



Integration of critically endangered Rüppell's Vultures with Griffon Vultures in a newly colonized European region

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Abstract

The critically endangered Rüppell's Vulture (*Gyps rueppelli*), originally from sub-Saharan Africa, has recently begun to establish itself in Europe, specifically in the Iberian Peninsula. This study focuses on understanding the spatial ecology of Rüppell's Vultures during the breeding season, analyzing movement patterns and home-range sizes of three individuals tagged with GPS in southern Spain. The results show significant differences in home-range sizes between adult and immature vultures, with the immature individual exhibiting larger ranges and exploratory behavior, while adults, particularly during breeding, displayed more localized movements. The integration of Rüppell's Vultures with Griffon Vultures (*Gyps fulvus*), including hybrid breeding attempts, raises conservation concerns regarding potential genetic amalgamation. The study highlights the need for transboundary conservation strategies, as some individuals occasionally enter Portuguese territory during the breeding season. These findings provide crucial insights for the conservation management of this species in Europe, where the vultures' expanding presence requires coordinated efforts to address threats such as energy infrastructures. Ongoing monitoring is necessary to assess whether these individuals represent a temporary presence or a long-term colonization process.

Keywords Biogeographic shift · Colonization · GPS telemetry · Endangered species management · Spatial ecology · Transboundary conservation

Zusammenfassung

Integration der vom Aussterben bedrohten Sperbergeier mit Gänsegeiern in einer relativ neu besiedelten Region Europas

Der vom Aussterben bedrohte, ursprünglich aus Subsahara-Afrika stammende Sperbergeier (*Gyps rueppelli*) hat sich seit kurzem auch in Europa, speziell auf der Iberischen Halbinsel, angesiedelt. In dieser Studie ging es darum, die Raumökologie von Sperbergeiern während der Brutzeit besser zu verstehen; dafür wurden die Bewegungsmuster und die Reviergrößen dreier mit GPS markierter Tiere in Südspanien analysiert. Die Ergebnisse zeigen signifikante Unterschiede in der Reviergröße junger und adulter Geier; das junge Individuum hatte ein größeres Reviere und zeigte ein erkundungsfreudigeres Verhalten, während die erwachsenen Geier insbesondere während der Brutzeit mehr in der näheren Umgebung blieben. Die Integration von Sperbergeiern mit Gänsegeiern (*Gyps fulvus*), einschließlich hybrider Brutversuche, wirft aus Sicht des Artenschutzes Bedenken hinsichtlich einer möglichen genetischen Vermischung auf. Unsere Untersuchung unterstreicht die Notwendigkeit

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grenzüberschreitender Artenschutzstrategien, da sich einige Tiere während der Brutzeit gelegentlich auch auf portugiesischem Gebiet aufhielten. Diese Ergebnisse liefern grundlegende Erkenntnisse für das Artenschutzmanagement dieser Art in Europa, wo die zunehmende Verbreitung der Geier koordinierte Anstrengungen erfordert, um z. B. den von Energieinfrastrukturen ausgehenden Gefahren begegnen zu können. Eine kontinuierliche Beobachtung ist notwendig, um herauszufinden, ob es sich bei diesen Tieren nur um einen vorübergehenden Aufenthalt oder um einen langfristigen Ansiedlungsprozess handelt.

Introduction

Rüppell's Vulture (*Gyps rueppelli*), a critically endangered species native to sub-Saharan Africa, has experienced a dramatic contraction in its historical range in recent decades (BirdLife International 2021). Its original range spanned the Sahel region of Africa, extending south through the savanna areas of East Africa (Kemp et al. 2020). During the last decades, the species has been regularly observed in Europe, typically in association with flocks of Griffon Vultures (*Gyps fulvus*) (Ramírez et al. 2011), with sightings reported consistently since the 1990s (Gutiérrez 2003; de Juana 2006). Its presence became so regular that by 2016 it was removed from the rare species list in Spain (Gil-Velasco et al. 2017). Although some research has been conducted on Rüppell's Vulture in northern Africa (El Khamlichi 2020; Garrido et al. 2022), there is still a significant gap in our understanding of its presence and movements in Europe, where, despite frequent observations, detailed studies are lacking. This represents a paradigmatic case, as a critically endangered species begins to breed in a new biogeographic realm and forms hybrid pairs with Griffon Vultures (Muñoz et al. 2024a), raising substantial concerns regarding its conservation and the potential genetic amalgamation with the more abundant Griffon Vulture.

