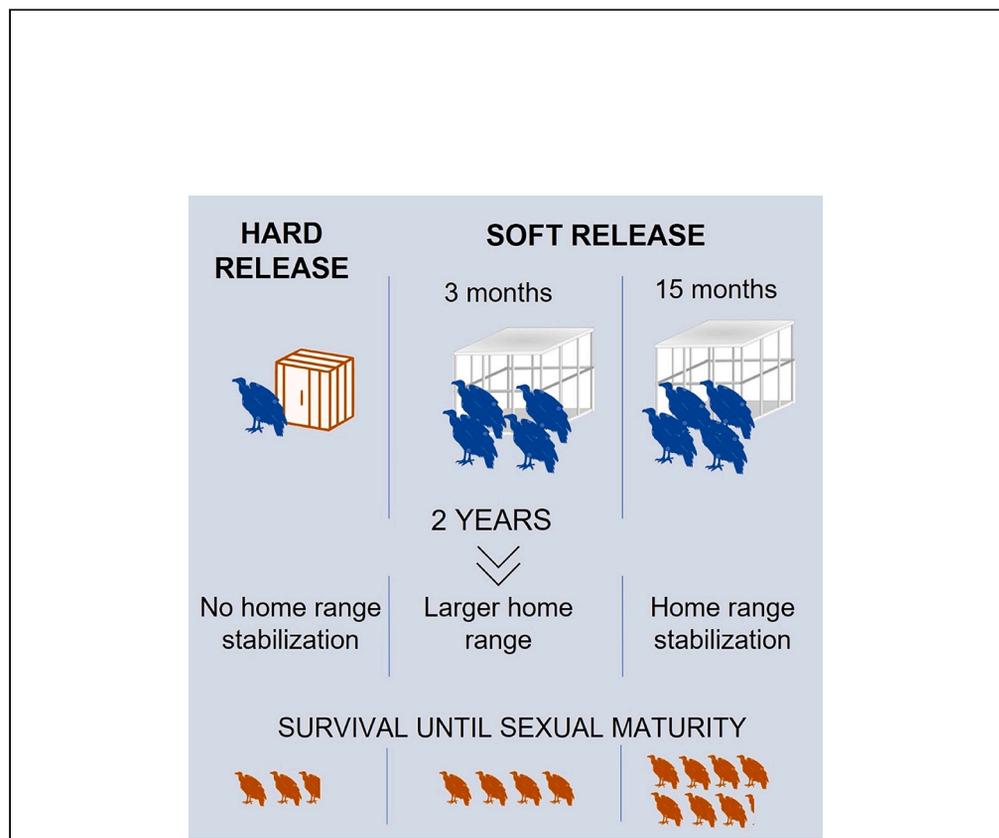


Article

Insights on the best release strategy from post-release movements and mortality patterns in an avian scavenger



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Highlights

Release strategies can affect the outcome of vulture conservation translocations

Long acclimatization favored home range size stabilization in Griffon vultures

More vultures reached sexual maturity when released after a long acclimatization

Long acclimatization seems the best practice for releasing Griffon vultures

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Article

Insights on the best release strategy from post-release movements and mortality patterns in an avian scavenger

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SUMMARY

Conservation translocations involving vultures rely either on soft- or hard-release strategies. To investigate whether these strategies affect home range stability and survival, we compared the spatial behavior and mortality of 38 Griffon vultures (*Gyps fulvus*) released in Sardinia. Griffons were released after no acclimatization or after 3 (short) or 15 (long acclimatization) months in an aviary. In the two years that followed their release, griffons without acclimatization did not stabilize their home range size, while those subjected to long acclimatization stabilized it in the second year. Short-acclimatized griffons always had a large home range, soon after their release. The number of individuals that reached sexual maturity was higher (71.4%) in long-acclimatized griffons than in short-acclimatized ones (40%) or in griffons that were hard released (28.6%). Soft release with a long acclimatization period seems to be the most successful method to ensure stable home ranges and the survival of griffon vultures.

INTRODUCTION

Conservation translocation is a practice where individuals of a focal species are deliberately moved and released into a certain area, usually with the 2-fold aim of improving its local/global conservation status and/or restoring ecosystem processes and function.^{1,2} The number of released individuals and the duration of release programs are critical for the success of vertebrate translocations.³ The two crucial phases affecting the dynamics of translocated populations are establishment, which starts with the first release and ends when post-release effects are no longer operating,¹ and persistence.⁴ However, a population persists only if it survives the establishment phase, often characterized by high mortality⁵ and dispersal,⁶ even when environmental conditions at the release site are favorable.⁵

Translocations are usually based on two different release strategies: soft and hard release (for translocation⁷; for reintroduction^{8–14}). Soft release is based on the delayed release of individuals from a temporary enclosure, while hard release involves the immediate and direct release of individuals without any previous acclimatization.¹⁵

Soft release has various potential advantages. By watching the release site from acclimatization enclosures, individuals could develop partial cognitive maps,¹⁶ an important component of spatial orientation.¹⁷ Gregarious species could also safely familiarize with conspecifics and create preliminary bonds that would facilitate their subsequent inclusion in social groups.¹⁸ Moreover, individuals could receive environmental enrichment and/or anti-predatory training, which would speed up the development of adaptive behavior.¹⁹ All these possibilities can optimize resource exploitation, increase survival, reduce post-release movements, and encourage site fidelity, ultimately increasing the chance of persistence.

Overall, Resende et al.²⁰ found that soft-release protocols tend to have a positive outcome and they are 45% more successful than hard-release ones in conservation translocations. Additionally, animals that were soft released tended to remain at or near the release site, and this increased the chance of conservation translocation success by 77%.

However, evidence-based conservation translocation still suffers from major gaps, including a focus on large iconic mammals,³ and the fact that few studies adopted a comparative approach, assessing the effect

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of different release strategies under similar environmental conditions.²⁰ These gaps are particularly critical for those species, such as large raptors, for which translocations/reintroductions are common and carried out worldwide with multiple release strategies (e.g., hacking,^{10,21,22} hard release,²³ soft release^{10,24,25}) and for which environmental and anthropogenic stressors are often highly heterogeneous in space (e.g., lead contamination,²⁶ human infrastructures,²⁷ poisoning²⁸). The exclusive existence of conservation translocation conducted with a single method, over a single area, does not allow to appreciate how different release strategies can affect the spatial ecology and survival of these species, in turn limiting our capacity to improve conservation programs.²⁹ This gap is even more concerning for Old World vultures, a group of raptors that suffered abrupt and extensive population declines over the last few decades.^{30,31} In fact, as the survival of many species of vultures depends upon connectivity between populations³² and the size of colonies,³³ many conservation programs for these species include reintroductions or restocking. This is particularly true for, but not limited to,^{10,34,35} programs focusing on vultures from the genus *Gyps*, which includes eight different species, distributed across Eurasia and the African continent, where they numerically dominate vulture guilds. All vultures from the genus *Gyps* are gregarious and rely on group foraging.³⁶ This makes them highly vulnerable to deliberate or accidental poisoning, and many species have been declining over the last few years, with 5 species being now critically endangered (*Gyps bengalensis*, *Gyps rueppellii*, *Gyps indicus*, *Gyps tenuirostris*, and *Gyps africanus*), one being vulnerable (*Gyps coprotheres*), and one being near threatened (*Gyps himalayensis*) according to the International Union for Conservation of Nature (IUCN).³⁷ As the population dynamics of *Gyps* vultures are subjected to important density-dependent effects,³⁸ conservation projects carried out in Europe,³⁹ sub-Saharan Africa,⁴⁰ or the Indian subcontinent⁴¹ included restocking as a tool to counteract the numerical decline of numerous populations.

However, while many studies identified release sites with suitable climatic conditions⁴² or biomass,⁴³ or established demographically³⁸ and genetically optimal⁴⁴ conservation planning, little efforts were made to compare how vultures subjected to soft and hard release could differ in their post-release spatial behavior and survival. To the best of our knowledge, the only two studies adopting a comparative approach focused on the origin of griffons, rather than on the methods through which they were released in the wild. Namely Peshev et al.⁴⁵ compared differences in post-release spatial behavior between captive-bred and wild-caught Griffon vultures (*Gyps fulvus*), while Jobson et al.,⁴⁶ between captive-bred and rehabilitated Cape vultures (*G. coprotheres*).

This is a major gap because many conservation programs for *Gyps* vultures, and other Old World vultures,¹⁰ do not only use animals with different origins but also use soft- and hard-release strategies. Moreover, since soft-release strategies may rely on an acclimatization lasting a variable amount of time, there is also a lack of information about how long an optimal acclimatization phase would last. Furthermore, pooling together findings from studies, each one using griffons that had been released with a single release strategy, is hardly indicative: without a comparative design,²⁰ any comparison would suffer from unquantified heterogeneities between study areas, including those in animal husbandry, supplementary feeding programs, the topography of the area, or different sources of mortality.

In this study we addressed this gap by comparing: *i*) the temporal trend of home range size and *ii*) the overall survival of three groups of griffons that had been released in Sardinia (Italy), within the LIFE “Under Griffon Wings” project.⁴⁷ This initiative, coupled with anti-poisoning campaigns and supplementary feeding, aimed to counteract the prolonged decline of the population in the island, caused by multiple mass mortality events and declining extensive livestock,⁴⁸ which had decreased the number of reproductive pairs since the 1980s.⁴⁹

Our sample included 38 griffons that were released between 2016 and 2021, in a common study area (Figure 1), and which were equipped with GPS (global positioning system) /GSM (global system for mobile communication) transmitters. However, some of them had been recovered from the wild, rehabilitated, and then subjected to hard release ($n = 10$), while others came from wildlife rehabilitation centers and zoological gardens and then were kept in aviaries for an acclimatization phase of 3 months (short acclimatization, $n = 21$) or 14 months (long acclimatization, $n = 7$), before being released.

