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Assessing the outcome of reintroduction efforts: Trends in population size and drivers of breeding success in alpine bearded vultures

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Abstract

Vulture populations have dramatically declined worldwide over the past few decades. In Europe, various programs have been implemented to reintroduce or restock these birds. In the Alps, the Bearded Vulture (*Gypaetus barbatus*) was eradicated in the early 20th century, prompting the launch of an international reintroduction program in 1986. Through intensive monitoring of Bearded Vulture breeding territories over 26 years (1995–2021), we observed spatial and temporal changes in population size and assessed environmental and individual factors influencing breeding performance across four countries in the Alpine arc. The number of breeding pairs increased steadily from 1 in 1995 to 65 in 2021, and the number of fledglings from 0 in 1995 to 42 in 2021, although we observed significant differences across areas, with slower growth in the Eastern Alps. The breeding success (proportion of clutches leading to a fledgling) of the entire Alpine population was 68%, higher than that of other European populations. Our analysis, which included individual and environmental variables, revealed that nest elevation positively influenced breeding success, while the proportion of open habitat in the territory had a negative effect. Additionally, breeding success significantly increased with the coverage of not strictly protected areas around the nest. In terms of individual factors, longer pair bonds positively affected breeding success, and pairs composed of wild-hatched individuals had higher breeding success compared to those including released individuals. Our results confirm the overall positive trend of the reintroduced Alpine population but also highlight the increased vulnerability of the population breeding in the Eastern Alps. Additionally, our findings suggest that an effective network of protected areas can support the establishment of reintroduced populations. We also identified directions for further research to better understand the drivers of Bearded Vulture breeding success in the Alps.

KEYWORDS

conservation, impact evaluation, mountain ecosystems, protected areas, raptor, reintroduction program

1 | INTRODUCTION

Biodiversity loss continues at an alarming rate (Rosenberg et al., 2019; Waldron et al., 2017) due to anthropogenic threats such as land use change, pollution, and overexploitation (Jaureguiberry et al., 2022). Effective conservation efforts to reverse species declines rely on accurate data regarding species abundance and the factors driving population trends. Additionally, monitoring the outcomes of conservation actions is essential to assess their success (Cazalis et al., 2020; Rodrigues et al., 2004) and to optimize conservation resources through adaptive management strategies.

Reintroductions are increasingly used, among other tools, to reverse species extinction in the wild and restore biodiversity. Reintroduction programs have significantly improved the conservation status of several vertebrate species on the brink of extinction, for example, the Yellow-shouldered Amazon *Amazona barbadensis* in Margarita Island (Venezuela) (Sanz & Grajal, 1998), the California Condor *Gymnogyps californianus* in the USA (Bakker et al., 2024) and the Alpine ibex *Capra ibex* in the Alps (Stüwe & Nievergelt, 1991). However, reintroduction success is not guaranteed, and failures have been linked to insufficient information on ecological needs, unresolved causes of decline, or inadequate long-term monitoring of population parameters and threatening processes following reintroduction (Bennett et al., 2013; Fischer & Lindenmayer, 2000).

Designation of protected areas (hereafter PAs) is another cornerstone of biodiversity conservation (Gray et al., 2016). However, although PAs have an overall positive impact on biodiversity, their local effectiveness can be variable (Barnes et al., 2016; Terraube et al., 2020), and global biodiversity is still declining (Butchart et al., 2010) despite PA coverage approaching the targets fixed by The Convention on Biological Diversity (Tittensor et al., 2014). This paradox can be partially explained by the difficulty to buffer against the impact of anthropogenic threats within PA boundaries. In this sense, effective PA management is crucial in influencing ecological outcomes and the overall effectiveness of land protection (Wauchope et al., 2022). Area-based conservation is often a key conservation tool to support wildlife reintroduction programs and increase their success (Wilson et al., 2014).

The Bearded Vulture *Gypaetus barbatus* was eradicated from many parts of its European range and disappeared from the Alps by the early 20th century (Mingozzi & Estève 1997). An international reintroduction program began in 1986 (Hirzel et al., 2004) and is now active across the entire Alpine arc. As a result, the Bearded Vulture population of the Alps is now the second largest in Europe after the Pyrenean population (Arroyo et al., 2021; Margalida et al., 2020), demonstrating the program's success. Despite this, the species is still classified as Near Threatened globally (BirdLife, 2022) and faces significant anthropogenic threats in Europe (Margalida, Donazar, et al., 2008; Margalida, Heredia, et al., 2008), emphasizing the need for further research on the key drivers of Bearded Vulture demographic variation.

