

Modelling the effect of environmental variables on the reproductive success of Griffon Vulture (Gyps fulvus) in Sardinia, Italy

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Old World vultures are experiencing dramatic population declines and now are among the species most threatened with extinction. Understanding the environmental variables that can influence the reproductive indexes of vulture populations can facilitate both habitat and species management. The aim of this study was to identify which environmental variables primarily affect the breeding successes of the Griffon Vulture Gyps fulvus in northern Sardinia by applying a Bayesian hierarchical model. A unique dataset of reproductive records (197 nests monitored over 39 years for a total of 992 breeding records) was used. Eight environmental and topographical variables describing the habitat at the nesting sites were considered as potential predictors of breeding success. These included mean annual temperature, mean annual precipitation, isothermality, elevation, the normalized difference vegetation index, wind speed, and the aspect and slope of the land surface. In addition, we also considered the effect of human disturbance and the type of nest. According to our best model, the probability of successfully raising a chick in Griffon Vultures was higher in nests exposed to a high wind speed, not covered by natural shelters, where the vegetation was mostly represented by shrub and pastures, with low human disturbance and in years with low rainfall. This model will be useful for management of the breeding habitat and to identify the area most suitable for Griffon Vulture reproduction. This information is crucial for programming conservation measures aimed at enlarging the area of occupancy of the species.

Keywords: cliff-nesting raptors, human disturbance, nest-sites, obligate scavengers, productivity.

A wide range of factors can influence breeding success in raptors in both the short and the long term. These factors are frequently complex and often specific to species, populations and habitats (Paviour 2013). Several studies have shown that in raptors, breeding success is highly dependent on the quality of their breeding territories and is

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influenced by local geomorphological, latitudinal as well as weather conditions (Amato et al. 2014, Anctil et al. 2014, Zabala & Zuberogoitia 2014). Understanding the factors which drive breeding performance is of crucial significance to preserve and monitor raptor populations. Therefore, several studies have addressed the effects of environmental variables on the reproductive processes of endangered raptors (as outlined in a meta-analysis study by Moreno-Opo et al. 2012).

Keystone species such as the 16 species of Old World vultures are experiencing dramatic population declines and now are among the species most threatened with extinction (Ogada *et al.*, 2012a, Safford *et al.*, 2019, Santangeli *et al.*, 2019). As the sole obligate scavengers, vultures comprise a unique functional guild among vertebrates and play an unparalleled role in maintaining ecosystem balance (Buechley & Sekercioglu 2016).

The Griffon Vulture Gyps fulvus, as a cliffnesting raptor, is constrained by nest-site availability that limits its breeding densities and ultimately its persistence in a territory (Fernandez *et al.* 1998, Mateo-Tomás & Olea 2011, Tapia & Zuberogoitia 2018). Griffon Vultures are colonial large vultures that feed mainly on carcasses of medium-sized and large animals (Cortés-Avizanda *et al.* 2014, Campbell 2015, Donázar *et al.* 2016). They forage in flocks and roost and nest on steep cliffs forming colonies ranging in size from a few pairs to several hundred nests; solitary breeding pairs also occur (Cramp 1985, Mundy 1992).

The Griffon Vulture population in Europe is increasing significantly and is estimated at 32 400-34 400 pairs (BirdLife International 2018), with Spain alone accounting for an estimated 30 000 pairs (SEOBirdlife 2018). Its range has also expanded thanks to reintroduction projects in France, the Italian peninsula and the Balkans (Deinet et al., 2013). However, in Italy the Griffon Vulture is still included on the Red List as 'Near Threatened' (Gustin et al. 2019), with the last natural population persisting on the island of Sardinia. In a population viability analysis of the Griffon Vulture population in Sardinia it has been shown that it transitioned rapidly from low to high probability of extinction when breeding propensity and reproductive success decreased (Aresu et al. 2020). Thus, understanding the environmental variables that can influence the reproductive indexes of the population would facilitate both habitat and species management.

