

**Title:** Weather conditions are systematically associated with long-range nonroutine movements in a large scavenger

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## Abstract

Movement data are valuable for the conservation of Old World vultures, as these move across large distances and experience a wide range of threats. As vultures rely on soaring flight, the interplay of solar radiation, as well as wind direction and strength, is crucial for both short- and long-range movements. However, no study explored the extent to which weather conditions can predict long-range nonroutine movements, such as those associated with forays, prospecting or dispersal.

We fitted Generalized Additive Mixed Models to predict the probability Griffon Vultures (*Gyps fulvus*, n.individuals = 20, n. GPS locations = 168,202) living in Sardinia (Italy) engaged in short-range, medium- and long-range movements under different weather conditions, in terms of solar radiation, wind direction and wind strength.

Under very weak wind conditions, Griffon Vultures restricted their movements in the areas around the colony, as exploring areas at the borders of their home range is more demanding. Conversely, under very strong winds, extra-home range movements were uncommon as Griffon Vultures could be less prone to venture outside well-known areas.

Extra-home range movements were more common for northwestern and southeastern winds of intermediate strength, in conditions of good solar radiation. However, the duration of long-range movements decreased with solar radiation. This might indicate that wind sometimes displaces Griffon Vultures and scarce solar radiation then prevents them from returning to the colonies, forcing them to engage in long journeys across unfamiliar landscapes.

Our findings indicates that some types of nonroutine movements in vultures are not entirely intentional and weather conditions can play a crucial role in triggering them. Combining high-resolution movement and weather data could allow researchers to them in advance and adaptively increase improve data acquisition from GPS tags, to study vulture behavior during nonroutine movements and improve conservation actions.

**Keywords:** foraging; scavengers; forays; vultures; biologging; soaring birds

1

## 2 **Introduction**

3 Movement data are increasingly used to attain a sounder understanding of animal ecology  
4 (Nathan et al., 2022) and inform conservation policies (Allen and Singh, 2016). Information  
5 derived from movement data are particularly valuable for the conservation of taxa such as  
6 Old World vultures (Ogada et al., 2012), which can move across large distances and therefore  
7 experience a wide range of threats.

8 Satellite telemetry (Alarcón and Lambertucci, 2018) shed light on the bioenergetics of flight  
9 in vultures (Duriez et al., 2014), as well as on the role played by social and heterospecific  
10 cues (Oliva-Vidal et al., 2024; Sassi et al., 2024). This technology also allowed to study  
11 routine movements (Newton, 2008) of several species of vultures, such as those associated  
12 with residency and seasonal migration (Arkumarev et al., 2019; Buechley et al., 2018; Kang  
13 et al., 2019; Martínez et al., 2024). Moreover, some studies also used telemetry and  
14 biologging to study long-range nonroutine movements (hereinafter referred as “nonroutine”  
15 movements), such as those associated with dispersal (García-Macía et al., 2023; Martínez et  
16 al., 2025; Tréhin et al., 2024; Tobajas et al., 2024). This knowledge in turn revealed the  
17 behavioral consequences of captive breeding (Jobson et al., 2021; Margalida et al., 2013) and  
18 release methods (Cerri et al., 2024a; Fozzi et al., 2023; Rousteau, 2022), predicted exposure  
19 to potential threats (Cervantes et al., 2023; Morant et al., 2024) and informed the design of  
20 protection areas (Kane et al., 2022) and ecotourism (Fozzi et al., 2025).

21 A frontier in research about the movement ecology of vultures is the integration between  
22 high-resolution environmental data and movement data, to assess the role played by weather  
23 conditions on the motion capacity of these species (Nathan et al., 2008). Soaring birds like  
24 vultures are strongly dependent on uplifts, which arise from the interplay of air temperature,

1 terrain morphology and wind conditions (Scacco et al., 2019, 2023). However, the few  
2 existing studies studying the link between weather conditions and vulture movements focused  
3 on the influence of solar radiation (Rivers et al., 2014; Poessel et al., 2017), with significant  
4 gaps still surrounding the role played by wind, such as the interplay between wind direction  
5 and strength. Addressing this gap would be particularly valuable both from a scientific and an  
6 applied perspective.

7 For short-range routine movements, such as foraging around colonies, considering that  
8 flapped flight is energetically costly for vultures (Duriez et al., 2014), they should prefer  
9 flying under optimal wind conditions for short-range routine movements (Alerstam et al.,  
10 2019). However, no study tested the extent to which vultures can fly under optimal conditions  
11 in terms of wind direction but suboptimal wind strength, and vice-versa. Moreover, vultures  
12 are prone to collide with wind turbines while foraging, due to their visual field and flight  
13 maneuverability (Martin et al. 2012). While the selective stopping of turbines reduces  
14 collisions (Ferrer et al., 2022), its implementation can be expensive. By knowing under which  
15 weather conditions vultures engage in short-range routine movements it is possible to  
16 improve the cost-effectiveness of selective stopping by intensifying its field monitoring at the  
17 most critical times.

18 For nonroutine movements, such as those associated with prospecting (Chaubet et al., 2025)  
19 or forays (Conradt et al., 2003), the informed dispersal theory (Reed et al., 1999) ignores the  
20 role of weather conditions. However, evidence from other large soaring raptors (e.g., *Aquila*  
21 *chrysaetos*, Poessel et al., 2022) indicates that optimal wind and radiation facilitate  
22 prospecting and empirical evidence indicates that at least on one occasion strong winds  
23 promoted the dispersal and colonization of an island by Griffon Vultures (Tavecchia and

Cortés-Avizanda, 2021). Therefore there is a need to address the systematic effect of weather conditions as a proximate driver of nonroutine movements in vultures. Considering that long-range movements are usually risky for individuals (Bonte et al., 2012), anticipating the occurrence of nonroutine movements can allow researchers to adaptively increase the acquisition frequency of GPS tags to better understand habitat selection (Orgeret et al., 2023) and assess the height at which vultures fly, two pieces of information that will improve the estimation of collision risk with human infrastructures (Schaub et al., 2024). In this study we explored how different wind conditions affected the probability that Griffon Vultures (*Gyps fulvus*) engaged in short-range and long-range movements. Our findings indicate that weather conditions are consistently associated with different types of movements in Griffon Vultures and it is reasonable to hypothesize that some long-range movements occur because individuals are first displaced by strong winds and then face unsuitable weather conditions, preventing them from returning to the colony.