We hypothesized that soft-release strategy would prove more successful because griffons in the aviary would have time to familiarize with their surrounding environment, by understanding patterns in wind intensity and direction, observing the surrounding area, and also meeting conspecifics. Thus, we expected this to reduce the

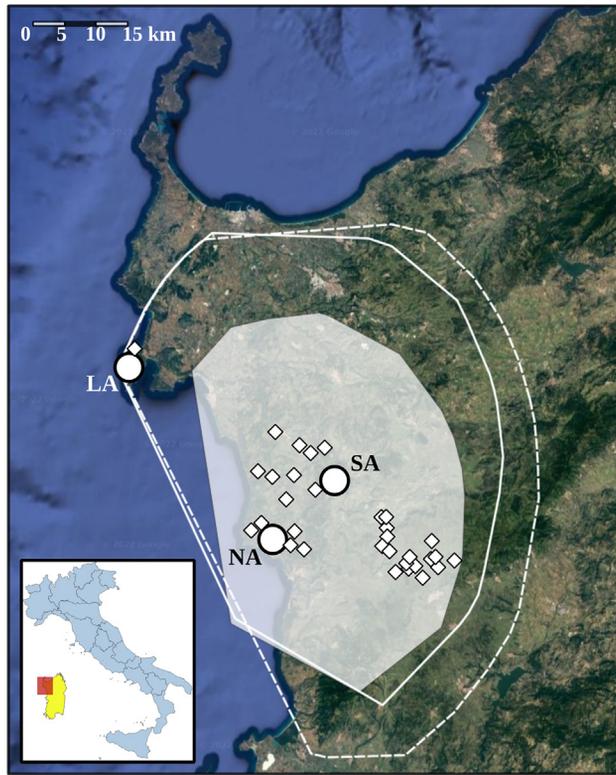


Figure 1. Study area map

Map of the study area, representing release sites (circles, “LA” = “long acclimatization”, “SA” = “short acclimatization”, “NA” = “no acclimatization”), supplementary feeding stations (squares), and the minimum complex polygon covered by griffon vultures released with no acclimatization (highlighted), with short acclimatization (dashed line), and with long acclimatization (solid line).

time needed for home range size stabilization, as well as the exposure of soft-released individuals to risks, increasing their survival up to five years of age, compared to individuals subjected to hard release.

RESULTS

Our final sample, used for data analysis, included a total of 699 observations of monthly home range size, belonging to 38 Griffon vultures (Table 1, 18.39 ± 12.81 home ranges/individual). All individuals were immature, except for one adult female, and were released at three different sites (Figure 1).

Average monthly home ranges were $1,005 \pm 1,302$ and 818 ± 980 km² (mean \pm SD) for female and male Griffon vultures, respectively. Model selection retained a generalized additive mixed model (hereinafter, “GAMM”), which explained 47.3% of variation in home range size, and which included the age of released individuals, the month of the year, the time from release in interaction with the release strategy, and the number of available spatial locations, as predictors (Table S1). According to the model, there were negligible differences in the home range size of female and male Griffon vultures, as well as in that of birds taken from the wild or coming from captivity.

Conditional effect plots showed that Griffon vultures decrease their home range size, in their first two years of life, passing from 1,500 km² for individuals with less than one year to 800–1,500 km² for individuals between two and six years of age (Figure 2A). The model detected a clear seasonal pattern in home range size, with Griffon vultures using smaller areas between November and December and larger areas between May and June (Figure 2B).

The temporal trend of home range size differed between the three groups of Griffon vultures. Individuals subjected to hard release had a home range of about 500 km² soon after the release, and then they linearly

Table 1. Released Griffon vultures with GPS type, release date and strategy, date and cause of death

Name	Origin	Sex	GPS model	Release method	Age in months	Date of birth	Date of first potential reproduction	Date of release	Date of the last GPS fix	Date of the last resight	Date of death	Sexual maturity achieved	Cause of death	Fix interval
Artis1	Netherlands	M	Ecotone Crex	LA	13	2017-04-01	2022-03-31	2018-04-14	2020-01-14			Unknown		60 min
Artis 2	Netherlands	F	Ecotone Crex	LA	13	2017-04-01	2022-03-31	2018-04-14	2019-02-15	2022-12-16		Yes		60 min
Artis 3	Netherlands	F	Ornitela 3G_50g	SA	15	2018-04-01	2023-03-31	2019-06-24	2022-06-28	2022-08-15		Unknown		15 min
Artis 4	Netherlands	M	Ornitela 3G_50g	SA	15	2018-04-01	2023-03-31	2019-06-24	2021-03-11			Unknown		15 min
Artis 5	Netherlands	M	Ecotone Crex	SA	15	2018-04-01	2023-03-31	2019-06-24	2020-08-18			Unknown		30 min
Barca	Spain	F	Ecotone Skua	LA	37	2015-04-01	2020-03-30	2018-04-14	2022-06-28	2022-12-22		Yes		60 min
Bonalva	Spain	M	Ecotone Crex	SA	20	2018-04-01	2023-03-31	2019-10-17	2020-01-04			Unknown		60 min
Bonassai	Sardinia	F	Ecotone Saker	HR	6	2017-04-01	2022-03-31	2017-09-26	2018-07-14	2022-08-15		Yes		60 min
Bulga	Spain	F	Ecotone Crex	LA	37	2015-04-01	2020-03-30	2018-04-14	2019-07-30		2019-07-31	No	Bird strike	60 min
Calmedia	Spain	F	Ecotone Crex	SA	20	2018-04-01	2023-03-31	2019-10-17	2020-10-13	2022-04-12		Yes		60 min
Caniga	Spain	F	Ecotone Crex	SA	19	2018-04-01	2023-03-31	2019-10-17	2022-06-28	2022-08-15		Unknown		120 min
Cannisone	Spain	M	Ecotone Crex	SA	33	2016-04-01	2021-03-31	2018-12-15	2019-09-25			Unknown		60 min
Corte	Spain	M	Ecotone Crex	SA	19	2018-04-01	2023-03-31	2019-10-17	2021-09-24			Unknown		60 min
Cristallo	Spain	M	Ecotone Crex	LA	37	2015-04-01	2020-03-30	2018-04-14	2022-06-28	2022-06-20		Yes		60 min
Cristina	Sardinia	U	Ornitela 3G_50g	HR	7	2021-01-01	2026-03-31	2021-08-01	2022-06-28	2022-12-22		Unknown		10 min

(Continued on next page)

Table 1. Continued

Name	Origin	Sex	GPS model	Release method	Age in months	Date of birth	Date of first potential reproduction	Date of release	Date of the last GPS fix	Date of the last resight	Date of death	Sexual maturity achieved	Cause of death	Fix interval
Cuada	Spain	F	Ecotone Crex	SA	106	2010-04-01	2015-03-31	2018-12-11	2022-06-28	2022-12-22		Yes		60 min
Doglia	Spain	F	Omitela 3G_50g	SA	19	2018-04-01	2023-03-31	2019-10-17	2022-06-27	2022-08-15		Unknown		1 s
Dresda1	Germany	U	Ecotone Crex	SA	11	2021-04-01	2026-03-31	2021-11-08	2022-06-28	2022-12-22		Unknown		60 min
Entulzu	Sardinia	U	Ecotone Skua	HR	11	2019-04-01	2024-03-30	2020-02-29	2022-06-28	2022-12-22		Unknown		60 min
Fenuggiu	Spain	M	Ecotone Crex	LA	37	2015-04-01	2020-03-30	2018-04-14	2021-09-12		2021-11-26	Yes	Electrocution	60 min
Hospiton	Sardinia	U	Ecotone Crex	HR	14	2020-04-01	2025-03-31	2021-05-19	2021-12-16	2022-02-04		Unknown		60 min
Idile	Spain	M	Ecotone Crex	SA	33	2016-04-01	2021-03-31	2018-12-11	2022-06-27	2022-12-22		Yes		60 min
Jana	Sardinia	F	Ecotone Saker	HR	12	2016-04-01	2021-03-31	2017-03-09	2017-12-22		2017-12-24	No	Poisoning	60 min
Life	Sardinia	M	Ecotone Saker	HR	39	2014-04-01	2019-03-31	2017-06-13	2017-07-11		2017-07-16	No	Probable collision with power lines	60 min
Lobo	Sardinia	M	Ecotone Skua	HR	14	2018-04-01	2023-03-31	2018-12-06	2019-10-09	2022-04-12		Unknown		60 min
Macomer	Spain	F	Ecotone Saker	SA	15	2018-04-01	2023-03-31	2019-06-24	2021-12-15	2022-12-22		Yes		60 min
Maddalena	Spain	F	Ecotone Crex	SA	15	2018-04-01	2023-03-31	2019-06-24	2019-07-20		2019-07-20	No	Injuries	60 min
Malvasia	Sardinia	M	Ecotone Crex	HR	15	2017-04-01	2022-03-31	2017-11-03	2018-08-27	2022-10-21		Yes		120 min
Meilogu	Spain	M	Ecotone Crex	SA	19	2018-04-01	2023-03-31	2019-10-17	2020-08-14	2022-12-16		Yes		60 min
Mina	Sardinia	F	Ecotone Saker	HR	8	2017-04-01	2022-03-31	2017-11-03	2019-11-30		2019-11-29	No	Electrocution	120 min

