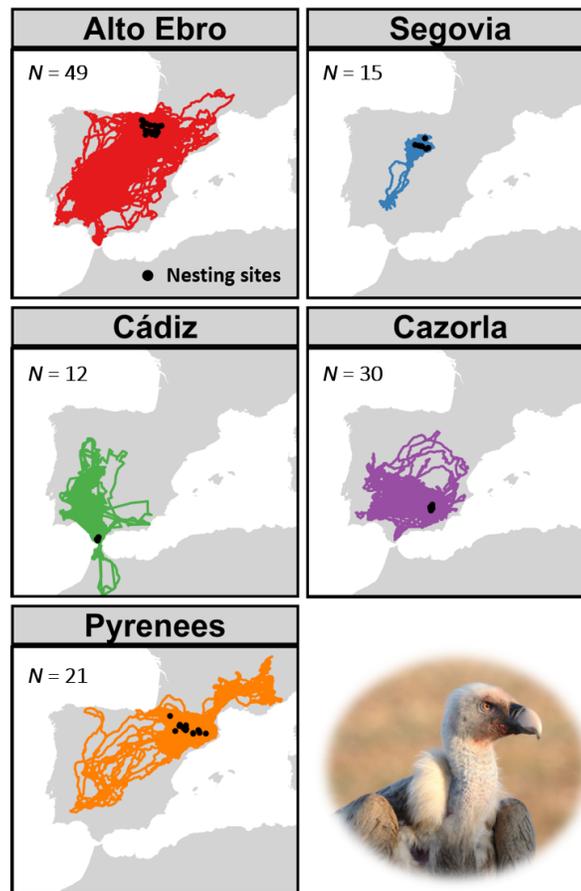


Fig.1

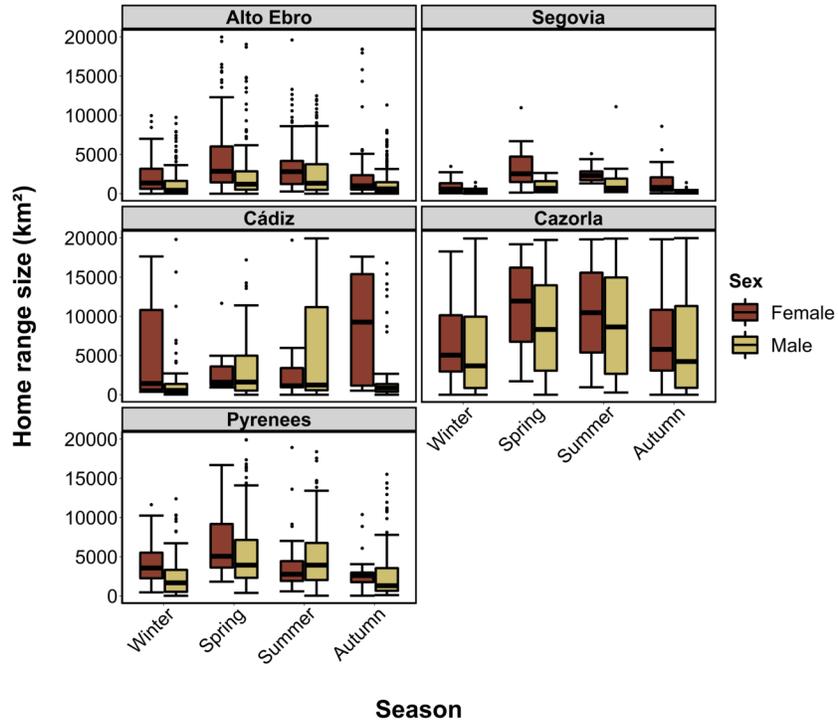


Fig.2

