Age class and natal origin drive foraging patterns in a reintroduced Cinereous Vulture population

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Abstract

Widespread vulture population declines are often counteracted by conservation strategies including reintroduction programs and supplementary feeding schemes. However, the role of supplementary feeding – focusing on specific, predictable, feeding sites - on movement behaviour, has been little explored, especially within populations in which reintroduced and wild born birds of different age-classes may show differing behavioural movement patterns. However, such information becomes crucial for improving conservation and management actions. We analysed GPS data from both reintroduced (n = 31) and wild born (n = 28) cinereous vultures *Aegypius monachus* in Catalonia, North-eastern Spain, collected during a long-term study (2009–2020), to assess SFS use patterns according to natal origin, release method, and age-classes of individuals. We found high age-related variation in SFS use; juveniles revisited fewer SFS, and spent much longer in these locations compared with immatures, subadults, and adults, pointing to a dependence of juveniles on social information, along with a lack of foraging and flight skills. Regular adult revisits to multiple SFS suggests that these vultures can develop a comprehensive spatial memory of SFS by adulthood. Additionally, birds that were released via an acclimatisation aviary showed lower affiliation with SFS compared with 'hacked' birds and wild-born nestlings perhaps suggesting a tendency to spend more time exploring the wider environment. Our study has particular relevance in light of the potential public health-related legislation changes within the European Union or the changes in management of SFS, which could alter movement patterns and demographic parameters of Iberian vulture populations.

Keywords: Foraging, revisitation analysis, supplementary feeding, movement ecology, spatial memory

Introduction

Anthropogenic activities are among the major drivers of the global decline in avian scavenger populations (Safford *et al.*, 2019; Harfoot et al., 2021). Key threats include illegal persecution(Margalida, Ogada and Botha, 2019), accidental poisoning (Berny *et al.*, 2015, Oliva-Vidal et al. 2022), and collision with anthropogenic infrastructure (Carrete *et al.*, 2009; Ives *et al.*, 2022). Conservation actions such as captive breeding and reintroduction programs, have to some extent mitigated these population declines (Lorand *et al.*, 2025). In combination with the establishment and provision of foraging resources through supplementary feeding sites (SFS) (Moreno-Opo, Trujillano and Margalida, 2015; Cortés-Avizanda *et al.*, 2016),

Populations of certain vulture species (Margalida and Colomer, 2012), as well as other bird species e.g., white storks *Ciconia Ciconia* (López-García and Aguirre, 2023), have become heavily reliant on predictable, human-modified resources, including landfill sites (Monsarrat *et al.*, 2013; Tauler-Ametller *et al.*, 2017; Cortés-Avizanda *et al.*, 2025). As a result, the spatial distribution, movement patterns, and home-range dynamics of these scavengers are therefore strongly influenced by the location, quality, and temporal stability of such anthropogenic resources (López-López et al. 2014, Margalida et al. 2016). However, some detrimental effects have been documented related to the use of supplementary feeding sites (SFS; Carrete et al. 2006, Cortés-Avizanda et al. 2016). Additionally, while predictable food resources generally increase foraging opportunities, it also promotes high-density aggregations that can exacerbate dominance hierarchies (Cortés-Avizanda, Carrete and Donázar, 2010; Moreno-Opo, Trujillano and Margalida, 2020), and cause negative density-dependent effects on fecundity (Carrete, Donázar and Margalida, 2006), as well as increasing the risk of disease and parasite transmission (Van Overveld, Gangoso, *et al.*, 2020).

Studies conducted on vulture species on the Iberian Peninsula have identified stratified age-related differences in the use of SFS. Juvenile foraging inefficiency is common across many species (Carmona, Aymí and Navarro, 2021), linked to inexperience in locating and competing for food resources (Fayet *et al.*, 2015). This means that although subdominant, non-breeding vultures prefer to exploit regularly stocked SFS, such as smaller, farm-based carcass deposition sites (Kane *et al.*, 2016; Morant *et al.*, 2020), their actual access to available food resources such as carcasses remains restricted by competitive exclusion from dominant adults (Duriez, Herman and Sarrazin, 2012; Van Overveld *et al.*, 2018; Moreno-Opo, Trujillano and Margalida, 2020). For example, adult griffon vultures (*Gyps fulvus*) tend to form foraging groups at SFS located within short distances (5 -10km) of their breeding colonies (Zuberogoitia *et al.*, 2013a; Cerri *et al.*, 2023), causing higher density competition that may exclude juveniles from profitable sites.

Despite both intra- and interspecific competition for such resources, time spent at locations with predictable food resources is also likely used as a way to form social relationships and identify suitable future breeding areas particularly among juveniles (Van Overveld *et al.*, 2018; Van Overveld, Gangoso, *et al.*, 2020). Such opportunities of social information exchange fit with the Information Centre Hypothesis (Buckley, 1996; Harel *et al.*, 2017), which may be particularly relevant for reintroduced individuals.

Vulture reintroduction has proved highly successful in several areas of Europe, with populations of Griffon, Bearded and Cinereous vulture *Aegypius* *monachus* translocated across Spain, France, Italy and Bulgaria primarily (Schaub *et al.*, 2009; Ivanov *et al.*, 2023; Monti *et al.*, 2023; Stoyanov *et al.*, 2023; Lorand *et al.*, 2025). Although many breeding populations have become well established, there is a potential hindrance to population maintenance and expansion because birds that are released from captive breeding or rehabilitation centres come with limited social and foraging experience (Fozzi *et al.*, 2023). Amongst reintroduced vultures, acclimated individuals observe the release site and their conspecifics from an aviary (as opposed to 'hacked' individuals that are released into a nest whilst flightless; Mihoub *et al.*, 2014), and have shown improved breeding success and survival as adults, particularly those acclimated for a longer period of time, as they are able to form partial cognitive maps to help them locate foraging sites (Fozzi et al. 2023). Reintroduced individuals overall often display more erratic dispersal movements (Rousteau *et al.*, 2022; Tréhin *et al.*, 2024a), and show species-specific differences in home range size compared to wild-born birds (Rousteau et al. 2022, Fozzi et al. 2023), both of which are likely to affect the dynamics of SFS use. Concentrating food resources in specific locations may unintentionally restrict juvenile dispersal among individuals and hinder population expansion (Margalida *et al.*, 2013; Cortés-Avizanda *et al.*, 2016; Reznikov *et al.*, 2024), and can also reduce the efficiency of vulture scavenging services throughout the wider landscape (Deygout *et al.*, 2009).