## Methods

### Study area

The study area includes the westernmost part of Sardinia (Italy), the second largest island of the Mediterranean sea (Fig. 1). Due to its Mediterranean climate, rainfalls are scarce and concentrated between November and December (Fратиanni and Acquadotta, 2017). The most common winds are the Mistral, which comes from northwest, and the Sirocco, which comes from southeast (Furberg et al., 2002).

Sardinia hosts a population of 424-470 (86 breeding pairs) Griffon Vultures (*Gyps fulvus*, Berlinguer et al., 2024). Griffon Vultures roost and nest at two main colonies in the northwest of the island, near the municipalities of Bosa and in Porto Conte Regional Park (Fig. 1, Cerri

et al., 2023). Griffon Vultures forage around the two colonies (Fozzi et al., 2025) and have smaller home-ranges than their conspecifics in mainland Europe (Cerri et al., 2023). Although long-range movements between Sardinia and Corsica have been recorded (Cerri et al., 2024), contrarily to what happens for Griffon Vultures from the Iberian peninsula or the Balkans (Arkumarev et al., 2019; Martínez et al., 2024), migration to sub-saharan Africa has never been observed in individuals from the Sardinian population.

## **Data collection**

Between 2016 and 2022, 79 Griffon Vultures were released in a conservation translocation program within the Life Under Griffon Wings project (LIFE14 NAT/IT/000484), to enhance the viability of the Sardinian population (Aresu et al., 2022). Released individuals had been recovered from the wild in the Iberian peninsula, or had been bred under different captivity breeding programs (LIFE14 NAT/IT/000484). Before being released in the wild, Griffon Vultures were tested for pathogens and lead poisoning and then kept at acclimatization aviaries, so that they could familiarize with the release site (Fozzi et al., 2023). They were also fitted with engraved metal rings from ISPRA (Istituto Superiore per la Protezione e la Ricerca Ambientale), placed on one tarsus, and with a plastic colored ring on the other tarsus to facilitate their identification. Before being released 45 individuals were also equipped with solar powered GPS/GSM transmitters, attached with a Teflon leg-loop harness comprised of 3 assembled strings (round silicone cord 2-mm + tubular Teflon ribbon 0.25 and 0.44), following Hegglin et al. (2004). GPS tags were programmed to collect the location of released griffons from dawn (approx. 6 a.m.) to dusk (approx. 6 p.m.) every  $158.3 \pm 620.8$  minutes (mean  $\pm$  sd). In this study we used locations from 20 individuals (n. GPS fix = 168,202). A complete overview of individuals from our sample is available in Table 1, while

extensive explanation about the release method and acclimatization is available in Fozzi et al. (2023).

#### **Quantification of extra-home range movements**

We quantified nonroutine movement as extra home range movements. These consisted of movement trajectories where a certain Griffon Vulture exited its home-range for a certain amount of time (Fig. 2). The home range of each individual was quantified from the 95% isopleth of its range distribution (Alston et al., 2022), obtained through Autocorrelated Kernel Density Estimation (AKDE, Fleming et al., 2015; Fleming and Calabrese, 2016) using continuous-time movement models with a perturbative Hybrid REML (pHREML) estimator (Silva et al., 2021). We generally preferred weighted AKDE (wAKDE Silva et al., 2021) due to the irregular acquisition of GPS locations by solar-powered tags and the lack of GPS location at night. Only for two individuals (Artis 4 and Artis 5) we used AKDE as wAKDE did not converge. Before estimating home ranges we screened the data and removed implausible GPS locations, falling more than 5 km away from the coast.

Whenever a Griffon Vulture exited its home range, we isolated its movement track until the moment when the individual re-entered its home range. Then, for each track we calculated: *i*) the median step length, *ii*) the median direction, expressed as degrees from the North, *iii*) the maximum distance, expressed as the Euclidean distance between the most distant point of the track and the home range, *iv*) its temporal duration, in hours and *v*) the straightness index, expressed as the ratio between maximum distance and the total length of the track. The straightness index ranges from 0 to 1, with 1 corresponding to a straight line (Benhamou et al., 2004). We believe these five metrics are useful to distinguish between long-range and

1 short-range movements of Griffon Vultures outside of their home range, which we found to  
2 differ in their duration, tortuosity and directionality.

3 Then we used Partitioning Around Medoids (PAM, Kassambara, 2017) cluster analysis to  
4 categorize individual movement trajectories outside the home-range, into different groups.  
5 The combined analysis of the average silhouette methods, elbow method and gap statistics  
6 method (Kassambara, 2017) identified 4 groups of extra-HR movements (Fig. S1). However,  
7 three groups were medium-range nonroutine movements (hereinafter MRM), characterized  
8 by short median step lengths, a short distance from the home range, intermediate to high  
9 values of the straightness index and differing in their mean orientation. In MRMs Griffon  
10 Vultures briefly exited their home range and then came back after a short period of time (Fig.  
11 1). However, cluster analysis also revealed a group of long-range nonroutine movements  
12 (hereinafter LRM) with a significantly longer duration, higher tortuosity and very high  
13 distances from the borders of the home range (Fig. S2). Although this last group was partially  
14 similar to one of the group that we classified as MRM, we preferred to keep it separated, to  
15 focus on the most extreme long-range movements only and reduce the categories used in the  
16 generalized additive mixed model.

17 Therefore, through cluster analysis we classified GPS locations as short-range movements  
18 (SRM) when falling inside the home range , as medium-range movements (MRM) when  
19 falling at a short distance outside the home range and having a short duration and as long  
20 range movements (LRM) when falling at a high distance outside the home range and having  
21 a long duration. We did not use other methods for behavioral classification (Gurarie et al.,  
22 2016), such Hidden Markov Models (Langrock et al., 2012) or Mixture Membership Models  
23 (Cullen et al., 2021), due to the high number of observations and the irregular collection of



1 GPS locations by our solar-powered tags, which did not collect locations at night or in  
2 conditions with low solar radiation.