Understanding population dynamics and identifying key areas for conservation are essential for informing management efforts, particularly through the study of animal movements and the factors influencing them (Fraser et al. 2018; Katzner and Arlettaz 2020; Arrondo et al. 2021; Pérez-García et al. 2022). Additionally, determining the extent of cross-border movements is critical for the implementation of effective transboundary conservation initiatives (Arrondo et al. 2018; Mason et al. 2020), which is especially important in the Iberian Peninsula, a single geographic unit shared by two countries that regularly host Rüppell's Vulture in Europe. Advancements in tracking and telemetry technologies like GPS have greatly enhanced the efficiency, affordability, and accuracy of collecting vast amounts of animal location data (Tomkiewicz et al. 2010; Nathan et al. 2022). These innovations offer unprecedented opportunities to study animal behavior, biotic interactions, and responses to environmental stimuli under natural conditions, allowing researchers to explore the movement ecology of free-ranging individuals (López-López 2016; Arrondo et al. 2025). Moreover, estimating home ranges and utilization

distributions (UDs) has become a widely used application of location data, offering valuable insights into the animals' spatial requirements, habitat preferences, and resource use patterns (Kie et al. 2010).

In an effort to improve our understanding of the spatial ecology of the critically endangered Rüppell's Vulture in Europe, this study provides a descriptive account of the movement patterns of three GPS-tagged individuals monitored during the breeding season. As this species, primarily native to Africa, has only recently begun to establish itself in Europe (Muñoz et al. 2024a), even limited data can yield valuable insights into its early colonization dynamics and potential conservation needs. By analyzing monthly home-range sizes, core-use areas, and spatial overlap among individuals of different age classes and reproductive status, we aim to explore variation in spatial behavior and document patterns that may signal emerging strategies of habitat use. These initial observations offer a first glimpse into how Rüppell's Vultures interact with European landscapes during a critical phase of their annual cycle, and may help inform future research and conservation planning as the species begins to settle and reproduce in non-native habitats.

Material and methods

Study area

The study was conducted in the Iberian Peninsula, located in southwestern Europe. The region comprises two major macrobioclimatic zones: temperate in the north and northwest, and Mediterranean in the rest, which support a mosaic of habitats from temperate forests to open woodlands and scrublands (Rivas-Martínez et al. 2017). Several mountain ranges, such as the Pyrenees, Sistema Central, and Baetic Systems, generate favorable conditions for soaring birds like vultures, which depend on thermal updrafts to locate unpredictable food resources (O'Neal Campbell 2016). The Iberian Peninsula supports the largest population of vultures in Europe, including Griffon Vultures and a presumed increase in Rüppell's Vultures, although this trend remains uncertain. The region sustains large quantities of ungulate carrion, primarily of anthropogenic origin, with livestock accounting for over 90% of the total estimated carrion biomass (Morant et al. 2023a). These abundant and spatially predictable food sources, combined with suitable breeding and soaring

habitats, make the peninsula a key area for studying vulture ecology and conservation (Santangeli et al. 2019).

Capture, tagging, age, and sex determination

Between November 2021 and May 2022, three Rüppell's Vultures were captured at the Natural Site of the Gaitanes Gorge (Paraje Natural Desfiladero de los Gaitanes; 36°54'34.5"N, 4°46'41.6"W), in southern Spain, near an active Griffon Vulture colony. The vultures were captured using a walk-in cage trap baited to attract the birds. The trap was actively monitored by researchers hiding nearby. Once trapped, the individuals were ringed, weighted, measured, and a blood sample was collected for genetic sex determination at the Center for Analysis and Diagnosis of Wildlife (CAD, Junta de Andalucía), as the species lacks obvious sexual dimorphism. Age classification was based on morphological traits such as plumage, beak, and eye characteristics (Rodríguez and Elorriaga 2016; Muñoz et al. 2024b), allowing the birds to be categorized as adult, immature, or juvenile. The tagged Rüppell's Vultures included two adults, a male and a female, and one immature male. Although the sample size is limited, it likely represents a considerable proportion of the total Rüppell's Vulture population currently present in Europe.