(Continued on next page)

Table 1. Continued

Name	Origin	Sex	GPS model	Release method	Age in months	Date of birth	Date of first potential reproduction	Date of release	Date of the last GPS fix	Date of the last resight	Date of death	Sexual maturity achieved	Cause of death	Fix interval
Monteleone	Spain	M	Ecotone Crex	SA	30	2016-04-01	2021-03-31	2018-09-13	2018-11-09		2018-11-09	No	Electrocution	60 min
Pabelanasa	Spain	F	Ecotone cDuck	SA	34	2016-04-01	2021-03-31	2018-12-12	2022-06-28	2022-08-15		Yes		60 min
Pituabile	Spain	M	Ecotone Crex	SA	33	2016-04-01	2021-03-31	2018-12-11	2021-01-31		2021-02-10	Yes	Drowning	60 min
Pozzomaggiore	Spain	M	Ecotone Crex	SA	15	2018-04-01	2023-03-31	2019-06-24	2021-11-18			Unknown		60 min
Tempestosa	Sardinia	F	Ecotone Saker	HR	12	2016-04-01	2021-03-31	2017-03-09	2017-09-29		2017-09-30	No	Collision with wind turbines	60 min
Timidone	Spain	M	Ecotone Crex	LA	37	2015-04-01	2020-03-30	2018-04-14	2021-02-22	2022-12-22		Yes		60 min
Tottubella	Spain	F	Ecotone Crex	SA	20	2018-04-01	2023-03-31	2019-10-17	2022-06-28			Unknown		60 min
Urinculè	Spain	M	Ecotone Crex	SA	30	2016-04-01	2021-03-31	2018-09-13	2021-03-10			Yes	Electrocution	60 min

"Name" = "individual name of the released Griffon vulture"; "Origin" = area of origin of the released individuals; "M" = "Male", "F" = "Female", "U" = "Unknown (the individual sex was not determined)"; "HR" = "Hard Release", "LA" = "Long Acclimatization", "SA" = "Short Acclimatization". Dates are in the yyyy-mm-dd format. Griffon vultures were deemed to have achieved sexual maturity if they were alive in December of the year before the one they were expected to have their first reproduction as this is the time of the year when nuptial flights begin. STAR Methods.

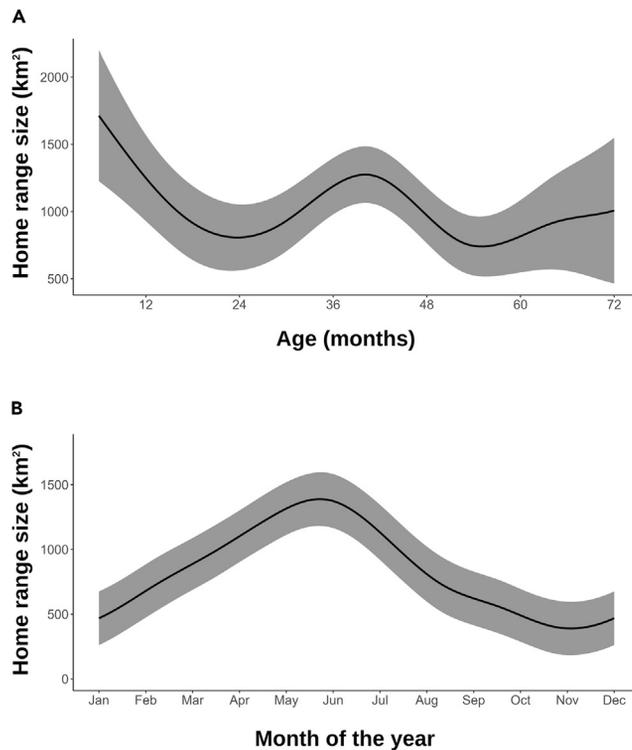


Figure 2. Age-specific and seasonal variability of monthly home range size of griffon vultures

(A and B) Variability of the monthly home range size of Griffon vultures across different ages (A) and months of the year (B), as predicted by the best generalized additive mixed model (see the [STAR Methods](#) section for more details). Estimated standard errors are represented by the color-shaded areas.

increased its size, reaching a home range of about 1300 km² 24 months after the release. Individuals subjected to soft release with long acclimatization had a home range of about 500 km² at the time of their release, and then they increased it to about 1500 km² at 12 months after the release and maintained it stable in the following two months. Finally, Griffon vultures released with a short acclimatization period initially showed a larger and stable home range size (around 2,000 km²), showing no significant variations along the two years after the release ([Figure 3](#)).

When considering griffons that could have already reached the age of their first reproduction, at the time of the study ($n = 34$), we noticed pronounced differences in survival between the three groups. Namely, 71.4% of griffons subjected to long acclimatization reached their fifth year of age, when they could enter the pool of potential breeders in the Sardinian population. This value was lower for griffons subjected to short acclimatization (40%) and to hard release (28.6%, [Table 2](#)). Moreover, 57.1% of griffons subjected to hard release were found dead before their fifth year of age ([Table 2](#)).

DISCUSSION

In the present study we analyzed home range size and its temporal trend, as well as mortality rates of Griffon vultures released following three different release strategies.

The results show that, among the factors analyzed, the individual age, the month of the year, and the time from release in interaction with the release strategy had the most significant effect in determining the monthly home range size.

Home range size

The mean size of the monthly home range for all individuals in our study turned out to be smaller than values from previous studies in Europe, as summarized in [Table 3](#). For example, Xirouchakis et al.⁵⁰ calculated a mean home range of $1,560 \pm 140$ km² (Kernel density estimation [KDE], 95%) by monitoring 32

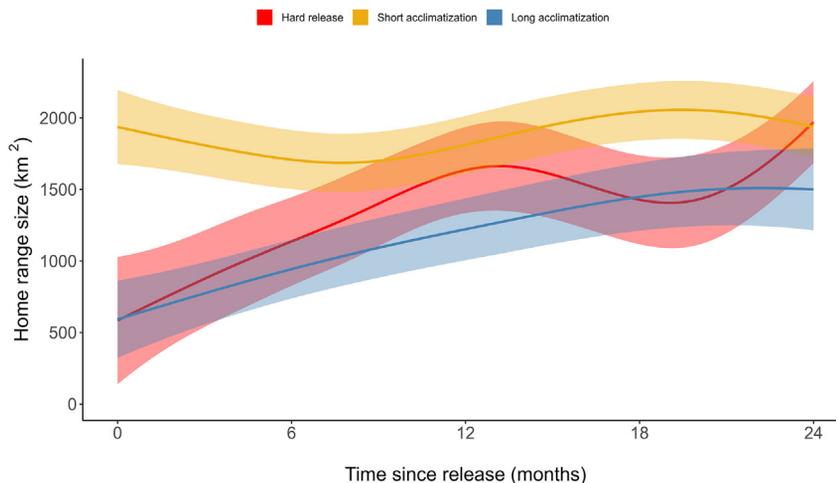


Figure 3. Post-release monthly home range size of griffon vultures

Variability of the monthly home range size of Griffon vultures after being released with short, long, or no acclimatization period (yellow, red, and blue lines, respectively), as predicted by the best generalized additive mixed model (see the STAR Methods section for more details). Estimated standard errors are represented by the color-shaded areas.

radio-tagged wild Griffon vultures in Crete, both adults and immatures, found with symptoms of poisoning and rehabilitated. Similar results, but with a higher variability, were reported by Peshev et al.⁴⁵ in Bulgaria, Greece, and North Macedonia (mean 95% home range area $1431 \pm 1472 \text{ km}^2$ - 51 GPS-tracked Griffon vultures of different ages and origin). Other authors, such as Arkumarev et al.⁵¹ in Bulgaria (overall foraging home range $3,204 \text{ km}^2$, 95% kernel - 13 GPS-tracked wild Griffon vultures, both adults and immatures) and Morant et al.⁵² in Spain (annual $5,027 \pm 2,123 \text{ km}^2$, monthly $4,889 \pm 1,753 \text{ km}^2$, KDE 95% - 127 GPS-tracked Griffon vultures), reported even larger values.

These differences could have arisen from actual differences in the behavior of populations studied but also from the methodological approach. In previous studies, the home ranges of Griffon vultures were only computed at the seasonal level⁴⁵ or even along the whole individual monitoring period⁵⁰ hindering any proper comparability with our results. Nonetheless, the substantial differences of the home range size observed with these works might also derive from different availability of suitable foraging habitats. In Crete, livestock is kept in pens and large enclosures from late October until late April, when herds are transferred to the summer pastures in the highlands;⁵⁰ thus Griffon vultures might travel longer distances to forage in summer.

On the other hand, in our study area, no seasonal movements of livestock exist: cattle and sheep are raised all year round in large traditional pastoral landscapes (similar to Delgado-González et al.⁵³), in a radius of a few hundred kilometers from colonies. Moreover, alternative resources are limited,⁵⁴ being restricted to wild boar densities lower than 15 individuals/100 ha and a population of approximately 300 fallow deer (*Dama dama*⁵⁵). These three factors probably limit foraging movements around areas characterized by high livestock densities, reducing home range sizes.