3 Finally, for each GPS location, we extracted hourly values of solar radiation, as well as wind  
4 direction and strength, at a 10 km scale, from the ERA5 climate reanalysis dataset  
5 ([https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-single-levels?](https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-single-levels?tab=overview)

6 [tab=overview](https://cds.climate.copernicus.eu/cdsapp#!/dataset/reanalysis-era5-single-levels?tab=overview)). Solar radiation was quantified as the mean surface downward short-wave  
7 radiation flux, representing the amount of solar radiation, both direct and diffuse, that reaches  
8 the ground. Downward short-wave radiation also accounts for partial reflection, and  
9 absorption, by clouds and aerosols, and corresponds to what would be measured by a  
10 pyranometer on the ground. Wind direction and speed were calculated from the eastward and  
11 northward component (ms<sup>-1</sup>) of wind, at a height of 100 metres above the surface of the  
12 Earth. Wind direction was expressed as degrees north, whereas wind speed in ms<sup>-1</sup>. While  
13 some studies quantified the tailwind and crosswind component (Cecere et al., 2020), we did  
14 not use these measurements, as we deemed them to be potentially misleading, given the  
15 relatively coarse resolution of our data, that were collected approx. every 60 minutes. We  
16 also did not use different altitudinal layers, as our GPS tags did not provide the height of a  
17 certain GPS location.

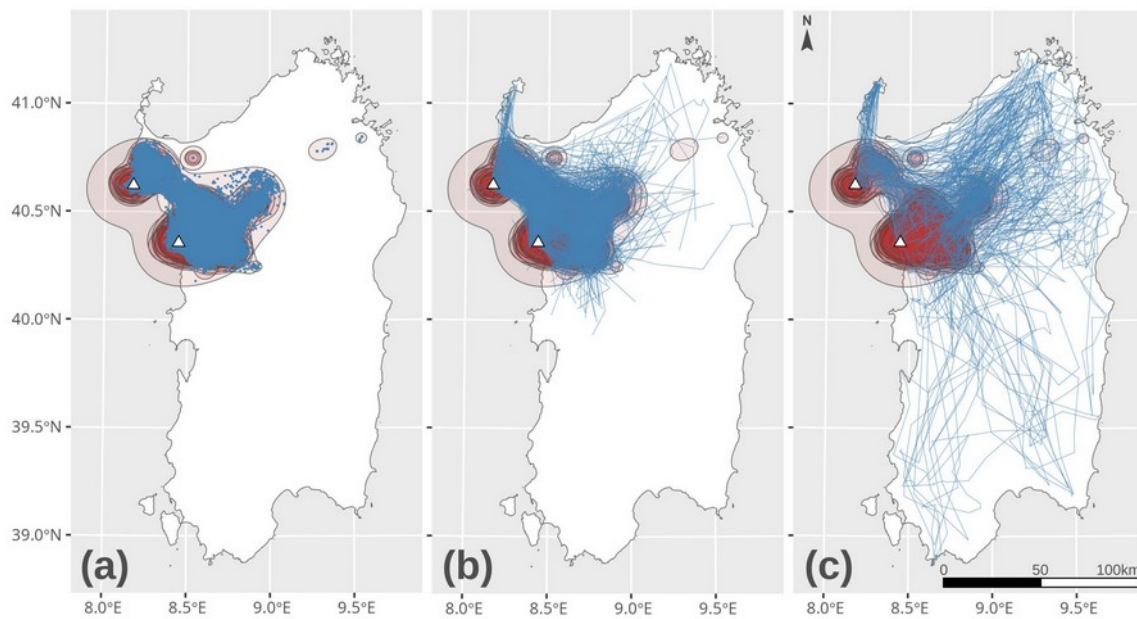


Fig. 1. Map of the study area with 95% isopleths of individual home ranges (HR, in red) and the three types of movement obtained from cluster analysis: short-range movements (left), medium-range movements (center) and long-range movements (right). The two colonies are represented as triangles.

## Statistical analyses

We used Generalized Additive Mixed Modeling (GAMM) to predict the probability that GPS locations belonged to SRMs, MRM or LRMs. We treated our three types of observations (SRM, MRM, LRM) as an ordered response, which was modeled through a linear predictor providing the expected value of a latent variable following a logistic distribution. Predictors included different weather variables and individual attributes that we deemed to potentially influence nonroutine movements by Griffon Vultures.

We included wind direction, as it can influence different types of movements of griffons in the study area. In northwest Sardinia colonies are on the west coast and foraging ground in

1 inner areas (Fozzi et al., 2025). Therefore, we hypothesized that griffons could be more active  
2 in case of western winds, that would allow to reach foraging grounds, but which can  
3 subsequently drift them away (Tavecchia and Cortés-Avizanda, 2021), increasing the  
4 likelihood of MRMs and LRMs. In turn we also included wind strength, because Griffons  
5 might be reluctant to fly around colonies with strong winds, as they can limit their aerial  
6 maneuverability around roosts (Shepard, 2019) or displace them on the open sea (Bildstein et  
7 al., 2009). We also accounted for solar radiation, as it is crucial for the generation of updrafts  
8 (Scacco et al., 2019) and therefore facilitates soaring flight in vultures (Fluhr et al., 2021;  
9 Poessel et al., 2017; Rivers et al., 2014), promoting MRMs and LRMs.

10 We also controlled for the release group of each individual, which was found to influence  
11 movement cohesion (Cerri et al., 2024) and therefore was believed to potentially influence  
12 their capacity to move across the landscape (Sassi et al., 2024). We also controlled for the age  
13 of each individual, as this variable could have potentially increased the probability of MRMs  
14 and LRMs due to the conjoint effect of increased flight experience, which makes vultures  
15 better at moving across the landscape (Efrat et al., 2023; Harel et al., 2016) and changes in  
16 the life stage of individuals (Acácio et al., 2023), which could increase long-range  
17 movements (e.g., related to prospecting, Chaubet et al., 2025). We also controlled for the sex  
18 of Griffon Vultures, as this variable was found to influence movement in individuals from  
19 populations of mainland Europe (Morant et al., 2023), and for the day of the year to capture  
20 long-range movements caused by unmeasured seasonal variations in the environment (e.g.  
21 food, Arrondo et al., 2023; Spiegel et al., 2013). Finally, we added a random intercept for  
22 each individual, to account for inter-individual differences in the probability of MRMs and  
23 LRMs due to unobserved attributes (e.g. personality, Nilsson et al., 2014).

1 We modeled wind direction, the effect of the day of the year and the effect of elapsed time  
2 since release, by means of cyclic cubic splines, which are highly effective at capturing  
3 periodic patterns. We rather used thin-plate splines to model the effect of solar radiation and  
4 wind strength. We used a tensor product to model the interactive effect of wind strength and  
5 direction (Wood, 2017). A complete script explaining model selection in GAMMs is  
6 provided in the Supplementary Information.