European sanitary regulations modified carcass availability and stocking densities at SFS, and in some cases led to their complete removal from the landscape (Margalida, Pérez-García and Moreno-Opo, 2017; Fernández-Gómez, Cortés-Avizanda, Arrondo, *et al.*, 2022). These changes altered resource distribution, and potentially population dynamics of both wild and reintroduced obligate scavengers (Cerecedo-Iglesias *et al.*, 2023; Colomer and Margalida, 2025).

Therefore, future legislation aiming to ‘clean up’ landscapes by closing open landfill sites and large carcass deposition sites has the potential to induce varying responses in productivity, survival, and alter the use patterns of remaining SFS (Zuberogoitia *et al.*, 2010; Cerecedo-Iglesias *et al.*, 2023). Empirical studies examining responses to site closures remain limited, but reveal declines in apparent survival, as well as changes in visit frequency and competitive behaviour (Zuberogoitia *et al.*, 2010; Margalida, Pérez-García and Moreno-Opo, 2017; Arévalo-Ayala *et al.*, 2023).

Collectively, these findings highlight how limited our understanding remains regarding the effects of SFS on vulture behaviour, including social associations and foraging strategies. A more comprehensive understanding of the dynamics of SFS use is needed to clarify how these sites support both reintroduced and wild vulture populations. Although vulture movement is well studied using bird-borne devices (Alarcón and Lambertucci, 2018), most GPS-based analyses have largely focused on estimation of metrics such as home range, or geometric information (Morant *et al.*, 2023; Tobajas *et al.*, 2024; Tréhin *et al.*, 2024a), rather than specific site use information, such as identifying which foraging locations are important to different groups of individuals (ages, origins), that could inform conservation prioritization and feeding site management regulation (Fernández-Gómez et al. 2022).

Here, we use GPS tracking data collected over a 12-year period in north-eastern Spain, to quantify use of SFS by both reintroduced and wild-born Cinereous vultures. Globally, while this species remains in decline, the Iberian Peninsula population has increased and is home of 90% of European population (Moreno-Opo & Margalida 2012; Terraube et al. 2012). Movement studies centred on Extremadura, Catalonia, and Aragón show that juveniles range farther than adults, especially during the breeding season when adults are constrained by nesting (Moreno-Opo, Trujillano and Margalida, 2015; Tobajas *et al.*, 2024). However, detailed information on their use of SFSs and other discrete foraging areas is lacking. Here, we quantify revisitation to SFS within and between age groups. Release origins, sexes, years and months. Revisitation behaviour, i.e., the tendency to return to a previously visited location, is associated with animals that possess the capacity for spatial memory to exploit resources that deplete and renew predictably within a heterogeneous environment (Berger-Tal and Bar-David, 2015; Bracis *et al.*, 2015). Such behaviour can enable individuals to optimize foraging efficiency, reduce uncertainty, and enhance survival in dynamic landscapes.

Our study had two main objectives: 1) to identify patterns of use of specific, known SFS by Cinereous vultures; 2) to investigate variation in site-use metrics (time spent there, number of revisits) between age classes (birds born or released as juveniles , became immature (IMM) in their third calendar year , subadults (SUB) in their fourth, and full adults (FAD) in their fifth; and between wild-born and reintroduced individuals.

Materials and methods

Tracking and data collection

We obtained GPS tracking data from 73 Cinereous vultures collected in Catalonia (NE Spain; Figure 1) between 2009-2020 (Supp Mat), all of which accrued more than 100 days tracked [113 – 4243 days]. Each bird was categorised as either ‘wild born’, ‘hacked’, or ‘acclimated’, and was molecularly sexed (Wink et al. 1998). The individuals were tagged as part of the project to recover the cinereous vulture in the Pyrenees managed by Catalan government and Grupo de Rehabilitación de la Fauna Autóctona y su Hábitat (GREFA). All cinereous vultures were classified into four age-classes based on plumage characteristics following Clark (2004) and De la Puente and Elorriaga (2012). Within the dataset, birds could age during the tracking period; we therefore applied a universal threshold date of 15 March, chosen to align with egg hatching, after which individuals were incremented in age (Ruby, Kumar and Kanaujia, 2018).