The presence/absence of supplementary feeding stations might also influence Griffon vultures foraging movements. In our study area 37 farm feeding stations (Figure 1) have been activated, providing approximately 20 tons of livestock carrion every year in a radius of less than 50 km.⁵⁵ Despite the fact that there is no universal consensus on the extent to which concentrated food resources affect the predictability of vulture movements,^{33,56} available evidence for Griffon vultures indicates that predictable supplementary feeding stations can reduce space utilization,⁵⁷ also through conspecific attraction.⁵⁸ As this dynamic could have negative long-term consequences for griffon conservation,⁵⁹ future studies should better clarify the role played by farm feeding stations over spatiotemporal habitat selection (e.g., through integrated methods⁶⁰), with the goal of improving supplementary feeding strategies to encourage exploratory behavior in Sardinia.

Finally, it should be considered that our study area was an island with obvious limitation of space available to search for food. Populations in continental Europe are also characterized by seasonal movements,⁶¹ as

Table 2. Number of individuals that reached their fifth year of age (n = 34), that were found dead before, or that were not re-observed, between the three groups of griffon vultures released with different strategies

	Age when released	Alive at 5 years of age	Found dead before	Not re-observed
Hard release	15.1 ± 10.9	2 (28.6%)	4 (57.1%)	1 (14.3%)
Short acclimatization	26.3 ± 20.09	8 (40.0%)	2 (10.0%)	10 (50.0%)
Long acclimatization	30.1 ± 11.7	5 (71.4%)	1 (14.3%)	1 (14.3%)

The average age, in months, at the time of release (mean ± standard deviation) was also reported. Four individuals from the initial sample were not eligible for this analysis as they were expected to reach sexual maturity after the time of the study.

well as by partial migration strategies during their first years of life,⁶² two characteristics that would increase the size of their home range (see also the [limitations of the study](#) section).

Individual age

Our results show that home range size decreases between six and 72 months of age, with a slight increase around 36 months of age. Beyond 72 months of age, home range size was estimated only for one adult female, which showed an extremely wide home range, presumably due to long-range forays. Nathan et al.,⁶³ in a study conducted in Israel, observed that some individuals showed similar long forays which, albeit energy demanding, did not include frequent foraging. Their results suggest that this behavior could have a social meaning, such as the search for a mate.

Immature individuals commonly show erratic behavior⁶⁴ as that they travel over long distances.^{51,65} In Crete, Xirouchakis et al.⁵⁰ found that immature Griffon vultures ranged on average about double the area than adults in winter and occupied significantly larger core areas. The home range size of Griffon vultures decreased with increasing experience (i.e., by age), and adult birds ranged over smaller areas than immatures. However, as in our study all released Griffon vultures were immatures, except for one adult, we were not able to make any comparison between different age groups.

Seasonal patterns of home range size

Our results also show a clear seasonal pattern in home range size, with Griffon vultures using smaller areas between November and December and larger areas between May and June. This result confirms previous findings as it is known that movement activity and home range size vary considerably during the annual cycle, with areas used in spring and summer that are larger than those used in winter.^{45,66} To the best of our knowledge, in the study area there are no seasonal shifts in livestock presence on pastures (e.g., due to transhumance), which remains constant across seasons, similarly to carrion provisioning to farm feeding stations. The observed pattern can therefore be explained by favorable weather conditions in spring and summer, in terms of daily temperatures and the formation of thermal updrafts, which allow vultures to travel further from roosting and breeding cliffs⁵¹ than in winter, when adverse weather prevents the creation of thermal updrafts and day length is reduced, constraining foraging.⁵⁷

Sex and origin

In our results the sex of Griffon vultures had a negligible effect on the size of their home ranges. The same result is shown in Xirouchakis et al.,⁵⁰ where the extent of home ranges of Griffon vultures was studied on Crete (Greece) and no differences were found between the two sexes.

Monsarrat et al.⁶⁷ deemed these results to be consistent with the limited sexual dimorphism of the species and, in adults, the equal investment of males and females in reproduction.⁶⁸ The origin of the Griffon vultures, either captive or wild caught, also had a negligible effect on the size of their home ranges. This finding aligns with Peshev et al.,⁴⁵ who found that there was no significant difference in home range sizes between “wild-caught”, “wild/rehabilitated”, and “re-introduced” Griffon vultures on the Balkan peninsula.

Release strategy and mortality

In conservation translocation projects, the spatial behavior of animals after their release may inform about the potential success of the translocation. During the establishment phase, individual movement is aimed

Table 3. Estimated home range size of Griffon vultures across different studies and methods used for computing them

Study	Area	Home range size (km ²)	Method	Age classes
Xirouchakis et al. ⁵⁰	Crete	1,560 ± 140	Mean, KDE 95%, all individuals and seasons pooled	Adults and immatures
Arkumarev et al. ⁵¹	Bulgaria	3,204	95% kernel, overall foraging range, Minimum Convex Polygon (MCP)	Adults and immatures
Peshev et al. ⁴⁵	Bulgaria, Greece, North Macedonia	1,431.22 ± 1,472.12	dynamic Brownian bridge movement model (dBBMM), mean 95% for all individuals	Adults and immatures
Morant et al. ⁵²	Spain	5,027 ± 2,123 (annual) 4,889 ± 1,753 (monthly)	KDE 95%	Adults
This study	Italy	1,005 ± 1,302 (females) 818 ± 980 (males)	average monthly HR size computed with local convex hull method (LoCoH)	Immatures

mostly to explore and acquire information about a new and unfamiliar environment, and thus decreased movements could indicate that translocated individuals found an area suitable for their establishment.^{20,69}

In our study, a factor that definitely affected home range size, and its temporal variation, was the release strategy. Our results show that both no- and long-acclimatized Griffon vultures exhibited relatively small home range right after the release. Regarding the former, as they did not spend any time in the acclimatization aviary, we might suppose that they could not adequately train flight muscles and were not proficient at flying soon after their release; the latter, on the other hand, by having spent 15 months in the acclimatization aviary, could also have developed a stronger relation with the release site, therefore showing smaller initial home range size.

While the home range size of the no-acclimatized Griffon vultures showed a steady increase within the two years after the release, the home range size of the long-acclimatized individuals reached its maximum size between 12 and 18 months after the release and then displayed a stable size at the end of the survey time, suggesting a different trend from the hard-released ones. The comparison of the home range sizes for the two groups at two years after the release shows a clear difference despite the partial overlap of confidence intervals. Assuming the continuation of this divergent pattern after two post-release years, we can expect that the difference between home range sizes of no- and long-acclimatized vultures will become even more evident in the long term.

Regarding the short-acclimatized individuals, they showed a larger and stable home range size soon after the release, with no significant variations along the survey time. Indeed, this might also increase mortality risk, since having a larger home range from the beginning might translate into incurring in greater risks.

These results are to be linked to those about mortality, as post-release survival rate is indeed another metric of success in the evaluation of conservation translocation programs.¹ Our findings indicate that a higher proportion of individuals subjected to a long acclimatization period reached sexual maturity, compared to individual subjected to short acclimatization or hard release. While these findings could have depended upon differences in griffon age at the time of the release (Table 1), with long-acclimatized griffons being on average older than individuals from the other two groups, this difference was noticeable: the number of griffons subjected to long acclimatization that reached adulthood was 2.5 times higher than that of griffons subjected to hard release, while the number of hard-released griffons that died before reaching sexual maturity was 4 times higher than that of long-acclimatized griffons.

Although this was only a descriptive result, we believe that such a preliminary evidence is promising for future ad-hoc studies on Griffons' post-release survival and to promote best practices within release projects.

Efrat et al.⁷⁰ proved that post-release survival of Griffon vultures in Israel was affected by different release sites and season, rearing methods, the age of released individuals, and the time elapsed after their release to the wild. They also found out that an age-related increase in survival most likely meant that vultures had acquired important skills during their time spent in captivity, either due to the properties of their captive environment during this critical period or because of the effects of maturation, regardless of their surroundings. This might explain why in our study long-acclimatized Griffon vultures showed an average survival rate that was higher than that of both short- and no-acclimatized ones. By spending their acclimatization period in large aviaries, specifically built for this purpose, they had the opportunity to perform small flights and to gain knowledge about the landscape where they would have been released. On the contrary, hard-released individuals came from a wildlife recovery center, where they were treated in hospitalization aviaries, which did not allow proper flight movements. This may have weakened the individuals physically over time and may have resulted into a reduced ability to fly after their release in an unfamiliar environment.

In conclusion, despite the persistence of Griffon vulture populations subjected to conservation translocations depending upon factors acting on breeding individuals (e.g., reproduction,⁷¹ mass mortality events^{48,72}), our findings indicate that release strategies can play an important role over the establishment of immature individuals, particularly for those populations, like those inhabiting Mediterranean islands, where juvenile dispersal is low. A soft release with a long acclimatization period was the most successful method, either by stabilizing home range size or by reducing mortality rates. Hard release may nevertheless be used as a complementary measure to inform and educate the general public by releasing animals in the wild at public events.

Limitations of the study

Both the sample size and the duration of the GPS transmitters lead to difficulties in the full interpretation of the results. Moreover, two years data for each individual were not clearly sufficient to fully describe home range size trajectory of the differently released category that in the two years of tracking showed different trends.

It is worth emphasizing that our griffons subjected to different release strategies also had inherent differences in their geographical origin and partially in their source. Namely, griffons subjected to hard release only came from the wild, not from captivity, and from the Sardinian population. Although we actually observed a rather similar pattern between Sardinian griffons (released without acclimatization) and non-Sardinian Griffon vultures (released with short acclimatization), future studies, adopting a factorial design, are needed to fully disentangle the interplay between these three components. Focusing on the impact of captive breeding would be particularly important, considering that this practice can relax selective pressures and produce behavioral changes,⁷³ as already hypothesized for other species of Old⁵⁸ and New World⁷⁴ vultures. Furthermore, we believe that studies randomly assigning animals to different release strategies, although challenging to implement, would ultimately be needed for making causal claims about release strategies.⁷⁵

Due to our low sample size, our conclusions about mortality were not based on structured sampling schemes but on a mixture of telemetry data and occasional resightings. Therefore, they did not include any probabilistic quantification of apparent survival, nor the effect of changes in detectability due to GPS battery expiration, and should be taken only as a preliminary evidence.