7 We used a combination of likelihood ratio test, AIC and generalized cross validation to  
8 select predictors and the numbers of basis in each spline. Namely, we selected the lowest  
9 number of basis after which we did not detect any improvement in model fitness to the data.  
10 Statistical analyses were carried out with the statistical software R (R Core Team, 2025).  
11 Namely, GAMMs were fitted with the *mgcv* package (Wood, 2017) and home ranges  
12 estimated with the *ctmm* package (Calabrese et al., 2016).

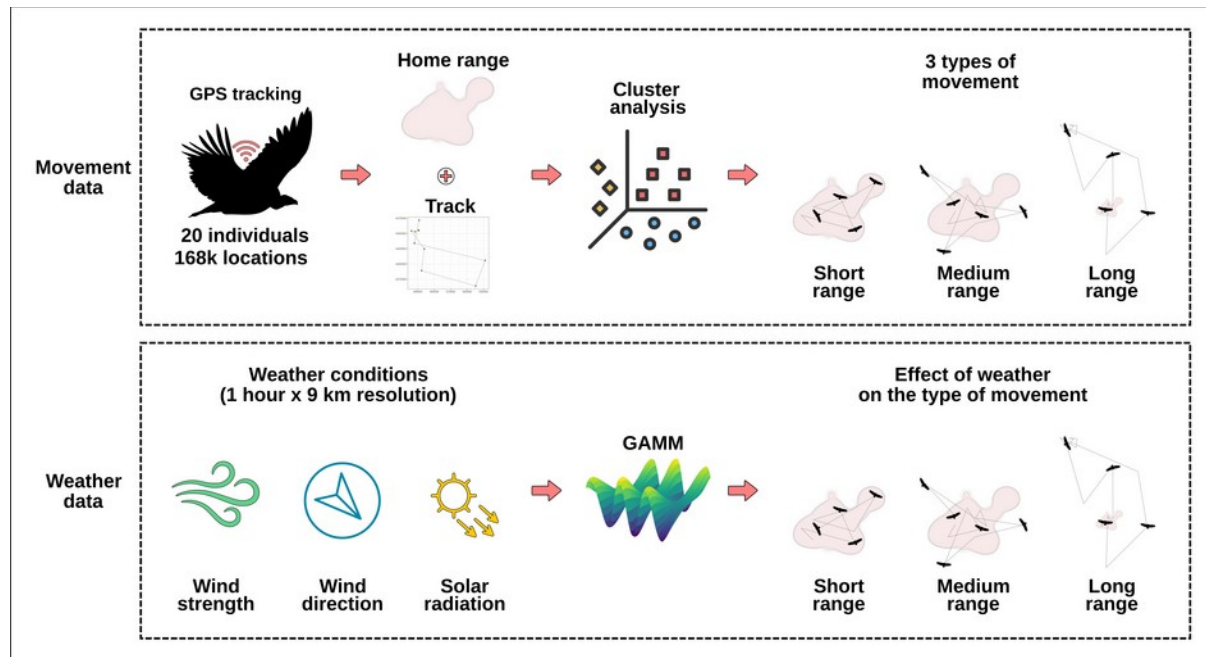


Fig. 2. Workflow of data processing: identification of the three types of movements from GPS telemetry data (top square) and integration of weather data to predict different types of movements (bottom square).

## Results

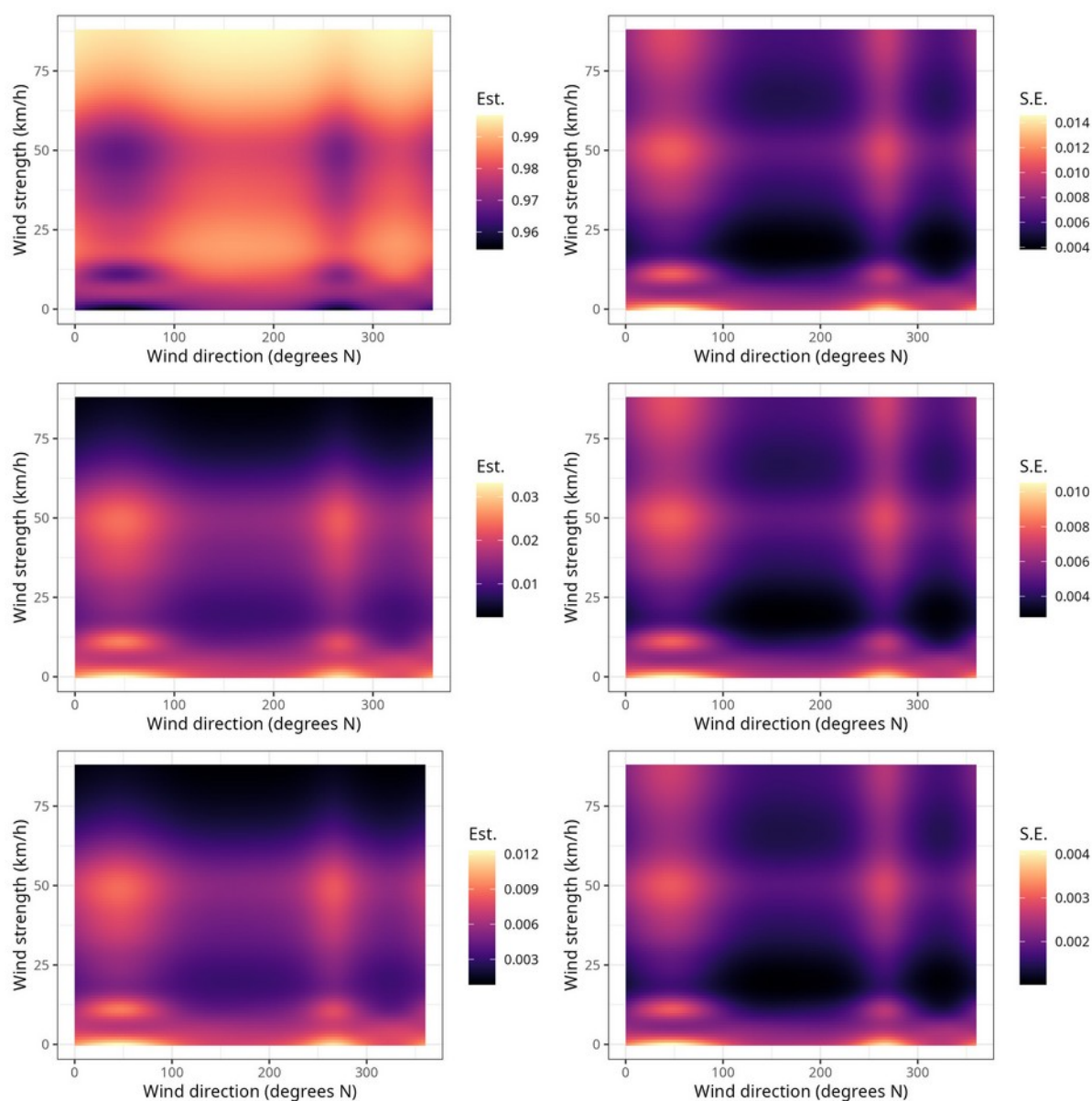
We identified 4,007 trajectories associated with MRMs and 593 trajectories associated with LRMs. Therefore, although most of our GPS fix (93.8%) belonged to SRMs, we also classified 4.4% and 1.8% of GPS locations as belonging to MRMs and LRMs, respectively. Although our final candidate model had a low overall accuracy at predicting these three movements (Table 1), model selection clearly identified a set of covariates which were systematically associated with them and which progressively improved the goodness-of-fit of a certain model to the data (Table 2).