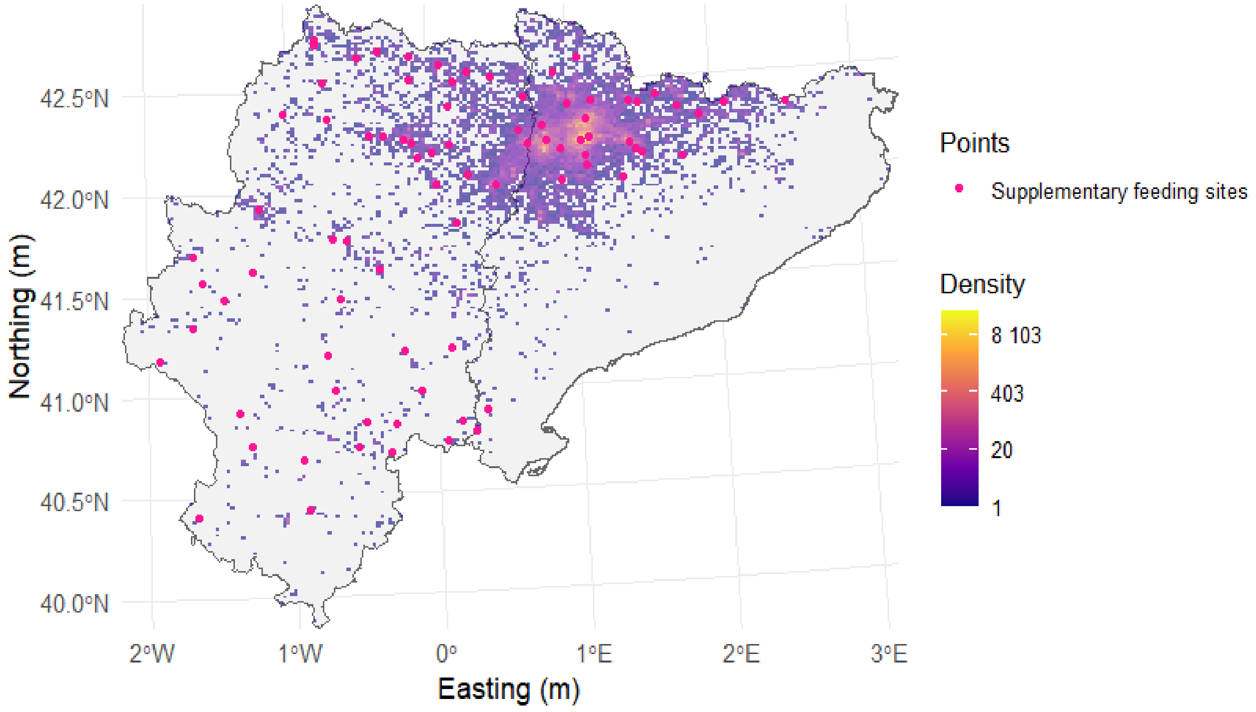

Figure 1: Density of GPS points from n = 59 Cinereous vultures per 2 km across Catalonia and Aragón, north-eastern Spain, from 2009 to 2020. Pink points represent Supplementary Feeding Sites (SFS).

Tracking data were categorised by season as follows; Spring: March – May, summer: June - August, autumn: September – November, winter: December – February. Phenologically, spring and summer correspond to the incubation and rearing period. Autumn and winter correspond to the post-fledging and pre-laying period. To ensure comparability among individuals with differing sampling intervals, the dataset was subsampled to retain one GPS location every four hours.

Revisitation analysis

After filtering the data, we conducted revisitation analysis on known feeding sites (SFS and landfills) using the package *recurse* (v. 1.4.0; Bracis et al. 2018) in R (v. 4.4.2). In order to understand how frequently SFS were revisited and whether this varied among different ages and origins, each SFS location was buffered at a biologically relevant distance; specifically, a 1 km buffer was applied to point locations of SFS and landfills across Spain (Monsarrat et al. 2013). This distance represents the approximate visual detection range from which vultures are able to see conspecifics circling in the sky, and thus become aware of a potential carcass or feeding opportunity, drawing them to that location (Jackson et al. 2008).

Revisits were defined as repeated visits to a specific SFS, having first exited the 1km boundary. In addition to quantifying the number of revisits to a given feeding site, the time spent at each feeding site was calculated using the function *getRecursionsAtLocations*. These metrics were then summarized across sites and individuals, and further aggregated by year and season, to describe the visitation patterns and the number of feeding sites visited in relation to age classes and origin.

Data analysis

Following filtering of individuals represented by only a single occurrence in the summarised dataset, and outliers in time spent at sites, the final dataset comprised 59 individuals. To examine variation in use of sites among age classes and release origins, we fitted three generalised linear mixed models (GLMMs).

Individual identity was included as a random effect, with observations grouped by year, to account for repeated measures across years. We tested for differences in the number of SFS visited using a Poisson error distribution; in the number of revisits to SFS using a negative binomial distribution; and in mean time spent at each revisited location (i.e. > one single visit) using a Gaussian distribution applied to log-transformed data. The fixed effects included season (as defined above), the number of days each individual was tracked per season, year, sex, calendar age, and origin (hacked, acclimated, or wild). Where model diagnostics indicated heteroscedasticity across years and season, we incorporated one or more dispersion parameters to improve model fit. For the gaussian model we report estimates and confidence intervals in the text; for the Poisson and negative binomial models we report incidence rate ratios and their confidence intervals (Brooks *et al.*, 2017). Full model output tables are available in the supplementary information.

Results

Overall use of supplementary feeding sites

There were 89 distinct feeding sites, all of which were SFS (not landfills), that were revisited during the 12-year tracking period (Figure 1). The most frequently revisited feeding sites were closely associated with the colony and release site (within 10 km). SFS were visited by an average of 5.8 (+/- se. 0.22 birds), although this mean was biased by the maximum of 23 birds, and many sites (per month and year) that were only visited by one bird. The number of vultures using the SFSs was also higher in winter (mean: 6.6 birds +/- se. 0.61), particularly compared to summer (mean: 5.3 +/- se. 0.37; figure 2).

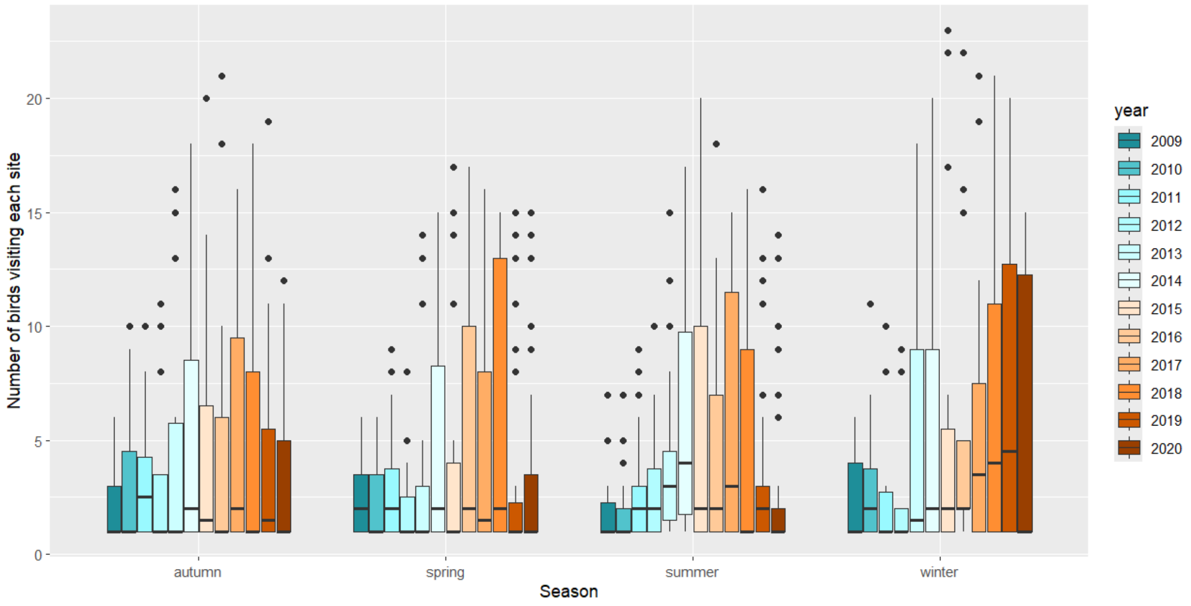

Figure 2: Number of Cinereous vultures visiting the 89 supplementary feeding sites (SFS) in Catalonia and Aragón, each season between 2009 to 2020.