Bearded Vulture breeding success is likely shaped by a combination of individual factors and environmental conditions (Arroyo et al., 2021; Margalida et al., 2003, 2014). Among environmental factors, studies in the Pyrenees have shown that harsh weather at high-elevation sites can negatively impact breeding outcomes (Arroyo et al., 2021; Donazar et al., 1993). Additionally, human disturbance is known to influence reproductive success in this species (Arroyo & Razin, 2006; Margalida et al., 2014), with disturbance levels generally higher in low-elevation territories, which tend to be more anthropized than those at higher elevations. Bearded Vulture reproductive success has been found to be higher in protected areas, which are typically characterized by lower levels of human disturbance and greater food availability, thereby providing higher habitat quality for the species (Arroyo et al., 2021). Additionally, studies in the Spanish Pyrenees have shown density-dependent effects on reproduction, with a reduction in productivity when local density increases (Carrete et al., 2006; Donazar et al., 1993; Margalida et al., 2003, 2020).

In relation to individual factors, and as with many species, Bearded Vulture breeding success has been shown to vary with laying date (Arroyo et al., 2021), this variable being related to age or individual quality (Jenny et al., 2018; Lequette & Weimerskirch, 1990). Some studies have suggested that the breeding performance for this and other long-lived monogamous birds is also influenced positively by the length of the pair bond (Arroyo et al., 2021; Sánchez-Macouzet et al., 2014). Additionally, in the case of reintroduced populations, where wild-hatched and captive-bred birds may coexist in the breeding pool, their origin might influence their breeding performance as captive-bred individuals may have lower fitness than wild-hatched conspecifics through maladaptive captive adaptations or as a result of translocation conditions (Bacon et al., 2019; Farquharson et al., 2018). Furthermore, inbreeding (mating between relatives) might lead to reduced reproductive success (Hedrick & Kalinowski, 2000; Keller & Waller, 2002). Captive populations as a source for reintroductions are often small and, usually, only offspring of a few pairs can be released into the wild. Therefore, the relatedness among breeders in the wild may be particularly high (Loercher et al., 2013).

Nevertheless, information on individual characteristics is usually sorely lacking, and studies investigating the factors driving variation in the reproductive success of the Bearded Vulture remain relatively scarce. Existing studies have so far focused mainly on the Pyrenean population (Arroyo et al., 2021; Arroyo & Razin, 2006; Donazar et al., 1993; Margalida et al., 2003; Seguin et al., 2010) and have rarely considered simultaneously individual and environmental factors. No research on this topic has been conducted on the reintroduced Bearded Vulture population of the Alpine arc.

Here, we take advantage of a unique dataset from a long-term monitoring program (1986–2021) of the Bearded Vulture population across the entire Alps, which includes 578 breeding events. The intensity of the monitoring enabled the collection of various data, including information about each reproductive attempt as well as individual data on many territorial pairs. This study aims to: (i) assess spatial and temporal trends in population size and breeding parameters; (ii) identify which individual and environmental factors influence the reproductive success of Bearded Vultures in the Alps; and (iii) evaluate the impact of two conservation actions, namely the reintroduction program and protected areas, on Bearded Vulture population size and breeding success.

2 | METHODS

2.1 | Study species and area

The Bearded Vulture is a large, long-lived raptor found in the mountains of Eurasia and Africa (Brown, 1997). It nests on cliffs, often in small caves (Arroyo et al., 2021), and has a low fecundity rate: typically, only one of the two eggs laid survives due to inter-sibling aggression (Margalida et al., 2003). Adults have a high survival rate (>0.96) (Margalida et al., 2020; Schaub et al., 2009), begin reproducing around 6–15 years of age (Antor et al., 2007; Margalida et al., 2020), and can breed up to 32 years old (Ferrer et al., 2014). Bearded Vultures defend an exclusive territory around the nest and are usually monogamous, though polyandric trios occur in saturated populations (Carrete et al., 2006), with lifelong pair bonds that can change if a partner dies (Arroyo et al., 2021). They are linked to mountain environments, high-elevation grasslands for food, and limestone cliffs for nesting and bone breaking (Krüger et al., 2014; Margalida et al., 2007; Vignali et al., 2021). Their diet mainly consists of mammal bones, especially from wild ungulates like Alpine ibex and chamois, as well as domestic sheep (Margalida et al., 2009).