All individuals were equipped with 50 g solar-powered GPS-GSM transmitters, manufactured by Microsentry (Cordoba, Spain, $n=2$) and Ornitela (Vilnius, Lithuania, $n=1$). The devices were attached to the vultures' backs using a loophole harness. The total weight of the equipment was less than 1% of the individual's body mass, which is within the recommended limit (Bodey et al. 2018), as the average weight of our Rüppell's Vulture ranged from 5.7 kg to 7.9 kg. Following tagging, intensive on-site observations and GPS tracking were conducted throughout the study period to document behavior, interactions with Griffon Vultures, and enrich the interpretation of the results.

Movement analyses

The study period extended from November 2022 to May 2023, overlapping with the breeding season, which includes courtship, nest building, egg laying, and fledging of the offspring (Donázar 1993). During this time, the number of GPS coordinates received per day fluctuated due to variations in battery charge levels, which needed to be maintained within specific limits. In the winter months, the number of acquired coordinates decreased because of the reduced solar panel recharge rate. No manual intervention was required for data download or transmitter reprogramming, as all operations were conducted remotely via the Internet and mobile antennas.

To ensure data quality, all GPS locations underwent a filtering process to remove spatial outliers and duplicates. The time intervals for location recording varied across transmitters, ranging from five minutes to 18 h. For consistency in data analysis, a standardized approach was applied, selecting one position per hour (the first location recorded for each hour) for all individuals. GPS locations were then projected onto the UTM coordinate system (WGS 1984 UTM Zone 30).

Home range size and overlap

To quantify the spatial extent used by each individual, total and monthly home range sizes (95% and 50% kernel density estimator, KDE) were estimated using the fixed kernel density method (Worton 1989), implemented through the *kernelUD* function from the *adehabitatHR* R package (Calenge 2006). The reference bandwidth (href) was selected as the smoothing parameter due to its robustness against potential outliers in large datasets (Hemson et al. 2005). Additionally, the total home ranges of all individuals were merged to identify key areas for the species. This analysis aimed to provide valuable insights for management planning, where the 50% KDE was considered the minimum area necessary for effective conservation efforts.

To assess home range overlap among individuals, we applied two probabilistic metrics based on UD. The Bhattacharyya index (BA) was used as a robust estimator to quantify the similarity between individuals' UD, with values ranging from zero (indicating no similarity) to one (indicating identical UD) (Fieberg and Kochanny 2005). Additionally, the UD overlap index (UDOI) was employed to measure the degree of spatial overlap between individuals. UDOI values range from zero, representing no overlap, to one, indicating complete overlap with uniformly distributed UD. In cases where UD are nonuniformly distributed but still exhibit significant overlap, UDOI values can exceed one (Fieberg and Kochanny 2005). We compared the overlap between three pairs—adult male and adult female, adult male and immature male, and adult female and immature male—to assess similarities in UD and spatial use. Furthermore, individual home range fidelity was evaluated by measuring the overlap of consecutive monthly home ranges.

Results

We collected a total of 36,015 GPS locations from the three Rüppell's Vultures between 1st November 2022 and 31st May 2023. After removing outliers, duplicates, and homogenizing the data, 9055 GPS locations were retained for analysis (Table 1).

Table 1 Summary of movement-related information (GPS locations, home range, and core areas) for the three Rüppell's Vultures tracked in this study, including their name, age, and captured date

Capture date	Age	Sex	GPS locations	Home range (95% KDE; km ²)	Core area (50% KDE; km ²)
30/05/2022	Adult	Male	4305	5831.1	492.4
18/11/2021	Adult	Female	2493	53,745.3	8335.3
15/11/2021	Immature	Male	2257	120,363.1	21,942.6
			9055	127,594.5	25,669.7

The two adult Rüppell's Vultures showed clear evidence of reproductive behavior. The adult male paired with a female Griffon Vulture and successfully raised a chick (Muñoz et al. 2024a), remaining linked to the breeding colony until the end of the breeding period. The adult female was observed copulating with male Griffon Vultures during December and January, but ultimately failed in her breeding attempt, as she did not lay an egg.