Number of supplementary feeding sites visited by age, sex and origin

Individuals revisited between one and 20 sites within a year (mean: 4.5, SD: 2.65). Accounting for annual variation, there were large inter-seasonal differences in the number of visits they made to these sites and the time spent in these sites (Figure 3, Supp Mat). Significantly fewer sites were revisited in winter (*IRR Winter: 0.78, CI: 0.68 – 0.89*), compared to all other seasons. Juveniles revisit significantly fewer sites than all other age groups (*IRR Juvenile: 0.53, CI: 0.45 – 0.61*), although this difference became smaller in winter. Hacked birds and wild nestlings revisited significantly more SFS than acclimated birds (*Hacked IRR: 1.42, CI: 1.17 – 1.72;*

Wild IRR: 1.24, CI: 1.08-1.41; figure 4). Lastly, males visited significantly fewer sites that females (*IRR Male: 0.89, CI: 0.81-0.98*).

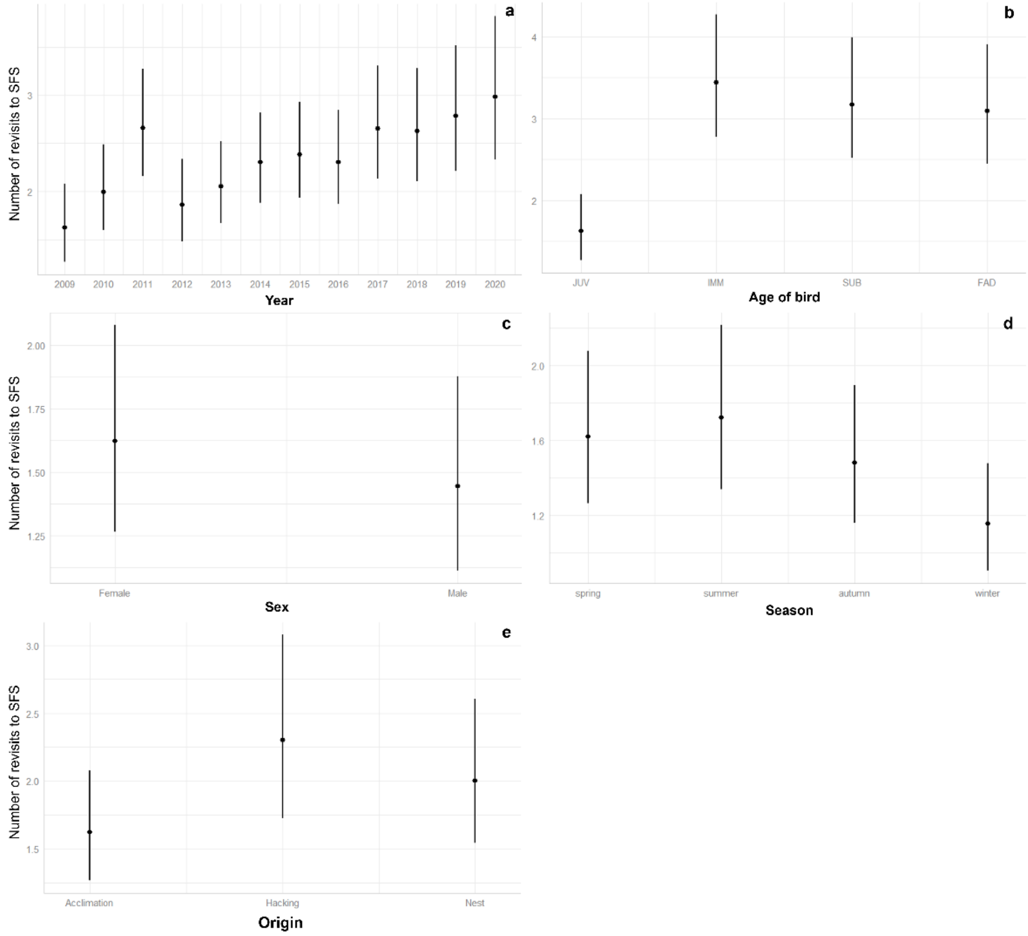

Figure 3: Model effects plots including upper and lower 95% confidence intervals, testing the factors driving the number of SFS revisited by a. year, b. age group (FAD = Full Adult, IMM = Immature, JUV = Juvenile, SUB = Subadult), c. sex, d. season and e. origin.