Starting from these premises, the aim of this study was to identify which environmental variables mostly affect the breeding successes of the Griffon Vulture in northern Sardinia by applying a Bayesian hierarchical model (BHM). The variables considered included human disturbance, the type of nest, mean annual temperature and precipitation, isothermality, elevation, vegetation coverage, wind speed, and the aspect and slope of the land surface. Bayesian methods have several advantages

over classical approaches. Indeed, whereas frequentist inference model parameters are treated as fixed variables. in Bayesian inference they are considered to be random (Costa et al. 2017). Furthermore, Bayesian statistics are able to integrate all types of uncertainties using probability as the exclusive metric. By combining uncertainty into the data (expressed by likelihood) with extra-data information (expressed by prior distributions), posterior probability distributions for all unknown quantities of interest (i.e. parameters) are built using Bayes' theorem (Banerjee et al. 2014). Intuitively quantifying uncertainty is fundamentally important for decision-makers and, to achieve more realistic scenarios, complex ecological models can be built straightforwardly by specifying successive modelling levels (also known under hierarchical models). We used a unique dataset of reproductive records (197 nests monitored over 39 years for a total of 992 breeding records). The model developed could help conservationists and decision-makers to optimize habitat management and to identify the most suitable area for Griffon Vulture reproduction. We hypothesize that human disturbance, the type of nest and climatic conditions in the nesting area, such as precipitation and wind speed, could affect the breeding success of Griffon Vultures.

METHODS

Nest data

The breeding success of the Griffon Vulture was defined as a binary variable that assumes a value of 1 when nest fate was successful (nests that fledged at least one juvenile) or 0 if it failed (nests that did not fledge a juvenile).

Griffon Vultures are monogamous, and breeding pairs give birth to only one chick per year. The incubation period is approximately 55 days, and both sexes incubate, feed, brood and shade the nestling (Cramp 1985, Xirouchakis 2010). The young leave the nest at an age of 110–120 days and continue to receive food from their parents for about 3 months after fledging (Schenk *et al.* 2008, Yaniv-Feller *et al.* 2018). During the study period (1979–2018), 197 nests were monitored, all of them located in the western part of Sardinia (Fig. 1), for a total of 992 breeding attempts monitored. Research efforts were focused on monitoring all the breeding pairs of the Griffon Vulture



Figure 1. Location map of the studied area. Black dots indicate the observed nests from 1979 to 2018.

population in Sardinia, except those belonging to a very small colony located in north-western Sardinia (only two territorial pairs from 2000 onwards).

Fieldwork in each breeding season was carried out between December and August to observe the entire breeding period of the species (courtship flights, building nest, egg-laying, brooding, hatching, feeding of the chicks and the first flight of juveniles). Observations were carried out from vantage points or by rubber dinghy at 300–600 m from the breeding sites with binoculars (8 × 42, 10 × 50) and telescopes (20 – 60 × 80). Each nest was visited 6–10 times during each year, and at least once every 40 days. A nest was classified as occupied if a territorial pair was observed in mating behaviour (display flights, nest construction/repair, mating). Nests were distributed in 16 colonies (12.9 \pm 3.6 nests per colony, mean \pm se; range 2–60) and six isolated sites. A cliff was

considered as a colony if it was occupied by at least two pairs and was at least 1000 m away from its closest neighbour (García-Ripollés *et al.* 2005).

Jointly with breeding success, we collected information about the geographical location (latitude and longitude), the level of human disturbance and the type of nest. The level of human disturbance was assigned depending on the accessibility of the nests and on the presence of paved and unpaved roads according to the following scoring system: 0: nest not accessible, no paved and unpaved roads in a 1-km radius of the nest; 1: nest not accessible, presence of unpaved roads in a 1km radius of the nest; 2: nest not accessible, presence of paved and unpaved roads in a 1-km radius of the nest; 3: nest accessible, presence of unpaved roads in a 1-km radius of the nest; 4 nest accessible, presence of paved and unpaved roads in a 1km radius of the nest.

The type of nest was described considering three categorical variables with three levels:

- 1 *Covered terrace*: open on three sides with a rocky overhang above the nest; a total of 22 nests of 197 (11.2%) belonged to this category, and this type of nest was occupied 91 times during the study period.
- 2 Not covered terrace: open on three sides with no rocky overhang above the nest; a total of 38 nests of 197 (19.3%) belonged to this category, and this type of nest was occupied 194 times during the study period.
- 3 *Cavity*: located in a natural cavity; a total of 137 nests of 197 (69.5%) belonged to this category, and this type of nest was occupied 707 times during the study period.