The two adult Rüppell's Vultures tracked in this study primarily moved within the southern region of the Iberian Peninsula, with overlapping movements near the capture site. In contrast, the immature Rüppell's Vulture exhibited more extensive movements, frequently traveling to the west and south of the peninsula, along with a single excursion to the north and east (Fig. 1). Both the immature and female vultures ventured into Portuguese territory, although the female made more frequent flights. The combined total home range (95% KDE) of all individuals covered 127,594.5 km², primarily concentrated in the western and southern regions of the peninsula (Table 1). Core areas (50% KDE) covered 25,669.7 km², mainly located in the southern part, predominantly in Spanish territory (Fig. 1). The average monthly home ranges (95% KDE) and core areas (50% KDE) were $25,992.6 \pm 38,297.3$ km² (range: 7.6–134,026.3 km²), and 5254.8 ± 8225.2 km² (range: 0.9–29,327.1 km²), respectively (Table 1). Home range sizes varied both between and within individuals, with the immature vulture occupying the largest home range, while the adult male had the smallest one, a pattern also observed in core areas (Table 1, Fig. 1).

The UDOI and BA estimates suggest that the female adult and the immature exhibit the highest degree of distribution similarity and space sharing among all individuals (Table 2).

During the first three months of the breeding season, both adults' home ranges remained within the Malaga region, Spain, and were the smallest in comparison to the rest of the study period (see electronic supplementary material Figs. S1, S2). Adult male's core area stayed in or near Malaga throughout the entire study, with an expansion of the overall home range starting in April, during the rearing period (Figs. 2 and S1). From February onward, the adult female's home range became more widespread, encompassing multiple core areas, one in Malaga and others in different

parts of the southwestern Peninsula, including incursions into Portuguese territory (Figs. 2 and S2).

The core area sizes of the adult male and female remained relatively constant and similar until February, after which the female's core area began to expand, while the male's remained stable (Fig. 2A). In contrast, the immature's core area size was relatively constant until March, despite variations in home range size throughout the study period. The largest core areas and home ranges for the immature were observed in the final months of the study (Fig. 2B).

The immature's home range was not confined to a specific location and exhibited the broadest territorial use among the three individuals. From November to March, its home range was concentrated in the southern part of the Iberian Peninsula, after which it expanded into Portuguese territory and the northern regions of the peninsula (Fig. S3).

Among the adults, the December to January period showed a high rate of overlap, while the March to April and April to May periods had the lowest overlap rates. The overlap indices between consecutive months for the adult male and the immature were variable, with some months showing high overlap and others displaying low overlap. In contrast, the adult female exhibited a progressive decrease in overlap between consecutive months (Table 3).

Discussion

Differences in movement patterns between adults and immatures

The results reveal a clear distinction in spatial use between adult and immature Rüppell's Vultures. The immature individual exhibited the most extensive home range. In November, during the days when the largest number of Griffon Vultures cross from Europe to Africa (Bernis 1980; Bildstein et al. 2009), and March, he approached the Strait of Gibraltar but did not cross it, instead heading to north-western Andalusia, where many juvenile and immature Griffon Vultures spend the winter (Del Moral and Molina 2018). This aligns with previous research conducted on Griffon Vultures, suggesting that younger individuals typically explore larger areas compared to adults during the breeding season