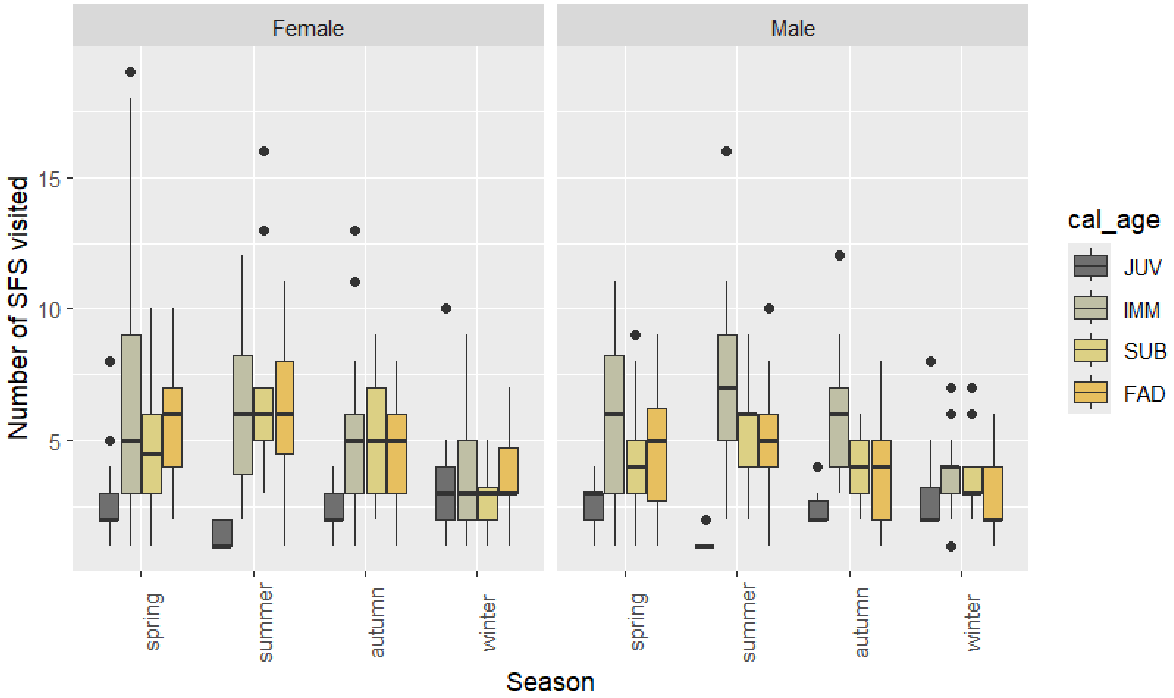

Figure 4: The number of different SFS revisited among age groups (acclimated, hacked, wild nestlings) across all four seasons, for both females (left) and males (right).

Number of revisits made supplementary feeding sites visited by age, sex and origin

Immature, subadult and adult birds made significantly more revisits to SFS than juvenile birds (*IRR Juvenile: 0.48, CI: 0.38 – 0.60*), but here only wild born birds made significantly more visits to SFS than acclimated birds (*IRR Wild: 1.45, CI: 1.20-1.75*; *IRR hacked: 1.30, CI: 0.97 – 1.73;* figures 5 & 6, Supp Mat).

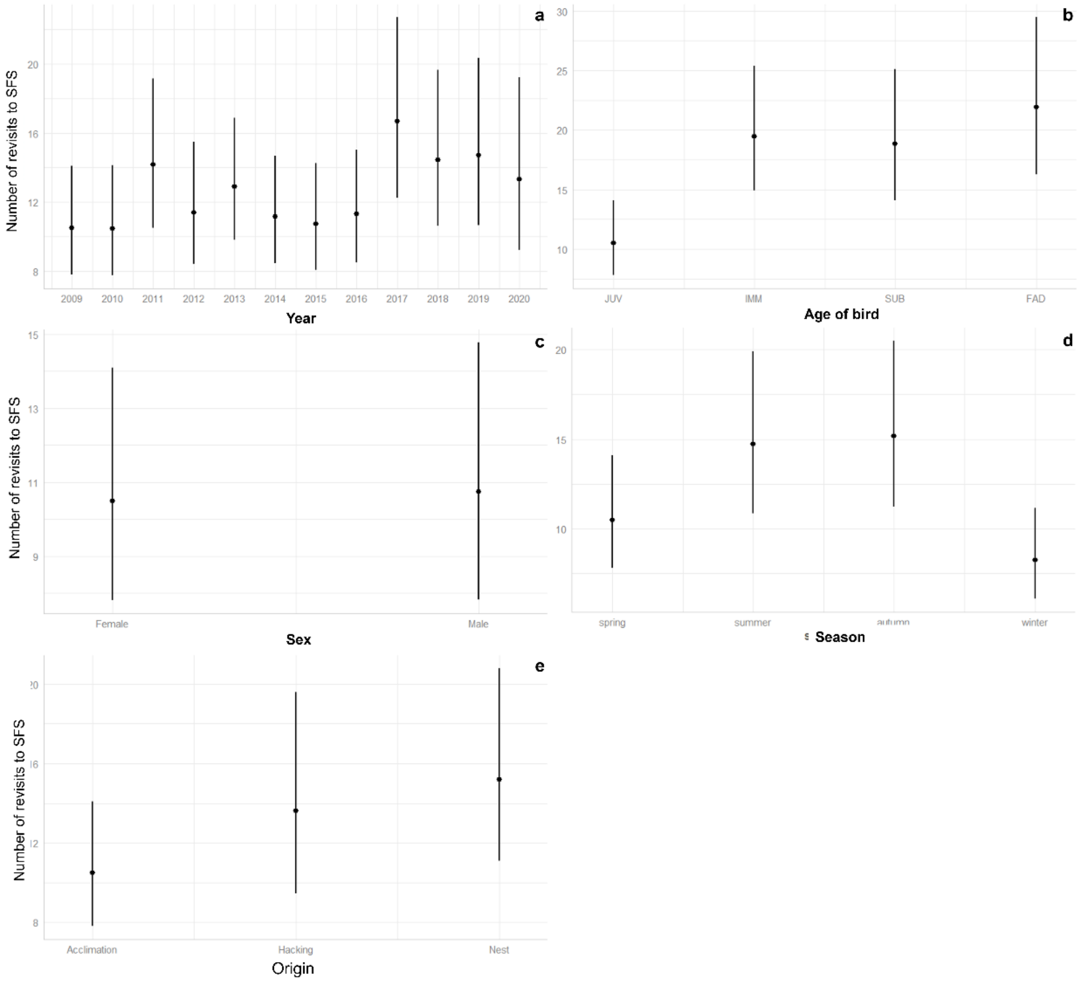

Figure 5: Model effects plots including upper and lower 95% confidence intervals, testing the factors driving the number of revisits made to SFS by a. year, b. age group (FAD = Full Adult, IMM = Immature, JUV = Juvenile, SUB = Subadult), c. sex, d. season and e. origin.