Finally, our findings were obtained from a griffon population living on an island. Griffons living in continental Europe are characterized by seasonal movements⁶¹ and by dispersal in their first years of life.⁶² Therefore, they usually have both larger home ranges and a different temporal trend in their spatial utilization. Moreover, as the dispersal phase sometimes involves sea crossings,⁷⁶ or areas with energy infrastructures,⁷⁷ these populations probably experience a higher mortality than those living on an island. Therefore, in a continental griffon population it is plausible that differences in both home range size variation and survival, between groups, would be different from the ones we detected. As wind energy development is increasing throughout Europe and the Mediterranean, assessing how differences in survival between griffon populations are affected by collisions with energy infrastructures is a priority because spatially varying mortality caused by collision hotspots²⁷ could lead to source-sink systems,⁷⁸ which should be accounted for in conservation programs.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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 - Statistical analyses

SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.isci.2023.106699>.

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AUTHOR CONTRIBUTIONS

Conceptualization, F.B. and M.A.; Formal Analysis, R.B., S.C., R.C., and I.F.; Writing – Original Draft, I.F. and R.B.; Writing – Review & Editing, I.F., R.B., J.C., F.B., and M.A.; Visualization, J.C., R.B., and I.F.; Supervision, F.B., D.D.R., and M.A.R.; Project Administration, F.B.; Funding Acquisition, F.B.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We support inclusive, diverse, and equitable conduct of research.

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REFERENCES

- IUCN/SSC (2013). Guidelines for Reintroductions and Other Conservation Translocations. <https://doi.org/10.13140/RG.2.1.1751.0003>.
- Evans, M.J., Pierson, J.C., Neaves, L.E., Gordon, I.J., Ross, C.E., Brockett, B., Rapley, S., Wilson, B.A., Smith, K.J., Andrewartha, T., et al. (2023). Trends in animal translocation research. *Ecography*, e06528. <https://doi.org/10.1111/ecog.06528>.
- Morris, S.D., Brook, B.W., Moseby, K.E., and Johnson, C.N. (2021). Factors affecting success of conservation translocations of terrestrial vertebrates: a global systematic review. *Glob. Ecol. Conserv.* 28, e01630. <https://doi.org/10.1016/j.gecco.2021.e01630>.
- Armstrong, D.P., and Seddon, P.J. (2008). Directions in reintroduction biology. *Trends Ecol. Evol.* 23, 20–25. <https://doi.org/10.1016/j.tree.2007.10.003>.
- Kreger, M.D., Hatfield, J.S., Estevez, I., Gee, G.F., and Clugston, D.A. (2006). Behavioral profiles of the captive juvenile whooping crane as an indicator of post-release survival. *Zoo Biol.* 25, 11–24. <https://doi.org/10.1002/zoo.20075>.
- Moehrensclager, A., and Macdonald, D.W. (2003). Movement and survival parameters of translocated and resident swift foxes *Vulpes velox*. *Anim. Conserv.* 6, 199–206. <https://doi.org/10.1017/S1367943003251>.
- H Clarke, R., L Boulton, R., and F Clarke, M. (2002). Translocation of the socially complex Black-eared Miner *Manorina melanotis*: a trial using hard and soft release techniques. *Pac. Conserv. Biol.* 8, 223–234. <https://doi.org/10.1071/pc030223>.
- Kmetova-Biro, E., Stoyanov, E., Ivanov, I., Peshev, H., Marin, S., Bonchev, L., Stoev, I., Stoyanov, G., Nikolova, Z., Vangelova, N., et al. (2021). Re-introduction of Griffon Vulture (*Gyps fulvus*) in the Eastern Balkan Mountains, Bulgaria - completion of the establishment phase 2010-2020. *Biodivers. Data J.* 9. <https://doi.org/10.3897/BDJ.9.e66363>.
- Liu, W., Liu, B., Liu, S., Zhang, J., Lin, S., and Zheng, G. (2016). Comparing post-release survival and habitat use by captive-bred Cabot's Tragopan (*Tragopan caboti*) in an experimental test of soft-release reintroduction strategies. *Avian Res* 776, 19–25. <https://doi.org/10.1186/s40657-016-0053-2>.
- Mihoub, J.-B., Princé, K., Duriez, O., Lécuyer, P., Eliotout, B., and Sarrazin, F. (2014). Comparing the effects of release methods on survival of the Eurasian black vulture *Aegypius monachus* reintroduced in France. *Oryx* 48, 106–115. <https://doi.org/10.1017/S0030605312000981>.
- Mitchell, A.M., Wellicome, T.I., Brodie, D., and Cheng, K.M. (2011). Captive-reared burrowing owls show higher site-affinity, survival, and reproductive performance when reintroduced using a soft-release. *Biol. Conserv.* 144, 1382–1391. <https://doi.org/10.1016/j.biocon.2010.12.019>.
- Nagata, H., and Yamagishi, S. (2016). Which factors affect post-release settlement of crested ibis *Nipponia nippon* on sado island, Japan? *Ornithol. Sci.* 15, 181–189. <https://doi.org/10.2326/osj.15.181>.
- Sasmal, I., Honness, K., Bly, K., McCaffery, M., Kunkel, K., Jenks, J.A., and Phillips, M. (2015). Release method evaluation for swift fox reintroduction at Bad River Ranches in South Dakota. *Restor. Ecol.* 23, 491–498. <https://doi.org/10.1111/rec.12211>.
- Saufi, S., Ravindran, S., Hamid, N.H., Abidin, C.M.R.Z., Ahmad, H., Ahmad, A.H., and Salim, H. (2020). Establishment of barn owls (*Tyto alba javanica*) in an urban area on penang island, Malaysia. *J. Raptor Res.* 54. <https://doi.org/10.3356/0892-1016-54.3.265>.
- Fritts, S.H., Mack, C.M., Smith, D.W., Murphy, K.M., Phillips, M.K., and Jimenez, M.D. (2001). Outcomes of hard and soft-releases of reintroduced wolves in central Idaho and the Greater Yellowstone Area. In *Large Mammal Restoration: Ecological and Sociological Challenges in the Twenty-First Century*, M. David, F.N. Reed, and L.L. Jeffery, eds. (Island Press), pp. 125–148.
- Kashetsky, T., Avgar, T., and Dukas, R. (2021). The cognitive ecology of animal movement: evidence from birds and mammals. *Front. Ecol. Evol.* 9. <https://doi.org/10.3389/fevo.2021.724887>.
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., and Smouse, P.E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad. Sci. USA* 105, 19052–19059. <https://doi.org/10.1073/pnas.0800375105>.
- Fuller, R., Venter, B., Venter, L., Venter, J., and Blue, S.K. (2021). Guidelines for the Rehabilitation, Release, and Post-release Assessment of Chacma Baboons (*Papio ursinus*) for Reinforcement. *Primate Conservation.* 35, 139–155.
- Tetzlaff, S.J., Sperry, J.H., and DeGregorio, B.A. (2019). Effects of antipredator training, environmental enrichment, and soft release on wildlife translocations: a review and meta-analysis. *Biol. Conserv.* 236, 324–331. <https://doi.org/10.1016/j.biocon.2019.05.054>.
- Resende, P.S., Viana-Junior, A.B., Young, R.J., and Azevedo, C.S. (2021). What is better for animal conservation translocation programmes: soft- or hard-release? A phylogenetic meta-analytical approach. *J. Appl. Ecol.* 58, 1122–1132. <https://doi.org/10.1111/1365-2664.13873>.
- Campbell-Thompson, E., Vargas, F.H., Watson, R.T., Muela, A., and Cáceres, N.C. (2012). Effect of sex and age at release on the independence of hacked harpy eagles. *J. Raptor Res.* 46, 158–167. <https://doi.org/10.3356/JRR-10-74.1>.
- López-López, P., Gil, J.A., and Alcántara, M. (2014). Post-fledging dependence period and onset of natal dispersal in bearded vultures (*Gypaetus barbatus*): new insights from GPS satellite telemetry. *J. Raptor Res.* 48, 173–181. <https://doi.org/10.3356/JRR-13-00072.1>.
- Naveda-Rodríguez, A., Campbell-Thompson, E., Watson, R.T., McCabe, J., and Vargas, F.H. (2022). Dispersal and space use of captive-reared and wild-rehabilitated harpy eagles released in central American landscapes: implications for reintroduction and reinforcement management. *Diversity* 14, 886. <https://doi.org/10.3390/d14100886>.
- Wallace, M.P., and Temple, S.A. (1987). Releasing captive-reared andean condors to the wild. *J. Wildl. Manag.* 51, 541–550. <https://doi.org/10.2307/3801266>.
- Woods, C.P., Heinrich, W.R., Farry, S.C., Parish, C.N., and Cade, T.J. (California Condors in the 21st Century. A. Mee and LS Hall. Washington, DC, and Cambridge, Massachusetts, USA, American Ornithologists Union, Nuttall Ornithological Club 2007;2:57-78). Survival and Reproduction of California Condors Released in Arizona.
- Mateo-Tomás, P., Olea, P.P., Jiménez-Moreno, M., Camarero, P.R., Sánchez-Barbudo, I.S., Rodríguez Martín-Doimeadios, R.C., and Mateo, R. (2016). Mapping the spatio-temporal risk of lead exposure in apex species for more effective mitigation. *Proc. Biol. Sci.* 283, 20160662. <https://doi.org/10.1098/rspb.2016.0662>.
- Gauld, J.G., Silva, J.P., Atkinson, P.W., Record, P., Acácio, M., Arkumarev, V., Blas, J., Bouten, W., Burton, N., Catry, I., et al. (2022). Hotspots in the grid: avian sensitivity and vulnerability to collision risk from energy infrastructure interactions in Europe and North Africa. *J. Appl. Ecol.* 59, 1496–1512. <https://doi.org/10.1111/1365-2664.14160>.
- Márquez, C., Vargas, J.M., Villafuerte, R., and Fa, J.E. (2013). Risk mapping of illegal poisoning of avian and mammalian predators. *J. Wildl. Manag.* 77, 75–83. <https://doi.org/10.1002/jwmg.424>.
- Smith, R.K., Dicks, L.V., Mitchell, R., and Sutherland, W.J. (2014). Comparative Effectiveness Research: The Missing Link in Conservation. *Conservation Evidence* 11, 2–62014.
- Ogada, D.L., Keesing, F., and Virani, M.Z. (2012). Dropping dead: causes and consequences of vulture population declines worldwide. *Ann. N. Y. Acad. Sci.* 1249, 57–71. <https://doi.org/10.1111/j.1749-6632.2011.06293.x>.
- Safford, R., Andevski, J., Botha, A., Bowden, C.G.R., Crockford, N., Garbett, R., Margalida, A., Ramírez, I., Shobrak, M., Tavares, J., and Williams, N.P. (2019). Vulture conservation: the case for urgent action. *Bird. Conserv. Int.* 29, 1–9. <https://doi.org/10.1017/S0959270919000042>.
- Le Gouar, P., Robert, A., Choisy, J.-P., Henriquet, S., Lécuyer, P., Tessier, C., and