Griffon Vultures in our study area were more prone to engage in MRMs and LRMs when wind came from northwest (Mistral) and southeast (Sirocco). However, the effect of wind direction varied considerably according to wind strength. When wind was very weak, vultures had a higher probability of engaging in MRMs and LRMs only with northwestern winds. Then the bimodal pattern of northwest and southeast winds became stronger up to intermediate values of wind strength: under moderately strong winds, wind direction had the most marked effect. Finally, under strong wind conditions, the effect of wind direction diminished (Fig. 3). The probability that Griffon Vultures engaged in MRMs and LRMs also increased markedly with solar radiation (Fig. 4) and in late summer (Fig. 5). The age of released individuals also influenced this probability, although without any clear pattern nor any clear difference between male and female Griffon Vultures (Fig. S3).

## Discussion

To the best of our knowledge this is the first study assessing weather conditions as a proximate driver of long-range nonroutine movements in an Old-World vulture. Our findings corroborate those from studies about other large soaring raptors (*Aquila adalbertii*, Ferrer, 1993; e.g. *A. chrysaetos*, Chaubet et al., 2025; Poessel et al., 2022; *Buteo buteo*, Walls et al., 2005; *Vultur gryphus*, Poessel et al., 2018 and Rivers et al., 2014) but highlight a potentially hierarchical effect of wind conditions and radiation over the decision making of moving vultures, which in turn can generate nonroutine movements.

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4 Fig. 3. Marginal effect plot, showing the interactive effect of wind strength and wind  
5 direction, over the probability that GPS fix belonged to short-range (left), medium-range  
6 (middle) and long-range movements (right). Estimated probabilities are on the left column  
7 and standard errors on the right column.

1

2 Our findings indicate that Griffon Vultures modulate their short-term and long-range  
3 movements according to wind conditions, both in terms of wind direction and strength.  
4 Namely, extra-home range movements (MRMs and LRMs) are more common for  
5 northwestern and southeastern winds of intermediate strength, while Griffon Vultures reduce  
6 long-range movements under both very weak and very strong winds. Under very weak wind  
7 conditions, they restrict their movements in the areas around the colony (Cerri et al., 2023)  
8 and foraging grounds (Fozzi et al., 2025), as exploring areas at the borders of their home  
9 range is more demanding. Conversely, under very strong winds, extra-home range  
10 movements are also less common, compared to winds of intermediate strength. Griffon  
11 Vultures might be less prone to move under potentially dangerous wind conditions, similarly  
12 to many other large soaring birds (Naveda-Rodríguez et al., 2023; Wilkinson et al., 2019),  
13 especially outside well-known areas where they cannot use conspecifics to detect updrafts  
14 (Sassi et al., 2024) and orientate (see Eisaguirre et al., 2020 for *A. chrysaetos*). We believe  
15 that future studies combining high-resolution telemetry with accelerometers will ultimately  
16 provide more accurate insights on the different flight strategies used by Griffon Vultures  
17 under different combinations of wind strength and direction. Particularly for short-range  
18 routine movement such as those related to foraging (Hernández-Pliego et al., 2014, 2017;  
19 Cecere et al. 2020).

20 We also found that Griffon Vultures engage in extra-home range movements when solar  
21 radiation is stronger. This effect, although not really surprising due to the strong correlation  
22 between solar radiation and updrafts (Scacco et al., 2019, 2022), is particularly interesting  
23 when considered in synergy with that of wind. In our model, the marginal effects of wind



direction, wind strength and radiation were almost identical for MRMs and LRMs, with Griffon Vultures engaging in these two movements under the same environmental conditions.