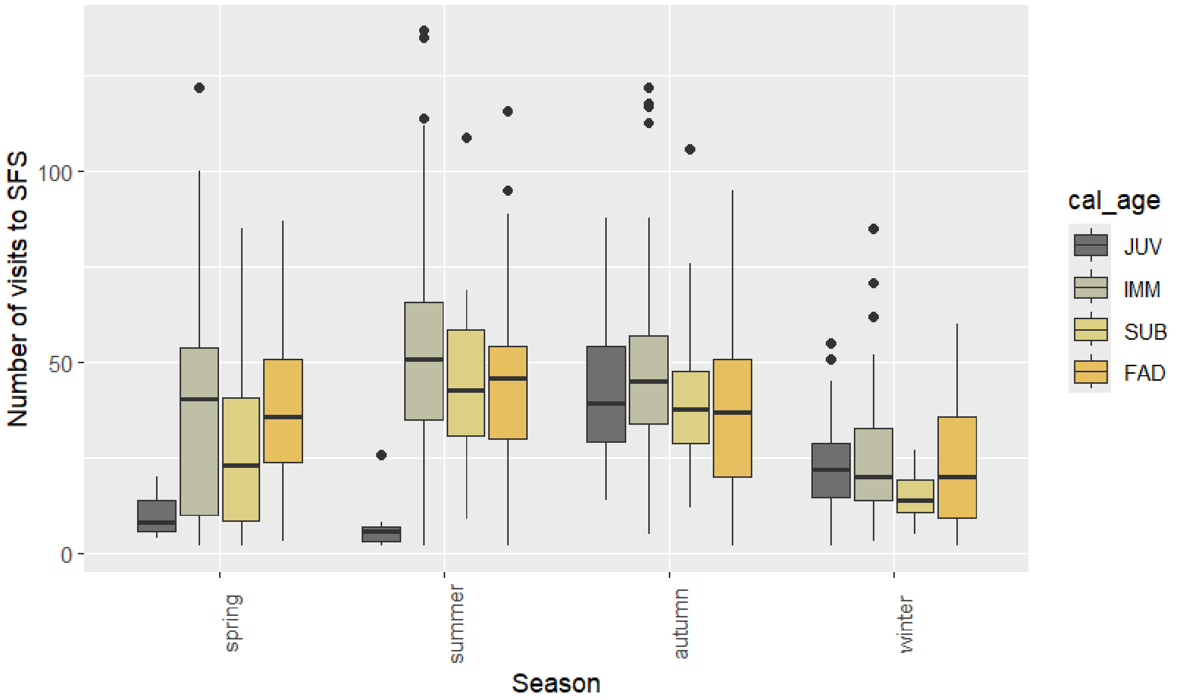

Figure 6: Number of revisits made to SFS by all four age classes across all four seasons.

Time spent at supplementary feeding sites by age, sex and origin

Birds spent an average of 9.7 hours (range: 4.1 - 175 hours) at SFS, but this declined significantly over the years included in the study period (Figure 7 and 8, supp mat). Mean time spent at sites was significantly lower in spring and summer, (*estimate spring: -0.13, CI: -0.22 – -0.03; estimate summer: -0.14, CI: -0.23 - -0.04;* Figure 8, Supp Mat). However, there was a large amount of heteroscedascity within and across years and seasons, represented by significant dispersion parameters (Supp Mat). Adults spent less time compared with the other age groups, particularly juveniles (*estimate juvenile: 0.51, CI: 0.3-0.72, immature: 0.19, CI: 0.02 – 0.36, subadult: 0.31, CI: 0.16-0.46*; Figure 7).

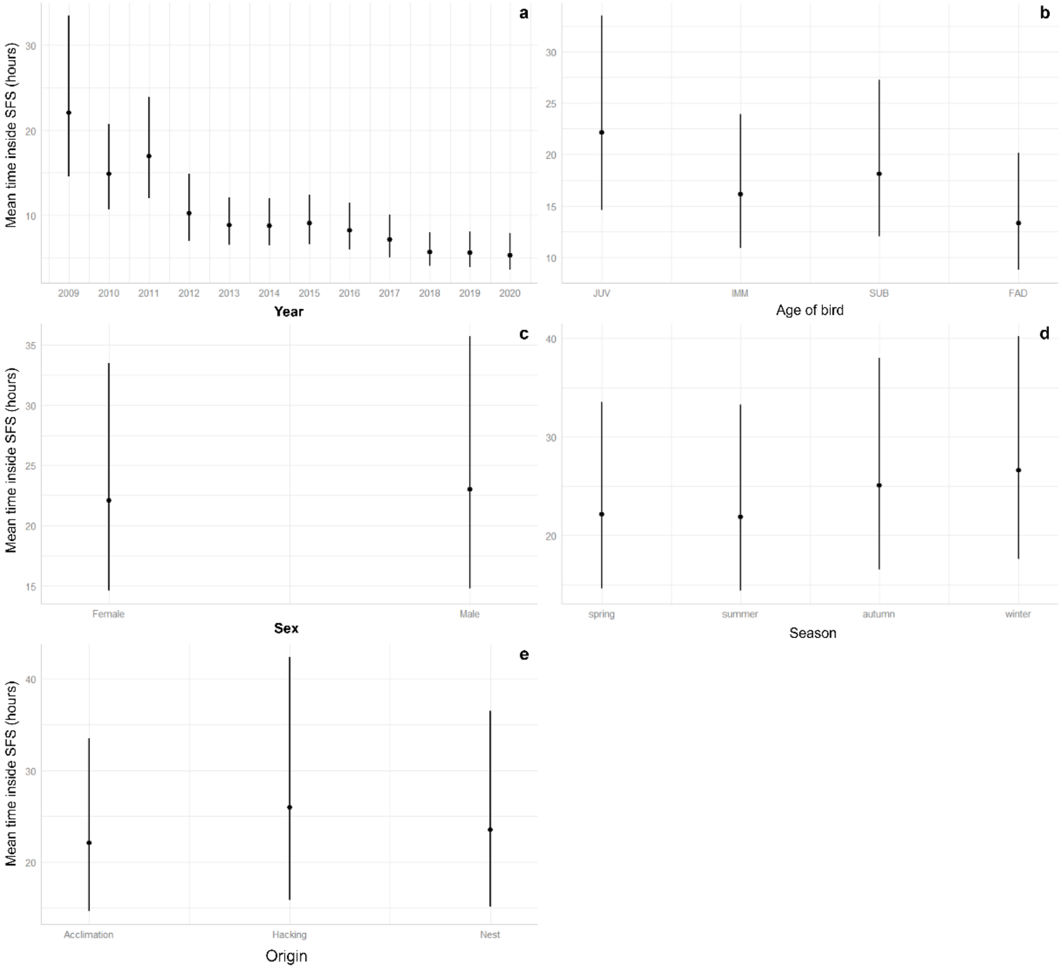

Figure 7: Model effects plots including upper and lower 95% confidence intervals, testing the factors driving the mean time spent at revisited SFS by a. year, b. age group (FAD = Full Adult, IMM = Immature, JUV = Juvenile, SUB = Subadult), c. sex, d. season and e. origin.