- Sarrazin, F. (2008). Roles of survival and dispersal in reintroduction success of Griffon Vulture (*Gyps fulvus*). *Ecol. Appl.* 18, 859–872. <https://doi.org/10.1890/07-0854.1>.
33. van Overveld, T., Blanco, G., Moleón, M., Margalida, A., Sánchez-Zapata, J.A., de la Riva, M., and Donazar, J.A. (2020). Integrating vulture social behavior into conservation practice. *Condor* 122. duaa035. <https://doi.org/10.1093/condor/duaa035>.
34. Colomer, M.À., Oliva-Vidal, P., Jiménez, J., Martínez, J.M., and Margalida, A. (2020). Prioritizing among removal scenarios for the reintroduction of endangered species: insights from bearded vulture simulation modeling. *Anim. Conserv.* 23, 396–406. <https://doi.org/10.1111/acv.12549>.
35. Efrat, R., Hatzofe, O., Miller, Y., Mueller, T., Sapir, N., and Berger-Tal, O. (2022). Postrelease survival of captive-bred Egyptian Vultures is similar to that of wild-hatched Egyptian Vultures and is not affected by release age or season. *Ornithol. Appl.* 124. duab065. <https://doi.org/10.1093/ornithapp/duab065>.
36. Bildstein, K.L. (2022). *Vultures of the World* (Cornell University Press).
37. (2022). The IUCN Red List of Threatened Species IUCN.Red List Threat. Species. <https://www.iucnredlist.org/en>.
38. Dermody, B.J., Tanner, C.J., and Jackson, A.L. (2011). The evolutionary pathway to obligate scavenging in Gyps vultures. *PLoS One* 6, e24635. <https://doi.org/10.1371/journal.pone.0024635>.
39. Deinert, S., Ieronymidou, C., McRae, L., Burfield, I.J., Foppen, R.P., Collen, B., and Böhm, M. (2013). *Wildlife Comeback in Europe. The recovery of selected mammal and bird species* (London, UK: Zoological Society of), p. 313.
40. Hirschauer, M.T., Hannweg, C.G., Kemp, R., and Wolter, K. (2022). VulPro: an overview of Africa's vulture conservation centre. *Vulture News* 81, 9–24. <https://doi.org/10.4314/vulnew.v81i1.3>.
41. Bowden, C.G.R., Prakash, V., Ranade, S., Routh, A., Jakati, R.D., Cuthbert, R.J., Rahmani, A.R., Green, R.E., Prakash, N., and Parry-Jones, J. (2012). Conservation breeding for the future release of the critically endangered Asian GYPS vultures - progress of the programme in South Asia and why it is so important. *J. Bombay Nat. Hist. Soc.* 109, 43–45.
42. Anoop, N.R., Babu, S., Nagarajan, R., and Sen, S. (2020). Identifying suitable reintroduction sites for the White-rumped Vulture (*Gyps bengalensis*) in India's Western Ghats using niche models and habitat requirements. *Ecol. Eng.* 158, 106034. <https://doi.org/10.1016/j.ecoleng.2020.106034>.
43. Margalida, A., Colomer, M.À., and Sanuy, D. (2011). Can wild ungulate carcasses provide enough biomass to maintain avian scavenger populations? An empirical assessment using a bio-inspired computational model. *PLoS One* 6, e20248. <https://doi.org/10.1371/journal.pone.0020248>.
44. Kleinhans, C., and Willows-Munro, S. (2019). Low genetic diversity and shallow population structure in the endangered vulture, Gyps coprotheres. *Sci. Rep.* 9, 5536. <https://doi.org/10.1038/s41598-019-41755-4>.
45. Peshev, H., Grozdanov, A., Kmetova-Biro, E., Ivanov, I., Stoyanov, G., Tsiakiris, R., Marin, S., Marinković, S., Sušić, G., Lisichanets, E., et al. (2021). New insight into spatial ecology of Griffon Vulture (*Gyps fulvus*) on the Balkans provides opportunity for focusing conservation actions for a threatened social scavenger. *Biodivers. Data J.* 9, e71100. <https://doi.org/10.3897/BDJ.9.e71100>.
46. Jobson, B., Wolter, K., Jordan, L., Monadjem, A., and Rowcliffe, J.M. (2020). Home range and habitat selection of captive-bred and rehabilitated cape vultures *Gyps coprotheres* in southern Africa. *Oryx* 55, 1–6. <https://doi.org/10.1017/S0030605319000814>.
47. Under Griffon Wings. LIFE project website 2020. <http://www.lifeundergriffonwings.eu/it/index.html>.
48. Aresu, M., Rotta, A., Fozzi, A., Campus, A., Muzzeddu, M., Secci, D., Fozzi, I., De Rosa, D., and Berlinguer, F. (2021). Assessing the effects of different management scenarios on the conservation of small island vulture populations. *Bird. Conserv. Int.* 31, 111–128. <https://doi.org/10.1017/S0959270920000040>.
49. Aresu, M., Pennino, M.G., De Rosa, D., Rotta, A., and Berlinguer, F. (2022). Modelling the effect of environmental variables on the reproductive success of Griffon Vulture (*Gyps fulvus*) in Sardinia, Italy. *Ibis* 164, 255–266. <https://doi.org/10.1111/ibi.13012>.
50. Xirouchakis, S.M., Grivas, C., Andreou, G., and Georgopoulou, E. (2021). Home range size, space use and resource selection of griffon vultures in an insular environment. *J. Zool.* 314, 116–131. <https://doi.org/10.1111/jzo.12868>.
51. Arkumarev, V., Dobrev, D., Stamenov, A., Delchev, A., and Stoychev, S. (2021). Seasonal and age-specific dynamics of the Griffon Vulture's home range and movements in the Eastern Rhodopes. *Ornis Hung.* 29, 81–92. <https://doi.org/10.2478/orhu-2021-0021>.
52. Morant, J., Arrondo, E., Sánchez-Zapata, J.A., Donazar, J.A., Cortés-Avizanda, A., De La Riva, M., Blanco, G., Martínez, F., Oltra, J., Carrete, M., et al. (2023). Large-scale movement patterns in a social vulture are influenced by seasonality, sex, and breeding region. *Ecol. Evol.* 13, e9817. <https://doi.org/10.1002/ece3.9817>.
53. Delgado-González, A., Cortés-Avizanda, A., Serrano, D., Arrondo, E., Duriez, O., Margalida, A., Carrete, M., Oliva-Vidal, P., Sourp, E., Morales-Reyes, Z., et al. (2022). Apex scavengers from different European populations converge at threatened savannah landscapes. *Sci. Rep.* 12, 2500. <https://doi.org/10.1038/s41598-022-06436-9>.
54. Margalida, A., Oliva-Vidal, P., Llamas, A., and Colomer, M.À. (2018). Bioinspired models for assessing the importance of transhumance and transboundary management in the conservation of european avian scavengers. *Biol. Conserv.* <https://doi.org/10.13039/501100009410>.
55. Berlinguer, F., Carta, S., and Terraube, J. (2021). ACTION A.2 Assess the Current and Potential Food Availability for Vultures in Sardinia. LIFE19NAT/IT/000732 Project.
56. Alarcón, P.A.E., and Lambertucci, S.A. (2018). A three-decade review of telemetry studies on vultures and condors. *Mov. Ecol.* 6, 13. <https://doi.org/10.1186/s40462-018-0133-5>.
57. Arkumarev, V., Dobrev, D., Stamenov, A., Terziev, N., Delchev, A., and Stoychev, S. (2021). Seasonal dynamics in the exploitation of natural carcasses and supplementary feeding stations by a top avian scavenger. *J. Ornithol.* 162, 723–735. <https://doi.org/10.1007/s10336-021-01865-1>.
58. Margalida, A., Carrete, M., Hegglin, D., Serrano, D., Arenas, R., and Donazar, J.A. (2013). Uneven large-scale movement patterns in wild and reintroduced pre-adult bearded vultures: conservation implications. *PLoS One* 8, e65857. <https://doi.org/10.1371/journal.pone.0065857>.
59. Cortés-Avizanda, A., Blanco, G., DeVault, T.L., Markandya, A., Virani, M.Z., Brandt, J., and Donazar, J.A. (2016). Supplementary feeding and endangered avian scavengers: benefits, caveats, and controversies. *Front. Ecol. Environ.* 14, 191–199. <https://doi.org/10.1002/fee.1257>.
60. Potts, J.R., and Börger, L. (2023). How to scale up from animal movement decisions to spatiotemporal patterns: an approach via step selection. *J. Anim. Ecol.* 92, 16–29. <https://doi.org/10.1111/1365-2656.13832>.
61. Genero, F., Franchini, M., Fanin, Y., and Filacorda, S. (2020). Spatial ecology of non-breeding Eurasian Griffon Vultures *Gyps fulvus* in relation to natural and artificial food availability. *Hous. Theor. Soc.* 67, 53–70. <https://doi.org/10.1080/00063657.2020.1734534>.
62. Onrubia, A. (2021). *Eurasian griffon vulture Gyps fulvus. In Migration Strategies of Birds of Prey in Western Palearctic* (CRC Press).
63. Nathan, R., Spiegel, O., Fortmann-Roe, S., Harel, R., Wikelski, M., and Getz, W.M. (2012). Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *J. Exp. Biol.* 215, 986–996. <https://doi.org/10.1242/jeb.058602>.
64. Zuberogoitia, I., González-Oreja, J.A., Martínez, J.E., Zabala, J., Gómez, I., and López-López, P. (2013). Foraging movements of Eurasian griffon vultures (*Gyps fulvus*): implications for supplementary feeding management. *Eur. J. Wildl. Res.* 59, 421–429. <https://doi.org/10.1007/s10344-012-0687-2>.
65. Peshev, H., Stoyanov, E., Parvanov, D., and Grozdanov, A. (2018). Seasonal and spatial dynamics of the population of the griffon vulture *Gyps fulvus* (hablizl, 1783)