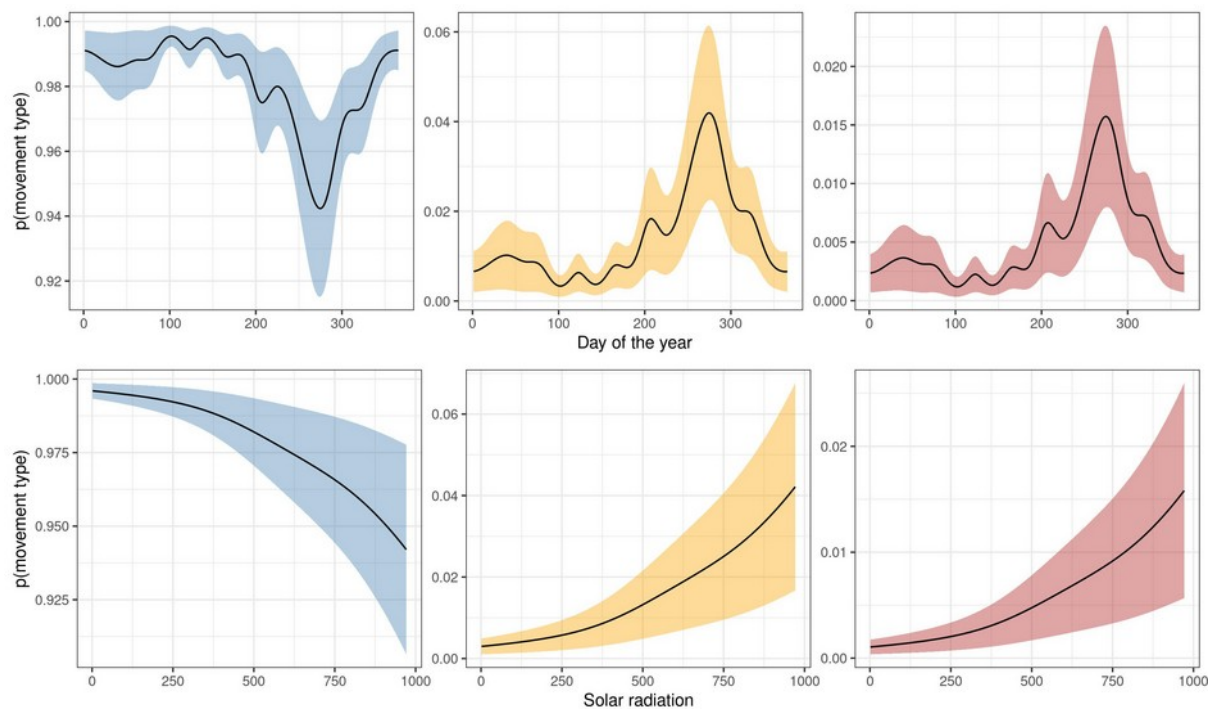


Fig. 4. Marginal effect plot, showing the effect of the day of the year and solar radiation on the probability that Griffon Vultures engaged in short-range (left), medium-range (middle) and long-range movements (right).

This might indicate that, under some specific weather conditions, Griffon Vultures venture outside the home range to explore new areas and locate resources (e.g., forays, Conradt et al., 2003). Being central place foragers, they would ideally limit the duration of extra-home range movements and return to the colony. However, on some occasions, they might fail to do so

because of scarce radiation (e.g., due to rain and cloud cover) and the lack of updrafts: at that point they would “go by the wind”, being thus displaced and forced to engage in long-range movements while attempting to re-orientate and return. We tested this hypothesis by fitting a Generalized Linear Mixed Model (see the script in the Supplementary Information) and finding that the duration of LRMs has a strong negative association with solar radiation, with prolonged journeys around Sardinia occurring when radiation was minimal (Fig. 5).

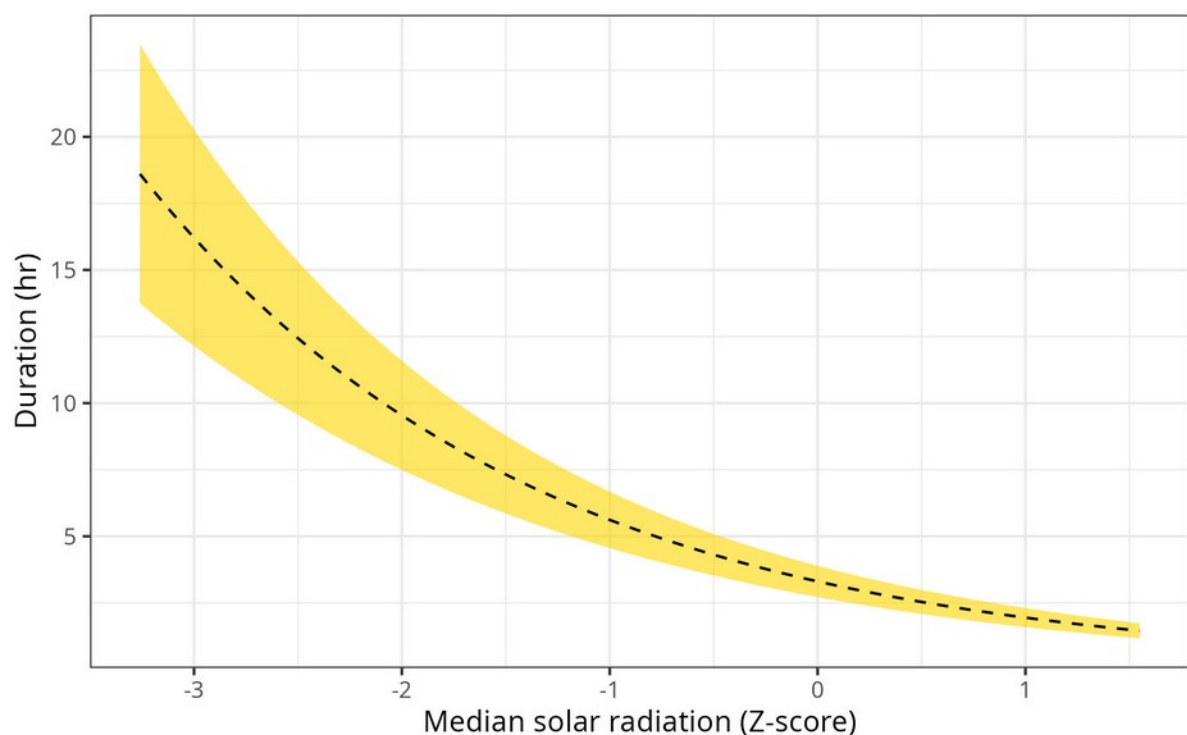


Fig. 5. Marginal plot, for the GLMM showing the effect of median solar radiation experienced during a long-range movement over its duration.

According to this explanation, long-range nonroutine movements would therefore arise, at least partially, as the wind displaces individuals. Although wind displacement by wind has

1 been proved for several bird species during migration (Newton, 2008) or foraging (e.g.,  
2 seabirds, Hass et al., 2012; Weimerskirch and Prudor, 2019), to the best of our knowledge no  
3 study suggested it as a mechanism driving long-range nonroutine movements in large soaring  
4 birds. The only empirical evidence was the displacement of Griffon Vultures from mainland  
5 Spain to Mallorca in 2008 (Tavecchia and Cortés-Avizanda, 2021). Our findings should  
6 encourage new studies about weather as a proximate cause of long-range nonroutine  
7 movements in vultures, which can also address some limitations of our case study. For  
8 example, our birds were tracked before they reached sexual maturity, while Griffon Vulture  
9 movements change throughout their whole lifetime (Acacio et al., 2023) and dispersal and  
10 prospecting movements in large birds also varies with age (Chaubet et al., 2025). Moreover,  
11 in our study area only two interconnected colonies of Griffon Vultures exist and individuals  
12 cannot move westward due to the presence of the sea. It would be important to replicate our  
13 findings in areas of mainland Europe, where colonies are more scattered across the  
14 landscapes and Griffon Vultures can move isotropically across larger areas (Delgado-  
15 González et al., 2022; Morant et al., 2023), benefitting from a higher number of social cues  
16 (Sassi et al., 2024). For gregarious vultures, such as the Griffon Vulture (van Overveld et al.,  
17 2020), future studies adopting high-frequency GPS telemetry should also explore the joint  
18 spatial behavior of multiple individuals (Kaur et al., 2024), to test for potential differences  
19 between individual and collective nonroutine movements.