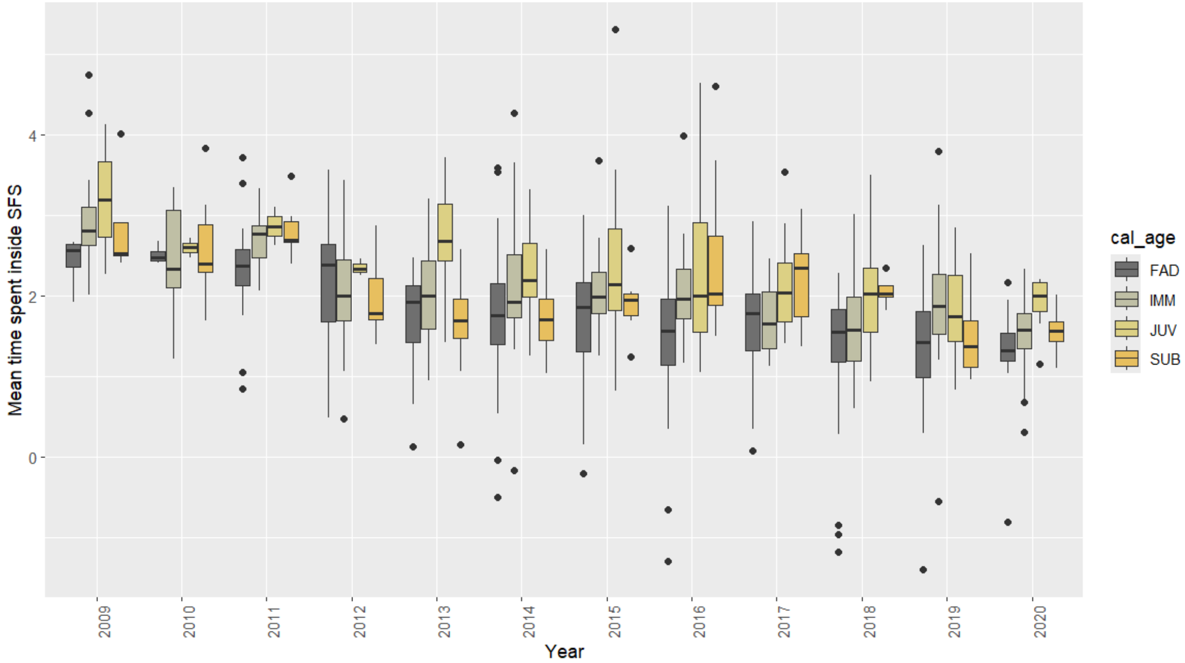

Figure 8: Mean time spent in SFSs (hours; log transformed) among age groups and across years.

Discussion

Our analyses revealed significant age-class and release origin differences in the number of SFS visited, the number of revisits to these SFS, and the time spent there. Supplementary Feeding Sites located in Catalonia and Aragón, were used frequently and for long periods of time by Cinereous vultures, both within and between years, and among individuals. Temporal differences were also evident, both seasonally and interannually, indicating that SFS use is influenced by dynamic ecological and life-history factors.

Overall population use

Overwhelmingly the most used SFSs were within 10 km of the release site and breeding colony, which aligns with the highly philopatric behaviour of Cinereous vultures (García-Macía *et al.*, 2023; Tobajas et al. 2024). Specifically, the most used

SFS were the three closest to the colony, located in the Boumort area. These received several hundred revisits a year by almost all of the individuals tracked, and outside of these three SFS the visitation rates declined swiftly.

Differential use among age classes

Our analyses consistently revealed strong age-class differences in SFS use. Immatures, subadults and adults made more revisits to a larger number of SFS, whereas juveniles revisited fewer SFS, less often, and spent much longer in these locations. This pattern aligns with known developmental constraints: juveniles are inexperienced, have lower flight efficiency (Van Overveld, Gangoso, *et al.*, 2020; Reznikov *et al.*, 2024), and lack detailed knowledge of the spatial distribution of the SFS throughout the region and so often explore more widely (García-Macía *et al.*, 2024).

Young birds are more social (Van Overveld, Gangoso, *et al.*, 2020), and by spending more time at specific SFSs, they may facilitate information transfer from older conspecifics, and gain information as well as competitive foraging skills. Kleptoparasitism has been recorded in a high percentage of juvenile Spanish Imperial eagles *Aquila adalberti* (Margalida, Colomer, *et al.*, 2017), as well as immature Bearded vultures (Margalida and Bertran, 2003), and Black vultures *Coragyps atratus* (Richard, Contreras Zapata and Angeoletto, 2022); perhaps for juvenile Cinereous vultures, whose foraging abilities are still underdeveloped, prolonged use of SFSs may therefore provide both energetic benefits and opportunities for learning, contributing to their relatively sedentary behaviour at these sites.

Foraging efficiency in vultures is developed over the first few years of life (Efrat *et al.*, 2023), thus by the time they reach potential breeding age (around five years old), they are likely to have developed a comprehensive map of SFS in the area and to move directly among known profitable locations. Adult Cinereous vultures, in contrast, are dominant at feeding sites, able to displace younger individuals (Duriez, Herman and Sarrazin, 2012; Moreno-Opo et al. 2020). Although our results show they revisit more SFS and do so often, they do not spend more time at such sites, suggesting perhaps that they are either 'monitoring' their environment using well-developed memory (McGrady *et al.*, 2018), or their dominance at active feeding stations allows them to feed and leave quicker. Similar patterns have been documented in adult Egyptian vultures, whose home range sizes are essentially dictated by the distribution of SFS (López-López, García-Ripollés and Urios, 2014), and which are smaller than the ranges of immature and subadult birds due to their ability to exploit these predictable resources efficiently, minimising roaming (Monsarrat *et al.*, 2013; Morant *et al.*, 2020).

The use of SFS by immature and subadult Cinereous vultures (between two and five years post-fledging) was highly variable, and represent transitional behaviour between the juvenile and adult life stage. These age classes show different seasonal patterns, visiting fewer sites in spring, but more sites in summer compared to adults, who are constrained by nest attendance during the breeding season (Zuberogoitia *et al.*, 2013a; Tobajas *et al.*, 2024). Despite prospecting widely, immatures and subadults still show their reliance on predictable food resources, including not only SFS but landfills that may be of lower quality but provide less competitive feeding (Fernández-Gómez *et al.*, 2022).