During the study period, supplementary feeding sites were not present continuously, only in limited periods. In particular, one feeding site was lightly provisioned between 1986 and 1989 and from 1994 to 1995, and another site from 2002 to 2004 and from 2007 to 2009. Thereafter, more feeding sites were activated only from 2017 onwards. Therefore, no predictable food sources were present during the study period and this variable could not be included in the model.

Environmental variables

Eight climatic and topographical variables describing the habitat at the nesting sites were considered as potential predictors of the breeding success of the Griffon Vulture. These included mean annual temperature (MT in °C), mean annual precipitation (MP in mm), isothermality (I in Joules per Kelvin, J/K; this quantifies how large the day-tonight temperatures oscillate relative to the summer-to-winter oscillations and is derived by calculating the ratio of the mean diurnal range to the annual temperature range), elevation (E in m), the normalized difference vegetation index (NDVI), wind speed (W in m/s), and the aspect and slope of the land surface (Fig. S1).

In particular, MT, MP, I, E and W were extracted as yearly means from the WorldClim database version 2 (Fick & Hijmans 2017) with a spatial resolution of 0.008×0.008 decimal degrees (corresponding to ~800 m).

The slope and the aspect of the land were derived from the elevation map using the *terrain* function of the *raster* package (Hijmans *et al.* 2014) in R software (R Development Core Team, 2017). This function measures the slope and aspect as the variation in the three-dimensional orientation of the grid cells within a neighbourhood. Aspect works as an indicator of land complexity by highlighting minor variations in the topography. Aspect values are scaled between 0 (no terrain variation) and 360 (complete terrain variation). This method effectively captures the variability and slope of the substrata in a single measurement (Sappington *et al.* 2007).

The NDVI is a quantitative index of greenness where 0 represents minimal or no greenness and 1 represents maximum greenness. NDVI is often used as a quantitative proxy measure of vegetation health, cover and phenology (life-cycle stage) over areas. Negative values of NDVI (values approaching -1) correspond to water and artificial materials (concrete, asphalt). Values close to zero (-0.1 to 0.1) generally correspond to barren areas of rock, sand or snow. Lastly, low, positive values represent shrub and pastures (approximately 0.2-0.4), and high values approaching 1 indicate dense vegetation (forest) (Savchenko et al. 2020). Annual maps of NDVI were extracted using the gimms R-package (Detsch 2018), which retrieves information about AVHRR GIMMS NDVI3g files currently available online.

All variables were aggregated at 0.008×0.008 degrees (corresponding to ~ 800 m) of spatial resolution and were explored for correlation, collinearity, outliers and missing data before their use in the models (Zuur *et al.* 2009). Variables with a

variance inflation factor (VIF) > 5 and a correlation > 0.80 were not included together in the models (Hahlbeck *et al.* 2017, Lezama-Ochoa *et al.* 2019, Lopez *et al.* 2020) (Figs S2–S4).

Finally, after an exploratory analysis, in order to better interpret the direction (positive or negative) and magnitudes (effect sizes) of parameter estimates in relation to the others, the explanatory variables were standardized (difference from the mean divided by the corresponding standard deviation) (Gelman 2008).

Statistical analysis

BHM was applied to identify which environmental variables mostly affect the breeding success of the Griffon Vulture in northern Sardinia. In addition to the environmental and topographical variables, we included in the models the factors 'type of nests' and 'level of human disturbance' as well as spatial-temporal effects to account for the rest of the data variability. In particular, the response variable Y_i represents the species breeding success (1 being yes; 0 being no) at each sighting location *i*.

Consequently, the conditional distribution of the data is $Y_i \sim \text{Ber}(\pi_i)$, where π_j is the probability of the species breeding success i (i = 1, ..., n), assuming that observations are conditionally independent given π_i . These probabilities were modelled using the following hierarchical model:

$$Y_i \sim Ber(\pi_i),$$

 $logit(\pi_i) = \alpha + X\beta + W_i + Z_k$

where α is the intercept, β is the vector of regression parameters and X is the matrix of the explanatory covariates. As the exploratory analysis revealed nonlinear relationships between environmental variables and breeding success, second-order random walk (RW2) latent models were used. RW2 performs as a Bayesian smoothing spline (Fahrmeir & Lang 2002) and thus this model can be seen as a general additive mixed model (GAMM). To account for interannual variability, the temporal variable 'Year' was fitted using an autoregressive model of order 1 (AR1). A remaining potential source of variation on breeding success could be due to intrinsic differences among nests due to unobserved characteristics. Consequently, we included a nest effect as a random effect Z_k . Similarly, differences could be due to the spatial variability, and thus a spatial random effect (i.e. latitude and longitude of the sampling observations) was included in the model. Finally, the 'type of nests' and 'anthropic effect' were fitted as factors. Effects of categorical variables were considered for k - 1 of the k factor levels, with the remaining one being considered as the base level. Hence the estimated coefficient of each factor level will indicate the deviation with respect to the value of the base level.

Following Bayesian reasoning, all model parameters were considered as random variables where their estimation was achieved through marginal posterior distributions. To do so, we relied on the integrated nested Laplace approximation (INLA; Rue *et al.* 2009) methodology and respective Rpackage (www.r-inla.org) within the R platform to estimate all fixed and random parameters.

Vague Gaussian priors centred at zero with a fixed large precision of 0.001 were assigned for all fixed-effect parameters as recommended by Held *et al.* (2010). These priors are designed to have little influence on the posterior distribution and thus the results are essentially similar to the frequentist approach. For RW2 effects, default Gamma prior distributions on the precision with parameters 1 and 0.00005 was used.

Model selection

Model selection was held following a forwardstepwise approach where the null model (containing only the intercept) was used as a base model and covariates were added subsequently. To evaluate the goodness-of-fit and predictive quality of the models, we considered the Watanabe information criterion (WAIC; Watanabe 2010) and the averaged logarithmic score of the conditional predictive ordinate (LCPO; Roos & Held 2011). Specifically, lower WAIC and LCPO values indicate better fit and predictive quality, respectively. Thus, the best model (and most parsimonious) was selected based on a compromise between the low WAIC and LCPO values (Fonseca & Ferreira 2017). Indeed, the LCPO is a 'leave-one-out' cross-validation index to assess the predictive power of the model. A relevant increase from one model to another is justified with differences equal to or greater than five units in both criteria.

Finally, functional responses between the selected variables and the observed values were plotted using the *ggplot2* package (Wickham 2016) of R software.

All the R codes used for the analysis can be found at https://github.com/MgraziaPennino/ Breeding_success_of_Griffon_Vulture

RESULTS

A positive trend was observed from 2008, with the highest numbers in both occupied and successful nests recorded from 2015 onwards (Fig. 2).

The best-fit BHM included as relevant predictors for the breeding success of the Griffon Vulture wind speed, precipitation P, NDVI, anthropic effect, type of nest, the temporal AR1 component and the random spatial effect. All other variables were less relevant as values of WAIC (Table 1). Note that in terms of prediction capability (i.e. LCPO), all models were very similar.

Wind speed showed a positive relationship with breeding success (Fig. 3). In contrast, precipitation and NDVI showed a negative relationship, meaning that a lower breeding success is expected with higher precipitation and NDVI values (Fig. 3). Breeding success appeared to be higher when little or no human disturbance was present, and decreased as disturbance increased (Fig. 3). The type of nest highlighted that nests in cavities have the lowest breeding success and not covered terrace nests had the highest success (Fig. 3).



Figure 2. Number of nests monitored from 1979 to 2018.

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No.	Model	WAIC	LCPO
1	β_0 + W + Y + MP + TN + A + WS + NDVI + ID	2569	0.20
2	β_0 + WS + MP + NDVI + A + TN + Y + W	2901	0.22
3	β_0 + WS + I + S + W + A + Y	2905	0.23
4	β_0 + As + E + TN + A + Y	2938	0.23
5	β_0 + WS + As + E + W + A + Y	2941	0.23
6	β_0 + WS + MP + NDVI + A + TN + Y	2945	0.23
7	β_0 + WS + MT + S + W + A + Y	2950	0.23
8	β_0 + WS + MP + NDVI + A + TN	2964	0.23
9	$\beta_0 + WS + MP + NDVI$	2966	0.23
10	$\beta_0 + A + TN + Y$	2971	0.23

Table 1. Selection of the most representative 10 models ordered according to WAIC and with their value of LCPO

Predictor acronyms: W = spatial effect, Y = year temporal effect, TN = type of nest, A = anthropic effect, WS = wind speed, NDVI = normalized difference vegetation index, MT = mean annual temperature, MP = mean annual precipitation, I = isothermality, E = elevation, ID = nest random effect, S = slope, As = aspect. The best model is highlighted in bold.