20 Our findings are also potentially useful from a conservation viewpoint. As the availability of  
21 high-resolution weather data is increasing rapidly, we believe that in a few years it will be  
22 possible to integrate them with high-resolution telemetry (Carrard et al., 2025) and predict  
23 movements in advance. By knowing when vultures increase their movements, researchers can  
24 activate geofencing (Sheppard et al., 2014) to reduce collisions with wind turbines and the

number of field observers for selective stopping (Ferrer et al., 2022) can be increased. At the same time researchers, by knowing in advance when vultures are more likely to engage in long-range movements, can increase the acquisition rate of GPS tags to generate collision risk models based on fly height (Schaub et al., 2024) and to better understand where supplementary feeding stations should be built, to sustain moving vultures.

## Conclusions

Our findings indicate that the decision-making of Griffon Vultures, while engaging in short and long-range movements across the landscape, accounts for wind direction and strength, as well as for solar radiation. However, the most extreme long-range nonroutine movements occur when wind displaces Griffon Vultures and scarce solar radiation prevent them from returning to the colonies. At that point individuals might engage in long journeys across unfamiliar landscapes, while attempting to re-orientate. This indicates that some types of nonroutine movements are not entirely intentional and weather conditions can play a crucial role in triggering them. In the future combining high-resolution movement and weather data could allow researchers to predict short and long-range movements in advance and improve data acquisition from GPS tags adaptively, to study vulture behavior during nonroutine movements and improve conservation actions.

## Data availability statement

Reproducible data and software code are available on GitHub at: <https://github.com/JacopoCeri7/Nonroutine-long-range-movements-in-Griffon-Vultures> and on Open Science Framework at: <https://osf.io/qb5jr/>

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8

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## 10 **Authors' contribution (CRediT)**

11 **Data curation:** DDR, IF, MA - **Formal analysis:** JC, CC - **Funding Acquisition:** FB, DS,  
12 MM - **Investigation:** JC, IF, DDR, FB - **Methodology:** JC, CC - **Project administration:**  
13 FB, DS, MM - **Resources:** FB, DS, MM - **Software:** JC - **Supervision:** JC, FB Validation:  
14 JC, CC, DDR, IF - **Visualisation:** JC – **Writing (original draft):** JC – **Writing (review and**  
15 **editing):** JC, IF, DDR, CC, MA, DS, MM, FB

## Supplementary figures

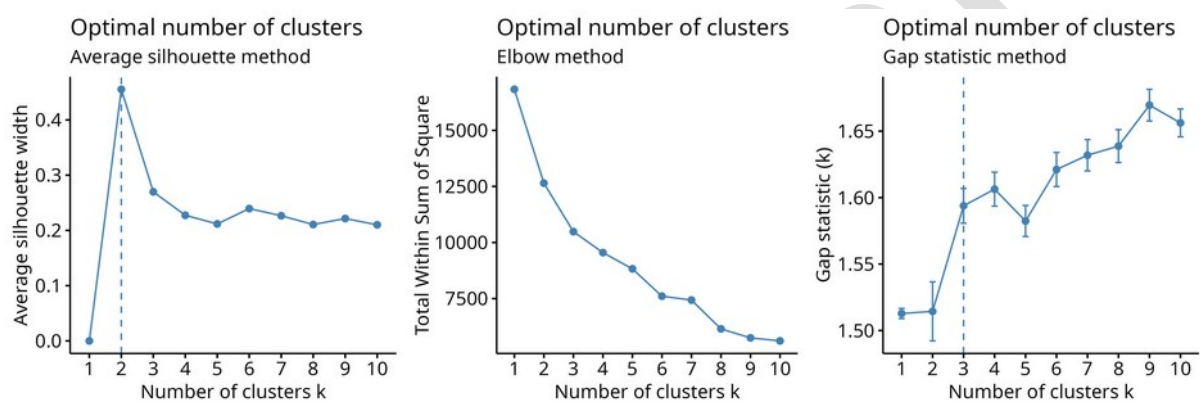
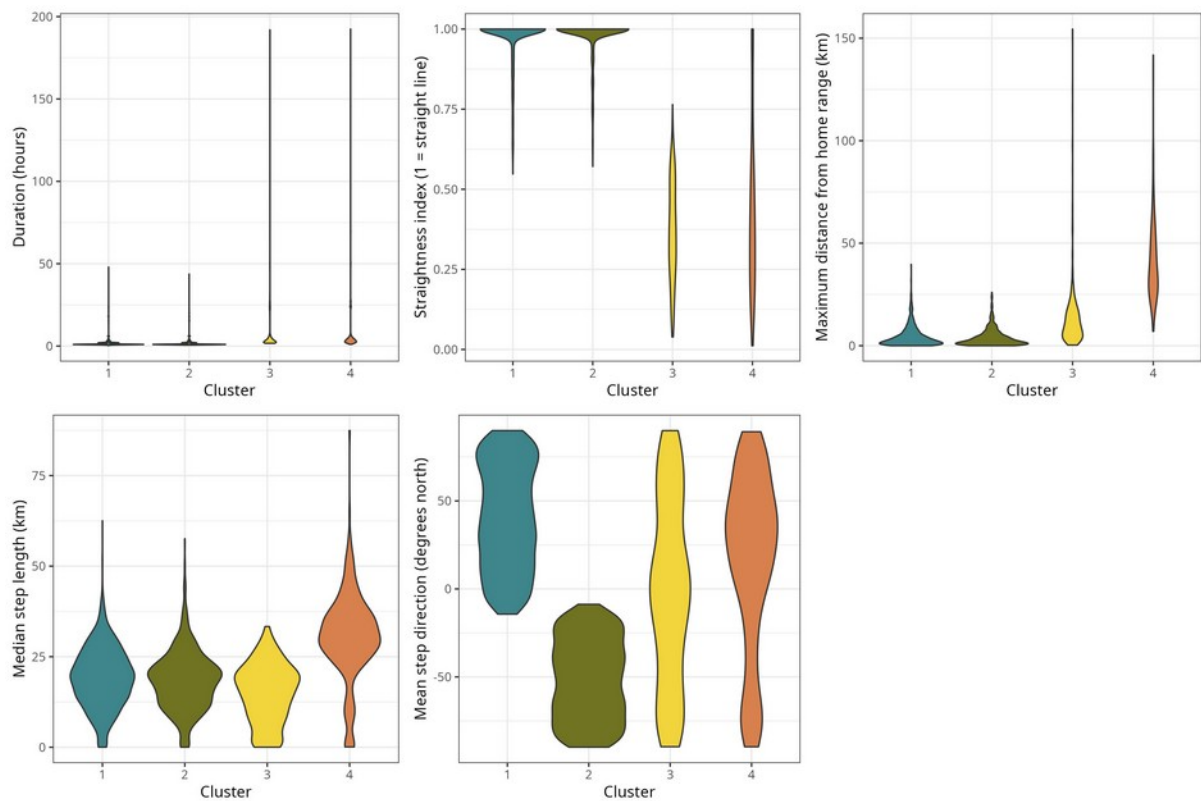