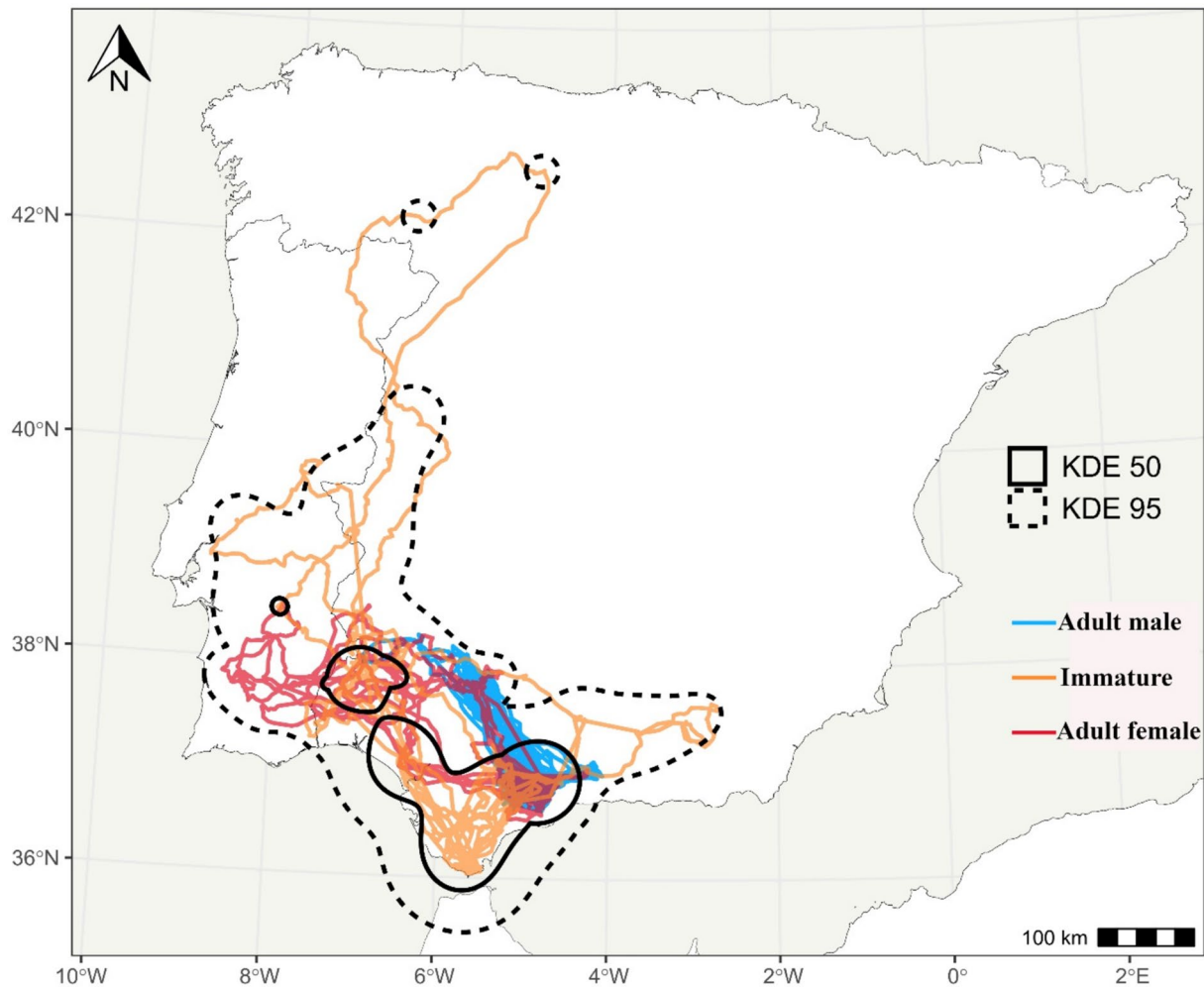


Fig. 1 Merged core areas and home ranges of tracked Rüppell’s Vultures during the breeding season. Diurnal flight paths are shown, with colors representing each individual: adult male in blue, adult female

in magenta, and immature in orange. Solid lines indicate 50% KDE, while dashed lines represent 95% KDE, respectively

(Zuberogoitia et al. 2013; Morant et al. 2023b), likely due

Table 2 Pairwise home range overlap estimates for the three tracked Rüppell’s Vultures during the breeding season, calculated at 50% KDE and 95% KDE

	BA _{UD50}	BA _{UD95}	UDOI _{UD50}	UDOI _{UD95}
Adult female—immature male	0.16	0.60	0.16	0.58
Adult male—adult female	0.14	0.49	0.02	0.47
Adult male—immature male	0.00	0.20	0.00	0.06

to their lack of reproductive duties and the need to develop efficient foraging strategies. In all direct observations conducted, the immature Rüppell’s Vulture was observed in the company of juvenile and immature Griffon Vultures. The

adult vultures, male and female, displayed more localized movements, particularly during the early stages of the breeding season, likely related to their nesting activities, which may require them to remain close to breeding grounds (Houston 1976; Fluhr et al. 2021). Unlike the immature, none of the adults approached the Strait of Gibraltar, which they would need to cross if they were returning to Africa, further indicating their settlement in Europe. The female had a larger home range and showed a lower site fidelity compared to the male, as already demonstrated for the Griffon Vulture (Morant et al. 2023b). Additionally, in all field observations, these adult Rüppell’s Vultures were consistently found in the company of Griffon Vultures, fully integrated into their groups and breeding colonies. These repeated associations suggest that Rüppell’s Vultures may already be playing a similar ecological role to Griffon Vultures within these mixed-species groups. Moreover, such patterns may be influenced by heterospecific facilitation processes, whereby