In addition, the temporal effect highlighted that the period 1993–1997 had the highest breeding success (Fig. 3). Considering the climatic variables and the vegetation, a higher probability of breeding success for the Griffon Vulture should be expected in south-eastern Sardinia (Fig. S1). Furthermore, breeding success is also influenced by hidden variability, as shown by the relevance of the nests and spatial random effects (Table 1).

DISCUSSION

The present study identified a set of environmental and topographical variables at nesting sites as



Figure 3. Smooth function of the functional response for the selected variables. The solid line is the smooth function estimate and shaded regions represent the approximate 95% credibility interval (CI). Estimated coefficients of the fixed effects are also shown with the respective 95% CI.

potential predictors of the breeding success of the Griffon Vulture in northern Sardinia. Breeding success was used as an indicator of the habitat suitability at nesting sites, and the results obtained indicated which habitat features influence reproductive success in this species.

Wind speed at the nesting sites was found to be positively related to the probability of successfully raising a chick in Griffon Vultures. Griffon Vultures, being obligatory scavengers, have evolved an extremely opportunistic lifestyle to cope with food resources that are unpredictable in time and space (Ruxton & Houston 2004). They are soaring-gliding birds which, by climbing in rising air columns, utilize energy from the environment, thereby dramatically decreasing movement costs. They thus rely heavily on thermal and linear soaring at sites of orographical uplift to minimize energy expenditure (Duriez et al. 2014). Griffon Vulture colonies are indeed located at the highest altitudes over sea level (García-Ripollés et al. 2005) or at the highest altitudes (Xirouchakis & Mylonas 2005). Wind speeds provide stronger updrafts along sloping topography, so nests exposed to higher wind speeds may facilitate the soaring flight and hence the search for food. In the Cape Vulture Gyps *coprotheres*, cliff roost sites with predominately east winds are favoured (Martens et al. 2020). However, other studies investigating the most influential habitat variables in the selection of breeding cliffs by the Griffon Vulture show nesting cliffs are located in sites protected against north winds (Xirouchakis & Mylonas 2005).

According to the best model, the probability of breeding success for the Griffon Vulture was negatively related to mean annual rainfall. Heavy rainfall is frequently reported to affect the breeding performance of raptors (Dawson & Bortolotti 2003, Morrison et al. 2009). This is due to the fact that in many raptor species, heavy rainfall reduces hunting efficiency by impairing flight, therefore increasing foraging costs and limiting the frequency with which parents can provide food for both their young and themselves (Paviour 2013). Our results confirmed previous studies which reported that abundant rainfall negatively affects the breeding success of Griffon Vultures (Donázar, 1987, Xirouchakis, 2010), although some studies have not confirmed this relationship (Fernandez et al. 1998). The Mediterranean region is an area potentially vulnerable to climate change. A recent study in Sardinia forecast a rainfall reduction in the winter months and an increase during the summer months (Caloiero *et al.* 2019). Based on our model, this change should favour the reproductive success of Griffon Vulture, though the impact on fledglings' ability to survive the first few weeks after leaving the nest should be evaluated.

Our model also showed that nests with higher breeding success were located in areas where the vegetation is sparse, e.g. in shrubs and pastures. The distribution of vultures is strongly related to the availability of carrion (Spiegel et al. 2013, Santangeli et al. 2018), which depends not only on the abundance and mortality rates of ungulates and on the presence of mammalian competitors, but also on carrion visibility and accessibility (Kane & Kendall 2017, Santangeli et al. 2018). Vultures rely mostly on visual cues to detect carrion (Ruxton & Houston 2004, Cortés-Avizanda et al. 2014, Martin-Díaz et al. 2020) and several studies report that carrion accessibility for vultures is higher in habitat with low vegetation coverage, such as pasturelands and open landscapes (Bamford et al., 2009a, 2009b, Ogada et al. 2012b, Arrondo et al. 2019, Pardo-Barquín et al. 2019). Adult Griffon Vultures range over a relatively small foraging area, showing a pattern of movement close to a 25-30 km radius (Van Beest et al. 2008, Zuberogoitia et al. 2013). Adult movements outside of the main foraging areas are scarce and restricted to the non-breeding period (Zuberogoitia et al. 2013). Thus, nests located in areas with low vegetation coverage might facilitate access to the feeding resources and hence breeding success. Habitat quality in terms of prey accessibility is frequently cited as a key influence on the success with which many raptors can raise young (Paviour 2013).