Release origin influence

Release origin also explained variation in the number of SFS revisited and the number of revisits made to these SFS, although it did not influence the time spent resident within 1 km of the SFS. Acclimated birds revisited fewer SFS, made fewer revisits overall, and spent (slightly) less time at these sites compared with hacked and wild-born birds. This pattern may indicate that acclimated birds are spending more time exploring the wider region rather than returning to known SFS, whereas particularly hacked birds rely more on supplemented food and the presence of con- and heterospecifics (Mihoub *et al.*, 2011), and may represent a lack of exploratory behaviours in such birds. Success of birds released via aviaries increases generally with longer periods of acclimation (Fozzi *et al.*, 2023), but is variable, dependent on the length of time they are acclimated for (Mihoub *et al.*, 2014; Ivanov *et al.*, 2023). However, lower survival rates of other hacked raptors e.g., hacked juvenile ospreys *Pandion haliaetus* compared to their wild-born conspecifics, particularly in winter, likely due to underdeveloped foraging skills, lack of parental care, and reliance on human-provided during early development (Monti *et al.*, 2014), demonstrating how captive breeding and translocations can influence social and population structure in potentially unpredictable ways (Van Overveld, Gangoso, *et al.*, 2020).

Seasonal and annual variation

Season and year also strongly influenced patterns of SFS use, which has also been found in other vulture research (Monsarrat *et al.*, 2013; Van Overveld *et al.*, 2018; Van Overveld, Gangoso, *et al.*, 2020; Genero *et al.*, 2020; Tréhin *et al.*, 2024b). The strongest differences occurred between winter (December- February) and the remaining seasons; during winter, individuals visited fewer SFSs, did so less frequently, and spent longer periods at the sites they used. During winter, flying conditions are generally poor (lower temperatures meaning fewer thermal uplift; Genero *et al.*, 2020), and hunting activity and subsequent carcass deposition provide higher food availability, affecting vultures movements and drawing birds to feeding sites for longer periods (Tobajas et al. 2024). This pattern is consistent with “encamped” foraging behaviour described in other vulture populations, in which experienced adults remain close to reliable resources under suboptimal flight conditions (Morant *et al.*, 2020), while juvenile dispersal has not fully begun resulting in a more intense concentration of multiple age classes (Ivanov *et al.*, 2023; Tréhin *et al.*, 2024b).

We also found a linear increase in both the number of revisits and number of SFS visited over time (i.e. across years), coupled with a decline in the time spent at these sites. This does not correspond to more birds being tagged in the later years; more birds were tagged between 2014-2017, yet the biggest increases in revisits and locations come after 2017. One plausible explanation is demographic, because from 2017 onwards, a greater proportion of experienced adults were present in the population, which had developed a comprehensive map of feeding sites, thereby driving this linear change. Another potential contributing factor may be also related to a slight delayed response to changes in Spanish sanitary legislation, approved in 2011 but implemented from 2014 (López-Bao and Margalida, 2018), which increased carcasses availability in the landscape (Fernández-Gómez *et al.*, 2022). Lastly, the growing presence of acclimated individuals, who have become accustomed to human-provisioned food during the early stages of reintroduction, may reinforce population-level reliance on predictable food resources.

Population affiliation with SFS and management implications

We observed consistently high use of SFS close to the colony throughout the 12-years study period. Such spatial concentration raises concerns that the population may fail to expand into the wider landscape, remaining dependent on a limited number of predictable feeding sites. Movement, including post-natal dispersal of vultures, whether released or wild born, are undoubtedly influenced by supplementary feeding and restocking frequency, and can change over time (see Fernández-Gómez *et al.*, 2022; Reznikov *et al.*, 2024; Tréhin *et al.*, 2024b). Large aggregations of vultures may not negatively impact survival, in fact the opposite is more commonly reported (Margalida, Martínez, *et al.*, 2017; Rousteau *et al.*, 2022), but they may push juveniles to disperse further, or use less frequently stocked or poorer quality sites to avoid heavy competition (Fernández-Gómez *et al.*, 2022; Reznikov *et al.*, 2024). However, movement data of cinereous vultures in the area show a high residence rate and low long-distance dispersal behaviour of individuals in all non-adult age classes (Tobajas et al. 2024), suggesting that a population threshold detrimental to young birds has not been reached.

Management of SFS must integrate both the ecological and social aspects of vulture foraging behaviour (Van Overveld, Blanco, *et al.*, 2020), and going forward, a more dispersed network of lightly stocked feeding sites could better mimic the natural carcass deposition in the landscape preventing extreme competition and encouraging more efficient scavenging behaviours (Deygout *et al.*, 2009; Cortés-Avizanda, Carrete and Donázar, 2010; Dupont *et al.*, 2012; Monsarrat *et al.*, 2013). Unfortunately, we lacked information on stocking patterns to contribute to the analysis conducted in this study, which could allow us to make a more detailed examination of the influence of food distribution on movements and behaviour. Previous research shows that distributing carcasses across a larger number of feeding sites and a further distances from colonies may encourage dispersal (Margalida and Colomer, 2012; Reznikov *et al.*, 2024), particularly during spring when vultures are expanding their ranges. In the context of European health regulations, the potential closure of SFS for public health reasons may impact vulture populations. Previous work on SFS closure found a change in diet composition in Griffon vultures (Donázar, Cortés-Avizanda and Carrete, 2010), and a decrease in survival, particularly of juveniles (Zuberogoitia *et al.*, 2013b), although it should be noted that Bearded vultures were not affected by regulations in the same way (Margalida, Pérez-García and Moreno-Opo, 2017).

Closure of large SFS in our study system is likely to change movement patterns, as seen in the removal of key 'node' sites in Cerecedo-Iglesias *et al.*, (2023). However, consequences on survival are harder to predict. Depending on the precise nature of future legislation, if farmers remain able to deposit carcasses on their land at lower densities, food would still be available in the landscape (Colomer & Margalida 2025). However, dominant adults that are more skilled at identifying carcasses in the landscape may push juveniles to disperse further, with potential survival effects, altering the spatial network use of these younger, non-breeding birds (Cerecedo-Iglesias *et al.*, 2023). The long-term implications of reduced volume or quality of predictable resources for future vulture population viability are still unclear; movements of birds in response to changes in SFS availability should be monitored and ideally linked to survival, and breeding performance in order to implement any necessary compensatory conservation measures and better plan future release locations of rehabilitated or captive bred birds.

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