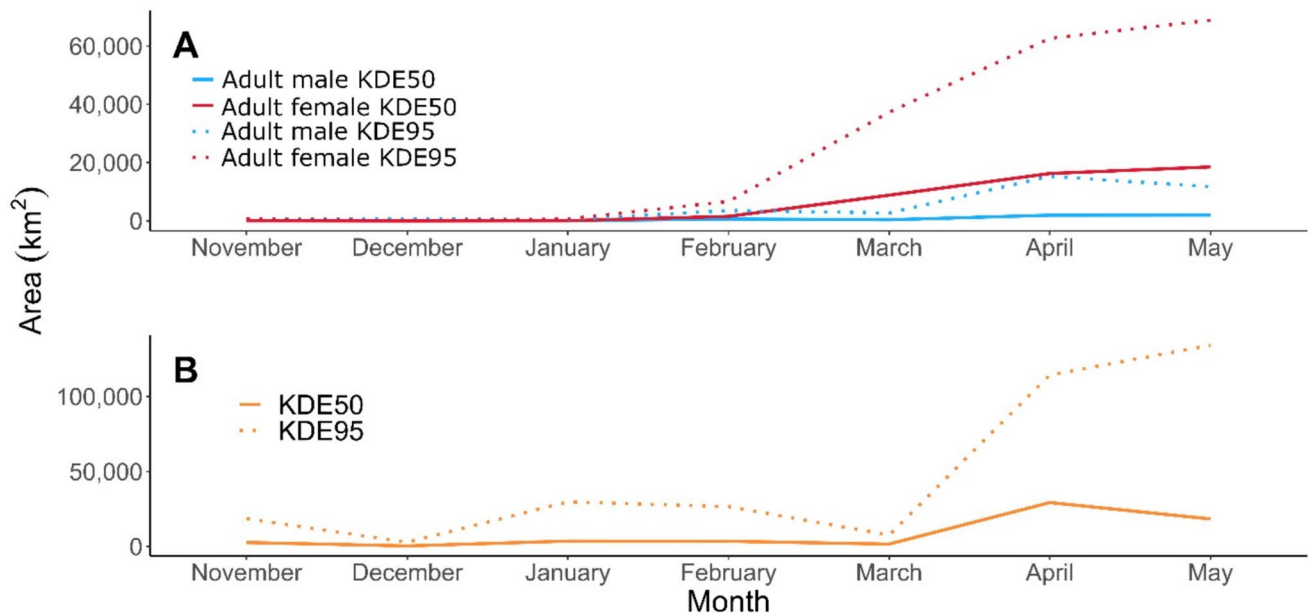


Fig. 2 Temporal changes in KDE for tracked Rüppell's Vulture during the breeding season. **A** Monthly KDE areas for the adult class, with adult male represented in blue and adult female in magenta. **B** Monthly KDE for the immature male shown in orange

Table 3 Estimated home range overlap values for consecutive months pairs for each Rüppell's Vulture in the Iberian Peninsula during the breeding season

	Adult male		Adult female		Immature	
	BA	UDOI	BA	UDOI	BA	UDOI
November–December	0.72	0.15	1.52	0.00	0.84	0.00
December–January	2.26	3.16	26.36	611.11	5.68	29.01
January–February	1.06	0.37	1.81	1.38	3.01	6.32
February–March	2.35	8.20	1.18	1.12	0.78	0.08
March–April	0.03	0.00	0.63	0.28	4.73	19.59
April–May	0.26	0.05	0.46	0.15	0.88	0.78

individuals benefit from the social cues provided by other species to enhance foraging efficiency (Oliva-Vidal et al. 2024).

The differences in home range sizes between age classes highlight the importance of understanding age-related behavioral differences when designing conservation strategies. These differences are likely shaped not only by age itself, but also by social factors such as dominance status and experience, which influence access to resources and movement decisions in vulture populations (van Overveld et al. 2020). Moreover, the observed movement patterns are consistent with those reported for the Griffon Vulture, suggesting that Rüppell's Vultures are already integrated into the Griffon Vulture population. This potential integration underscores the need for comprehensive studies to assess the implications for both species, particularly concerning hybridization and resource competition.