In the present study, the probability of successfully raising a chick was higher where no human disturbance was present or was slight, but it decreased when disturbance became frequent. Several studies assessing the environmental variables affecting nest-site selection have reported that vultures select nest-sites located away from human infrastructures or anthropogenic factors than can provoke disturbances (Donázar et al. 2002, Morán-López et al. 2006, Bamford et al. 2009a, 2009b, Mateo-Tomás & Olea 2009, Moreno-Opo et al. 2012). Other studies have shown that human disturbance also reduces breeding success (Donázar et al. 2002, Morán-López et al. 2006) but this finding has not always been confirmed (Fernandez et al. 1998).

We found that the type of nest used had a significant effect on Griffon Vulture breeding success. Nests with an overhang might be expected to have a higher breeding success as a result of shelter provided during inclement weather. However, our results showed that productivity was not improved in sheltered nests, as nests not covered by terraces were those with the highest success. Other studies. while confirming that the type of nest has an influence on Griffon Vulture breeding success, report that nests in caves were more successful and were used for more breeding attempts compared with nests that were exposed from above (Freund et al. 2017). This may be due to parents at exposed nests investing substantially more time in thermoregulation (i.e. brooding or shading the young) (Freund et al. 2017). In our study area, inclement weather is not extreme, and the large size of the Griffon Vulture probably protects it sufficiently, as confirmed by a previous study (Fernandez et al. 1998).

In conclusion, according to our results, the probability of successfully raising a chick in Griffon Vultures is higher in nests exposed to a high wind speed, not covered by natural shelters, where the vegetation is mostly represented by shrub and pastures, with low human disturbance and in years with low rainfall. Breeding success is also influenced by hidden variability, as shown by the relevance of the random effects of spatial and nests in our model. Besides environmental variables, other factors can influence breeding productivity in raptors, such as the age and experience of the pair and the density of the population (see for examples in Fernandez et al. 1998, Paviour 2013) or other biotic factors that are spatially structured but that were not included in our model (prey availability, competition trends, etc.). The model developed in the present study will facilitate breeding habitat management by allowing spatially explicit decisions about conservation planning (Mateo-Tomás & Olea 2010). Recently, a LIFE project (LIFE Safe for Vultures - LIFE19 NAT/IT/ 000732) aiming at enlarging the area of occupancy of the species has been approved, and the information gathered in this study will help identify the area in which to create a second nucleus of Griffon Vultures in Sardinia. Considering the climatic variables and the vegetation, a higher probability of breeding success for the Griffon Vulture should be expected in south-eastern Sardinia. Further studies will develop predictive models to identify the most suitable areas for Griffon Vulture reproduction in the future.

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CONFLICT OF INTEREST

None.

AUTHOR CONTRIBUTIONS

Mauro Aresu: Conceptualization (equal); Data curation (lead); Investigation (lead); Methodology (supporting); Writing-review & editing (supporting). Maria Grazia Pennino: Conceptualization (supporting): Data curation (equal): Methodology (lead); Writing-review & editing (equal). Davide De Rosa: Conceptualization (supporting); Data curation (supporting); Writing-review & editing (supporting). Andrea Rotta: Conceptualization (supporting); Funding acquisition (equal); Project administration (lead); Writing-review & editing (supporting). Fiammetta Berlinguer: Conceptualization (lead); Funding acquisition (supporting); Investigation (supporting); Writing-original draft (lead).

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig S1. Spatial map of the eight predictors used to define the reproductive breeding successes of

the Griffon vulture (*Gyps fulvus*) in the northernwestern part of the Sardinia Island (Italy).

Fig S2. Sperman's correlation matrix of explicative variables used in models.

Fig S3. Plot of the Generalized variance-inflation factors (GVIF) obtained for all the environmental variables.

Fig S4. Plot of the Generalized variance-inflation factors (GVIF) obtained for the environmental variables used in the final model.