- (aves: accipitridae) in Southwestern Bulgaria. *Acta Zool. Bulg. Suppl.* 12, 67–75.
66. Hribšek, I., Plečaš, M., Skorić, S., and Marinković, S. (2021). First description of movement and ranging behavior of the Griffon vulture (*Gyps fulvus*) from Serbia using GPS satellite tracking. *Arch. Biol. Sci.* 73, 185–195. <https://doi.org/10.2298/ABS201210013H>.
 67. Monsarrat, S., Benhamou, S., Sarrazin, F., Bessa-Gomes, C., Bouten, W., and Duriez, O. (2013). How predictability of feeding patches affects home range and foraging habitat selection in avian social scavengers? *PLoS One* 8, e53077. <https://doi.org/10.1371/journal.pone.0053077>.
 68. Cramp, K.E.L. Simmons, and C.M. Perrins, eds. (1982). *Handbook of the Birds of Europe, the Middle East and North Africa, 1982–1994* (Oxford University Press).
 69. Berger-Tal, O., and Saltz, D. (2014). Using the movement patterns of reintroduced animals to improve reintroduction success. *Curr. Zool.* 60, 515–526. <https://doi.org/10.1093/czoolo/60.4.515>.
 70. Efrat, R., Hatzofe, O., Miller, Y., and Berger-Tal, O. (2020). Determinants of survival in captive-bred Griffon Vultures *Gyps fulvus* after their release to the wild. *Conserv. Sci. Pract.* 2, e308. <https://doi.org/10.1111/csp2.308>.
 71. Almaraz, P., Martínez, F., Morales-Reyes, Z., Sánchez-Zapata, J.A., and Blanco, G. (2022). Long-term demographic dynamics of a keystone scavenger disrupted by human-induced shifts in food availability. *Ecol. Appl.* 32, e2579. <https://doi.org/10.1002/eap.2579>.
 72. Murn, C., and Botha, A. (2018). A clear and present danger: impacts of poisoning on a vulture population and the effect of poison response activities. *Oryx* 52, 552–558. <https://doi.org/10.1017/S0030605316001137>.
 73. Elsbeth McPhee, M. (2004). Generations in captivity increases behavioral variance: considerations for captive breeding and reintroduction programs. *Biol. Conserv.* 115, 71–77. [https://doi.org/10.1016/S0006-3207\(03\)00095-8](https://doi.org/10.1016/S0006-3207(03)00095-8).
 74. Utt, A.C., Harvey, N.C., Hayes, W.K., and Carter, R.L. (2008). The effects of rearing method on social behaviors of mentored, captive-reared juvenile California condors. *Zoo Biol.* 27, 1–18. <https://doi.org/10.1002/zoo.20151>.
 75. Pynegar, E.L., Gibbons, J.M., Asquith, N.M., and Jones, J.P.G. (2021). What role should randomized control trials play in providing the evidence base for conservation? *Oryx* 55, 235–244. <https://doi.org/10.1017/S0030605319000188>.
 76. Bildstein, K.L., Bechard, M.J., Farmer, C., and Newcomb, L. (2009). Narrow sea crossings present major obstacles to migrating Griffon Vultures *Gyps fulvus*. *Ibis* 151, 382–391. <https://doi.org/10.1111/j.1474-919X.2009.00919.x>.
 77. Ferrer, M., Alloing, A., Baumbush, R., and Morandini, V. (2022). Significant decline of Griffon Vulture collision mortality in wind farms during 13-year of a selective turbine stopping protocol. *Glob. Ecol. Conserv.* 38, e02203. <https://doi.org/10.1016/j.gecco.2022.e02203>.
 78. Grainger Hunt, W., David Wiens, J., Law, P.R., Fuller, M.R., Hunt, T.L., Driscoll, D.E., and Jackman, R.E. (2017). Quantifying the demographic cost of human-related mortality to a raptor population. *PLoS One* 12, e0172232. <https://doi.org/10.1371/journal.pone.0172232>.
 79. Bodey, T.W., Cleasby, I.R., Bell, F., Parr, N., Schultz, A., Votier, S.C., and Bearhop, S. (2018). A phylogenetically controlled meta-analysis of biologging device effects on birds: deleterious effects and a call for more standardized reporting of study data. *Methods Ecol. Evol.* 9, 946–955. <https://doi.org/10.1111/2041-210X.12934>.
 80. Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J., and Wilmers, C.C. (2007). LoCoH: nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS One* 2, e207. <https://doi.org/10.1371/journal.pone.0000207>.
 81. Signer, J., Fieberg, J., and Avgar, T. (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecol. Evol.* 9, 880–890. <https://doi.org/10.1002/ece3.4823>.
 82. Wood, S.N. (2017). *Generalized Additive Models: An Introduction with R, Second edition* (CRC Press/Taylor & Francis Group).
 83. Wood S.Package ‘mgcv’. R package version 2015;29:729.
 84. Liaw, A., and Wiener, M. (2022). *Classification and Regression by randomForest*. *R News* 2, 18–22.
 85. Bartoń, K. (R package version 2022. <https://cran.r-project.org/package=MuMIn>). *MuMIn: Multi-Model Inference*.
 86. Symonds, M.R.E., and Moussalli, A. (2011). A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike’s information criterion. *Behav. Ecol. Sociobiol.* 65, 13–21. <https://doi.org/10.1007/s00265-010-1037-6>.
 87. Kruschke, J.K., and Liddell, T.M. (2018). The Bayesian New Statistics: hypothesis testing, estimation, meta-analysis, and power analysis from a Bayesian perspective. *Psychon. Bull. Rev.* 25, 178–206. <https://doi.org/10.3758/s13423-016-1221-4>.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Griffon vultures' GPS location and monthly home range size datasets and R code used for analyses	Mendley Data repository	https://data.mendeley.com/datasets/94kjxx4ddg/2

RESOURCE AVAILABILITY

Lead contact

Further information and requests for data and code should be directed to and will be fulfilled by the lead contact, dr. Rudy Brogi (rbrogi@uniss.it).

Materials availability

This study did not use newly generated materials or reagents.

Data and code availability

- Griffon vultures' GPS location and monthly home range size datasets have been deposited on the Mendley Data repository and are publicly available at <https://data.mendeley.com/datasets/94kjxx4ddg/2>.
- The code used to analyze the variability of monthly home ranges is deposited together with the raw datasets as indicated above.
- Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

METHOD DETAILS

Release of the individuals

With permission from the National Institute for Environmental Protection and Research (ISPRA, representing the Ministry for the Environment) and the Sardinian Regional Department for the Environment, a total of 76 Griffon vultures were released between 2016 and 2021. Animals were released within the LIFE Under Griffon Wings project (LIFE14 NAT/IT/000484), funded by the European Commission through the LIFE program.

Released individuals had a different origin, coming from wildlife rescue centers in Spain (n = 57), captive breeding programs in the Netherlands (n = 5), Spain (n = 1) and Germany (n = 1), as well as a wildlife rescue center in Sardinia (n = 12). However, from a biogeographical viewpoint, animals also had different geographical origin, coming from the local Sardinian population (n = 12) or from the outside (n = 64).