The study area encompasses the entire Alpine massif (Figure 1), spanning five countries. Due to its extensive geographical range, varying elevations, and diverse topography, the region experiences a variety of climatic influences (Rubel et al., 2017). Specifically, the Northern Alps have an oceanic climate, the Inner Alps are characterized by continental and subcontinental conditions, while the Southern Alps exhibit an Insubric climate, marked by warm, wet winters and hot summers (Vignali et al., 2021). This range of climatic conditions and geological substrates, such as limestone, sandstone, and granite, creates an extensive and heterogeneous landscape that provides favorable breeding habitats for the Bearded Vulture. The reintroduction program using captive-bred birds began in the Austrian Alps in 1986 (Frey & Walter, 1989) and was later extended to other Alpine countries including France, Switzerland, Italy, and more recently Germany (since 2021). Between 1986 and 2021, a total of 227 birds were released across Austria, France, Switzerland, and Italy. The birds are released at approximately 3 months of age using the hacking method (Frey, 1992): chicks, 2–4 weeks prior to fledging, are placed in a cave with supplemental food provided. The cave is designed with an open structure, enabling the birds to fledge when they are physically ready. All released birds are marked with rings, whereas only 27 wild-hatched birds (up to 2021) have been ringed. Wild-hatched birds are primarily tracked through genetic methods (i.e., genetic analyses of shed feathers found in nest areas, see below).

2.2 | Breeding monitoring

The monitoring of the breeding units and population size was performed by the IBM partners (International

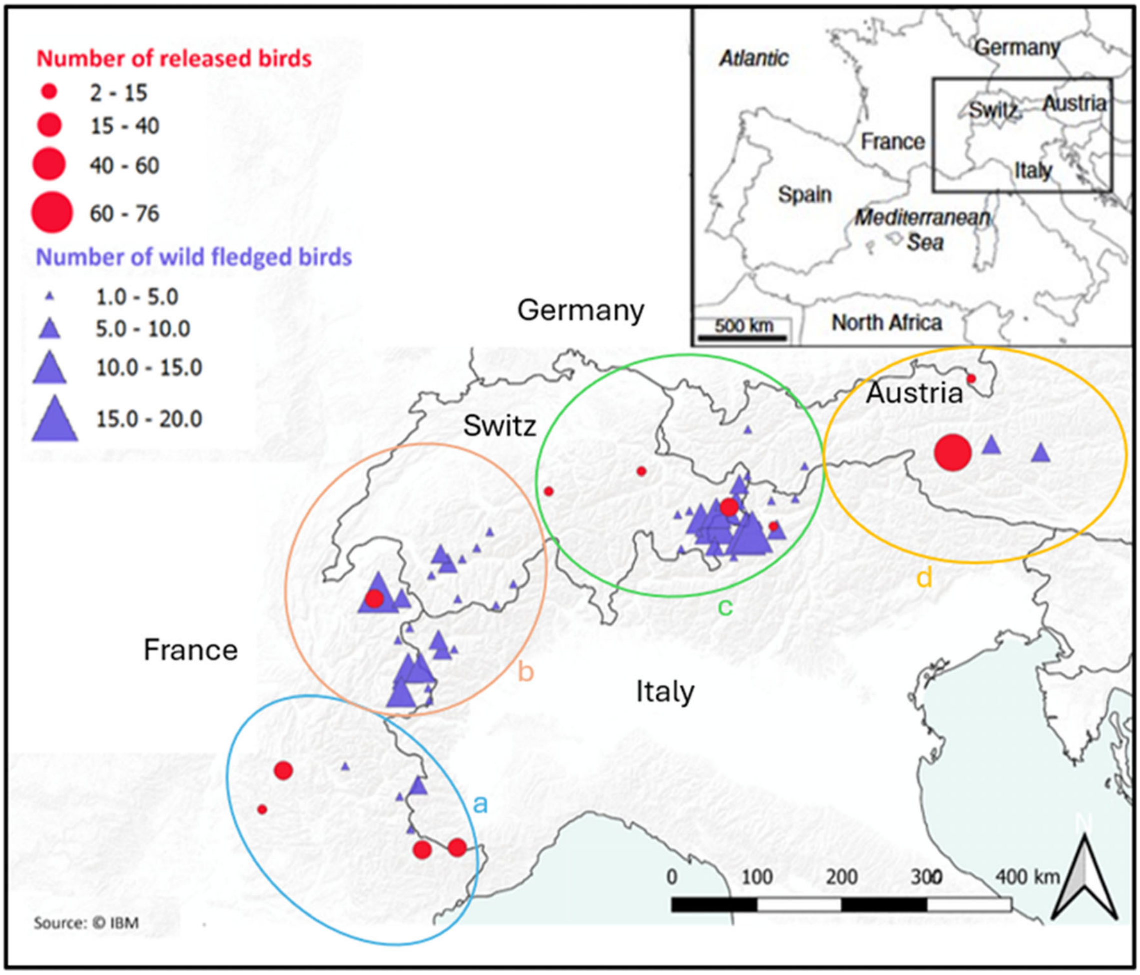

FIGURE 1 Location of study area and countries involved. The geographic distribution of the total number of released and wild-hatched fledglings from 1986 to 2021 is also shown for each of the four Bearded Vulture subpopulations across the Alpine arc, represented by circles: (a) the South-western Alps, blue; (b) the North-western Alps, orange; (c) the Central Alps, green; and (d) the Eastern Alps, yellow.