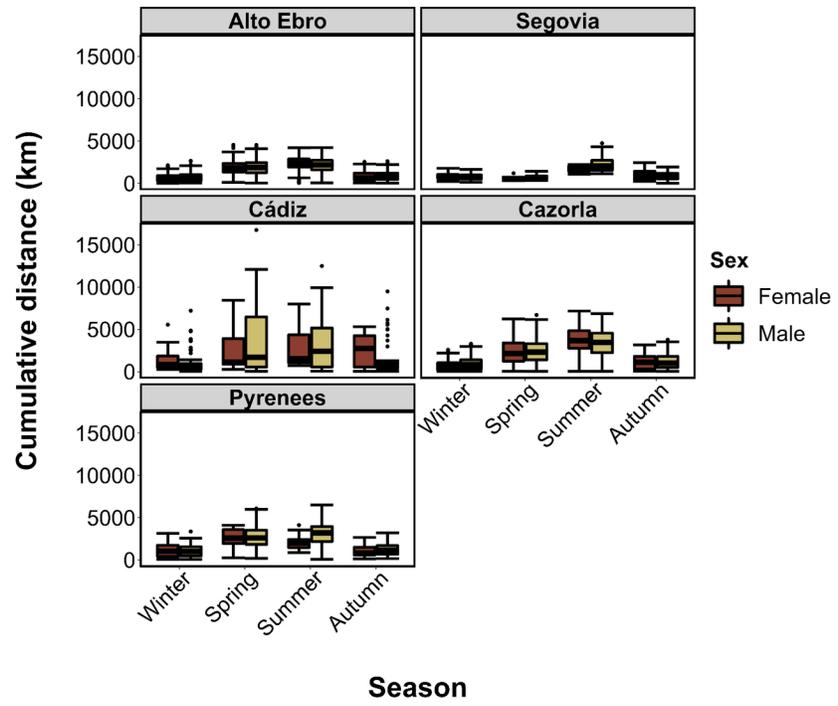


Fig.3

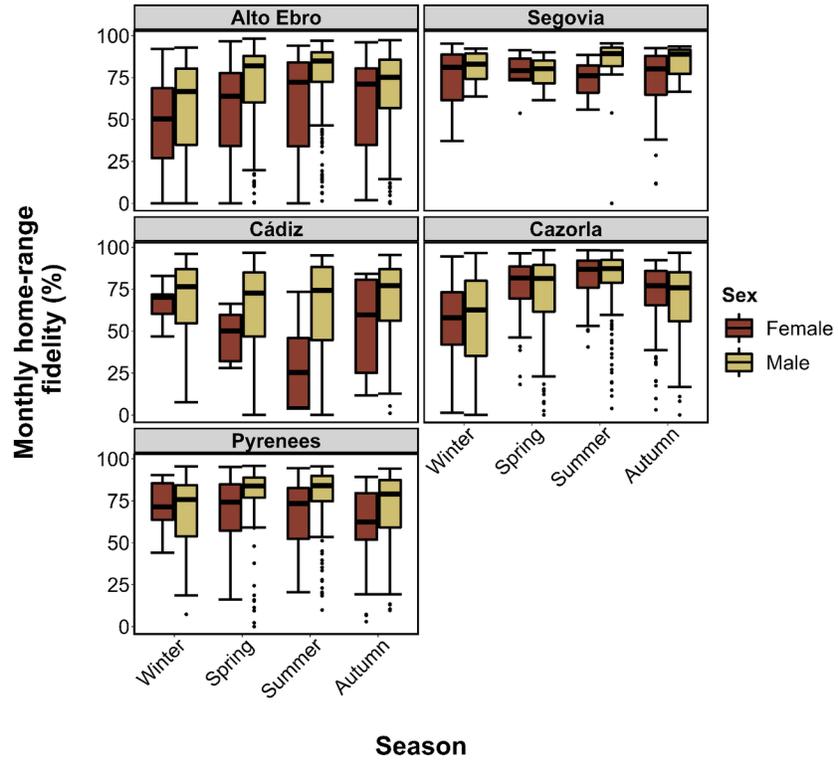


Fig.4