Fig. S1. Overview of the average silhouette method, the elbow method and the gap statistics method, to identify the optimal number of cluster for PAM cluster analysis. A complete description of the three methods is available in Kassambara (2017).

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6 Fig. S2. Comparison between the four groups of extra-home range movement trajectories,  
7 identified by PAM cluster analysis. The four groups are compared in terms of their duration,  
8 the tortuosity, the maximum distance, the median step length and their mean step direction.

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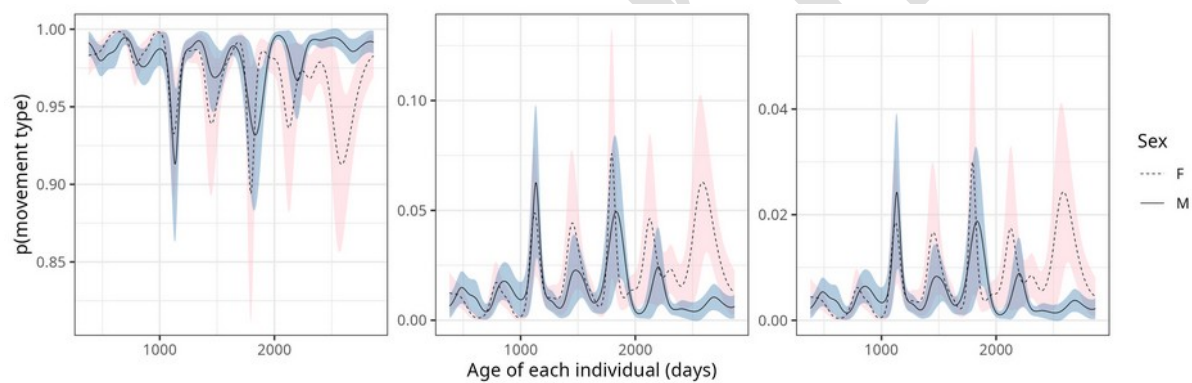


Fig. S3. Marginal effect plot, showing the effect of the age of each individual over the probability that male and female Griffon Vultures engaged in short-range (left), medium-range (middle) and long-range movements (right).

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Preprint

# 1 Tables

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Individual	GPS locations	Sex	GPS model	Date of birth	Date of release	Cohort	Locations from MRMs	Locations from LRMs
Artis 1	5,485	M	Ecotone Crex	Around 2017-04-01	2018-04-14	1	291	56
Artis 2	2,810	F	Ecotone Crex	Around 2017-04-01	2018-04-14	1	153	43
Artis 3	19,278	F	Ornitela 3G_50G	Around 2018-04-01	2019-06-24	2	666	64
Artis 4	9,309	M	Ornitela 3G_50G	Around 2018-04-01	2019-06-24	2	156	227
Artis 5	2,384	M	Ecotone Crex	Around 2018-04-01	2019-06-24	2	91	44
Barca	15,784	F	Ecotone Skua	Around 2015-04-01	2018-04-14	1	1227	358
Bulga	4,618	F	Ecotone Crex	Around 2015-04-01	2018-04-14	1	164	74
Calmedia	2,816	F	Ecotone Crex	Around 2018-04-01	2019-10-17	3	175	84
Caniga	8,960	F	Ecotone Crex	Around 2018-04-01	2019-10-17	3	290	214
Corte	4,890	M	Ecotone Crex	Around 2018-04-01	2019-10-17	3	209	135
Cristallo	13,505	M	Ecotone Crex	Around 2015-04-01	2018-04-14	1	487	426
Doglia	18,090	F	Ornitela 3G_50G	Around 2018-04-01	2019-10-17	3	468	274
Fenuggiu	10,255	M	Ecotone Crex	Around 2015-04-01	2018-04-14	1	486	94
Macomer	8,012	F	Ecotone Saker	Around 2018-04-01	2019-06-24	2	488	72
Meilogu	2,484	M	Ecotone Crex	Around 2018-04-01	2019-10-17	3	103	3
Pabelanasa	10,526	F	Ecotone cDuck	Around 2016-04-01	2018-12-12	4	614	251
Pituabile	6,231	M	Ecotone Crex	Around 2016-04-01	2018-12-12	4	222	73
Pozzomaggiore	6,574	M	Ecotone Crex	Around 2018-04-01	2019-06-24	2	680	108
Timidone	8,451	M	Ecotone Crex	Around 2015-04-01	2018-04-14	1	279	121

Tottubella	7,740	F	Ecotone Crex	Around 2018-04-01	2019-10-17	3	159	303
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Table 1. Overview of the data used in this study, for all the 20 Griffon Vultures. Further information on the same individuals are available in Fozzi et al. (2023) and Cerri et al. (2024).

Behavior	SRM (predicted)	MRM (predicted)	LRM (predicted)
SRM (observed)	157,754	16	0
MRM (observed)	7,397	11	0
LRM (observed)	3,021	3	0

Table 2. Confusion matrix comparing observations classified as short-range (SRM), medium-range (MRM) and long-range movements (LRM), with predicted values from the GAMM.

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