Animals were released using both soft and hard release, on the basis of human resources available to run acclimatization aviaries, and on the predictability of their arrival. Hard-released individuals had all been recovered from the wild, and then released after a rehabilitation period, as it was impossible to plan the functioning of an acclimatization aviary at the last moment. In soft release, individuals spent a period of time at an aviary, then, after a period of acclimatization, the door of the aviary was left open and individuals were free to leave. The aviary in Porto Conte Regional Park was built with a modular structure in galvanized iron, 27 × 8 meters big, with a minimum height of 3 meters and a maximum height of 4.5 meters, closed with rhomboidal galvanized metal mesh equipped with flap windows with 180° opening in the front part of the aviary; access for cleaning and for the supply of food and water was ensured through three side doors. The aviary in Monte Minerva had a supporting structure, made of galvanized iron, 4.5 meters high and with a base of 10 meters × 8 meters; it was closed with a rectangular galvanized metal mesh, anchored to the main structure with metal staples. The base part of the aviary was shielded with a shading mesh. To access into the aviary for cleaning and for the supply of water and food two doors were built on the side walls of the aviary (facing north and south), while in the front part, facing east, two 1-meter-wide doors were built to

allow the easy and natural release of the griffon vultures. In both aviaries several wood perches were installed. Birds had free access to water and they were provided with food once per week, mostly sheep. Nearby, aviaries had a feeding station that was regularly provisioned with sheep carcasses. While some individuals were kept in an aviary built in Monte Minerva for 3 months (hereinafter named “short acclimatization”, $n = 50$), others were kept in an aviary built in the Porto Conte Regional Park for 15 months (hereinafter named “long acclimatization”, $n = 14$). Finally, a third group of individuals (hereinafter named “no acclimatization”, $n = 12$) was subjected to hard release, being put in transport boxes and brought to a site close to the Griffon vulture colony of Bosa, where they were immediately released (Figure 1). These individuals had been recovered from the wild in Sardinia and rehabilitated in the aviary of a wildlife rescue center for a period of 2–4 months, before being subjected to hard release.

Therefore, griffons from the “no acclimatization” group had always been born in the wild, and came from the local Sardinian population, while individuals from “short” and “long acclimatization group” were born either in the wild or in captivity, but always came from other griffon vulture populations.

Environmental conditions at these three sites are similar, as the vegetation is constituted mainly by Mediterranean maquis, Holm oak (*Quercus ilex*) and Cork oak (*Quercus suber*) woodlands and planted *Pinus* sp. woods, and there are large areas of pastures used for extensive livestock rearing. Moreover, around the three areas there are many cliffs, mostly on calcareous and volcanic rock substrate. In the study area, there was a uniform network of farm feeding stations (Figure 1) and two centralized feeding stations, that ensured to griffons from the three groups homogeneous trophic resources across the landscape.

Prior to their release, all individuals were fitted with PIT tags, and with an ISPRA engraved metal ring around one tarsus and a plastic ring on the other tarsus, to facilitate long-distance identification. Moreover, to facilitate individual recognition during fieldwork, the remiges or the rectrices were bleached, with a characteristic pattern for each individual.

Post release monitoring

Out of 76 vultures that were released, 43 were equipped with solar powered GPS/GSM and VHF transmitters. Devices were attached to individuals with a Teflon leg-loop harness, constituted by three assembled strings (round silicone cord 2 mm + tubular teflon ribbon 0.25” and 0.44”). This structure was recommended by the Vulture Conservation Foundation. Overall, 39 vultures were tagged with Ecotone GPS/GSM transmitters (2 with Ecotone cDuck model, 25 with Ecotone Crex model, 7 with Ecotone Saker model and 5 with Ecotone Skua model), and 4 vultures with Ornitela 3G_50g transmitters. Ecotone transmitters weighed 33 grams, while Ornitela transmitters weighed 50 grams. The transmitter harness and rings did not exceed 3% of the total body mass of a bird, following recommended limits to avoid adverse effect on individual behavior and fitness.⁷⁹ Transmitters were fitted by following best practices to safeguard animal welfare, with the head of each individual that was covered to minimize stress and the manipulation time that was reduced below ten minutes.

Transmitters were programmed to acquire a GPS fix with different time intervals (Table 1), during the day, although in winter the frequency of data acquisition was lower due to scarce solar charging. When a tagged individual did not move for more than 24 hours, field technicians tried to locate it on the field, to establish its eventual death and the eventual carcass was subjected to autopsy, to determine the cause of death (Table 1).

Movement data were collected soon after release, and for the next three years, depending on transmitters lifespan. Data collected for the first two years of the project were used to acquire information on Griffon vulture movements. As for survival, we combined all available information until January 2023, including GPS fix, individual resightings from camera trapping and direct observations, altogether with recoveries of dead griffon vultures.

QUANTIFICATION AND STATISTICAL ANALYSES

Monthly home range computation and dataset preparation

Monthly home ranges were computed through the Local Convex Hull (hereinafter “LoCoH”, sensu Getz et al.⁸⁰). LoCoH adopts the minimum convex polygon method on spatially localized data and it adopts kernel analysis with a form that arises from the data.⁸⁰ To compare findings from different individuals,

having different GPS models with a different intensity of data acquisition, we adopted a common sampling rate of 1 fix every 2 hours. LoCoH also allowed to use different GPS transmitters, or to have an irregular data acquisition due to low power input from solar panels, as the method does not require location errors, or the continuous acquisition of locations. LoCoH were fitted through the “hr_locoh” function of the “amt” package of the software R.⁸¹ We considered only those individual months with at least 60 recorded spatial locations. This criterion led us to retain a final sample of 38 tagged individuals.

For each month and each individual we measured the surface covered by each monthly home range (hereinafter, “home range size”) and assigned to each record some variables that were specific to a certain individual or the release session, to use them as predictors of home range size, namely: *i*) sex, a categorical predictor assuming three possible levels (female, male and unknown), *ii*) age, calculated as the number of months elapsed since the 1st April of the individual year of birth to the first day of the reference month, *iii*) month of the year, *iv*) time after release, calculated as the number of months since the date when each individual was released to the first day of the reference month, *v*) release strategy, a categorical predictor referred to the length of the acclimatization period underwent before being released (“no acclimatization”, “short acclimatization” and “long acclimatization”, as specified in the previous section), *vi*) the origin of released individuals, a categorical predictor distinguishing between individuals that had been bred in captivity or born in the wild, *vii*) the geographical provenience, a categorical predictor with two levels (“local” for individuals from the Sardinian population and “non-local” for individuals from external populations), *viii*) the number of available spatial locations, referred to the number of fixes acquired by GPS/GSM transmitters in the reference month.

Statistical analyses

We adopted GAMMs⁸² to model the monthly home range size of individual griffon vultures according to chosen predictors, while accounting for inter-individual variability through a random term. Models were fitted with the “mgcv” package⁸³ in the statistical software R.

Before they were included in the model predictors were tested for: *i*) collinearity by converting all of them to continuous categorical covariates and calculating the Pearson’s correlation coefficient (variables were deemed to be collinear if coefficients were above 0.7) and by *ii*) calculating the Variance Inflation Factor (VIF, deemed to indicate collinearity if higher than 3). As we detected a non-negligible collinearity between the release strategy and the geographical provenience of each bird, we performed a Random Forest algorithm (with the “randomForest” package in R⁸⁴) and discarded the geographical provenience of each individual, on the basis of its low potential to explain variability in home range size. Indeed, griffons with a different release strategy also had inherent differences in the geographical origin and this second effect was captured by the covariate measuring the release strategy adopted for each individual.

The sex and age of each individual were treated as categorical and continuous predictors, respectively, while the month of the year was included as a circular predictor, to account the continuity between December and January. Time after release was treated as having an interactive effect with the release strategy and the origin of each individual. However, to avoid collinearity among the release strategy and the origin of each individual, during model selection we considered only those models including a maximum of one interaction term. Release strategy and the individual origin were also included as categorical predictors in the full model. Finally, the number of available spatial locations was inserted as a continuous control variable, in order to prevent potential bias related to sample size. We adopted the “dredge” function of the “MuMIn” package in R⁸⁵ to create a complete set of models with all possible predictor combinations, then we selected the best model by keeping the one with the lowest value of the Akaike’s Information Criterion (hereinafter, AIC), with a maximum threshold of 2 among competing models.⁸⁶ As model averaging is not possible for GAMMs, because splines do not have coefficients which could be averaged, we just selected a best candidate model, rather than averaging models with similar performances. Then we used conditional effect plots to compare the association between model predictors and the size of monthly home ranges, for the best candidate models.

To establish whether the three release strategies affected the mortality of Griffon vultures, we compared the number of individuals that had survived up to five years of age. As the restocking initiative aimed to increase population size and the number of breeding couples in Sardinia, this age was chosen as we wanted to quantify the number of griffon vultures that reached the age of first reproduction. For each

individual, based on its expected date of birth, we quantified the date in spring at which the first reproduction was deemed to occur. Then, since reproduction begins with nuptial flights between December and January, we classified griffon vultures as having reached sexual maturity in case they were alive in the December of the year before their first potential reproduction. We discarded 4 griffons, which were expected to reach sexual maturity after the time when this study was conducted, and so we quantified survival for 34 griffon vultures (Table 1). We did not carry out any statistical comparison (e.g. through null-hypothesis testing), between the three groups, as p-values are often flawed and misleading for observational data,⁸⁷ and our low sample size would have led us to have a low statistical power.