Temporal changes in spatial use and overlap

Both adults demonstrated relatively small home ranges during the early breeding season, particularly from November to February, when vultures are most occupied with nest defense and egg laying. The localized movements observed at the beginning of the breeding season in the adult male, who successfully reproduced, are likely associated with the spatial constraints imposed by parental duties. As the breeding season progressed and the chick required less parental investment, his home range expanded, indicating a shift in foraging strategy in response to changing reproductive demands (Fluhr et al. 2017). The adult female, who had no reproductive commitments, expanded her movements, including excursions into Portuguese territory, yet she regularly returned to the same breeding colony, indicating her integration into the Griffon Vulture breeding colony. This individual has been

observed consistently at the same colony from 2020 up to the time of writing this text (November 2025).

In contrast, the immature maintained a broader and more variable home range throughout the study period, reflecting the exploratory behavior typical of immature vultures. The overlap indices (UDOI and BA) indicated that the highest degree of spatial overlap was observed between the female adult and the immature, which may be due to both individuals converging on high-quality foraging grounds in south-western Iberia (Delgado-González et al. 2022). However, the progressive decrease in overlap between consecutive months in the adult female's movements supports the idea of increased exploration as the breeding season progressed. The areas used by Rüppell's Vultures align with those predicted as highly favorable for African species colonizing Europe, as identified by López-Ramírez et al. (2024).

Conservation implications and future research directions

The results from this study provide the first insights into the spatial ecology of Rüppell's Vultures during the breeding season in Europe, specifically in the Iberian Peninsula. This region already hosts established individuals that are mixing with the Griffon Vulture (Muñoz et al. 2024a), making it essential to generate comprehensive knowledge about their behavior and ecology. Further research is needed to assess the long-term establishment of Rüppell's Vultures in Europe, particularly as sightings of adult individuals increase; based on our monitoring work, at least four different adults have been identified so far in breeding colonies of Griffon Vultures, all of them in Andalusia, although only two are known to be integrated as breeders within Griffon Vulture colonies. Continued monitoring through GPS tracking could provide valuable data on how this species adapts to new habitats and interacts with native Griffon Vulture populations. The immature's proximity to the Strait of Gibraltar during the migration periods, without actually crossing it, raises questions about whether he will make future crossings or permanently settle in Europe. While it is known that some Rüppell's Vultures cross to Africa, leaving the European continent and returning to their natal areas (Ramírez 2012), the immature did not depart, which is something other Rüppell's Vultures may also do. It remains unknown whether he will do so in the future or if this marks the beginning of his establishment and potential reproduction in Europe. Understanding how individuals from different biogeographical regions establish themselves in Europe may be crucial.

One limitation of our study is the small number of individuals monitored, although increasing the sample size would be extremely challenging given the very limited number of Rüppell's Vultures present in Europe, which likely numbers only a few dozen individuals (Molina et al. 2023

and own data). For now, this remains the only available information on the species in this region.

Determining whether the presence of Rüppell's Vultures in Europe represents sporadic events or a colonization in progress will ultimately require continued monitoring. The colonization of Europe by Rüppell's Vulture will depend on ongoing arrivals from Africa, their settlement in Europe, and whether hybrid pairs participate in breeding events or Rüppell's Vultures reproduce among themselves, which has not been observed to date and seems unlikely. This knowledge would provide insights into how species expand their ranges and adapt to new environments, which is of great importance for anticipating the future of the Rüppell's Vulture population in Europe.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10336-026-02364-x>.

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Data availability Data supporting the findings of this study are available from the corresponding author upon reasonable request.

Declarations

Conflict of interest The authors declare that non-financial interests exist that could be perceived as influencing the work reported in this manuscript.

Ethics approval Capture and marking procedures were carried out with authorizations granted by regional authorities (Consejería de Agricultura, Ganadería, Pesca y Desarrollo Sostenible, Junta de Andalucía). To minimize stress on the vultures, handling time was kept to a minimum. All the individuals were captured and tagged outside the breeding season to avoid influencing their behavior during this critical period.

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