Bearded Vulture Monitoring, www.gyp-monitoring.com). Monitoring followed standardized methods, that is, homogeneous monitoring protocols across the entire study area and curation of a central database (Lauper, 2022). Since the establishment of the first breeding pair, Bearded Vulture territories have been monitored to identify new pairs and record breeding activity and reproductive output. As new breeders typically establish a territory a few years before their first reproduction, the likelihood of detecting all breeding attempts is high (Margalida et al., 2020; Schaub et al., 2024). Each breeding territory was visited at least three times during the breeding season to record egg laying, hatching, and fledging dates. Additional visits were conducted if dates could not be determined during the three visits. This approach allowed us to estimate lay rate (proportion of breeding attempts resulting in a clutch), hatch rate (proportion of clutches reaching the hatching stage), and fledging success (proportion of clutches resulting in a fledged young). Trios were rare in our study area (only nine trios detected over the years), so this variable was not included in the analyses. A total of 578 breeding attempts were monitored over 27 years.

Given that countries are connected by demographic and genetic flows, when discussing the results we considered that the Bearded Vulture range across the Alpine arc is delineated in four regions based on geographic characteristics, habitat quality, and reintroduction timing: (i) the Central Alps and (ii) the North-western Alps (both constituting the core area) and (iii) the South-western and the Eastern Alps (peripheral areas).

2.3 | Individual variables

Laying date was assessed through observations, as described above. Breeding birds were identified when possible using rings, unique plumage features (like molt or feather coloration, confirmed by regular observations and photographs), or genetic methods on feathers collected at nest sites (Gautschi, 2001). This identification allowed attributing to identified individuals their origin (wild-hatched or captive-bred), age, and the time (years) each breeding pair has been together.

Annual genetic monitoring under the IBM includes genotyping all captive-bred and released birds, as well as feathers collected in the wild in or close to nesting areas (for the latter, we assumed that feathers collected there belonged to either breeding adults or fledglings produced). Genotyping follows the methods described in Gautschi et al. (2000). Using the reconstructed pedigree, we calculated individual inbreeding coefficients and kinship between pairs, with parental kinship equating to the offspring's inbreeding coefficient (Keller & Waller, 2002; Speed & Balding, 2015). Genetic monitoring was crucial for detecting changes in pair composition (Jenny et al., 2018).

Overall, we had individual data on all assessed variables (age/sex, years paired, kinship, origin, laying date) from birds of 257 breeding events.

2.4 | Environmental variables

The exact position of the nest and the height of the cliff were recorded during field monitoring. Elevation of the nest was calculated with QGIS 3.20.10 from the coordinates. Around each nest, we drew a buffer of 6.4 km radius (hereafter called "breeding territory"), that represents the average home-range size of the species (Gavashelishvili & McGrady, 2007; Krüger et al., 2014; Margalida et al., 2016; Subedi et al., 2020). We extracted eight variables (see Table S1) for each buffer using QGIS 3.16.10 and R.4.2.0. First, we calculated the proportion of "open areas", considered as the main foraging habitat available for the Bearded Vulture (Bogliani et al., 2011), using Corine Land Cover (CLC). The land use categories used by CLC were simplified into four categories, "open", "forest", "urban", "other". From the CLC categories, we considered the following as open areas (usable for foraging by the study species): pastures, natural grasslands, moors and heathland, sparsely vegetated areas, land with significant areas of natural vegetation, and bare rocks. As no major differences in the proportion of these CLC categories were observed between the different versions available, we used the 2018 layer for analyses. We also calculated the density of roads (as the total length of paved and unpaved roads divided by buffer area).

As a proxy for food availability, we used data on Alpine ibex abundance in the breeding territories. The carcasses of Alpine ibex and other large ungulates serve as a primary food source for Bearded Vultures (Hirzel et al., 2004; Vignali et al., 2021). In addition, temporal series on Alpine ibex populations are the only ones available at such a large scale (Brambilla et al., 2020). We calculated yearly Alpine ibex abundance within each breeding territory and assigned it to the corresponding reproductive year of the Bearded Vulture pair. Yearly values of ibex density were extracted for each ibex colony from the model presented by Brambilla et al. (2020). To estimate the number of ibex present in each Bearded Vulture breeding territory, we calculated the area of the ibex colony included in the 6.4 km buffer around the Bearded Vulture nest and multiplied it by the ibex density of that colony. The Alpine ibex model only covers the years 2004 to 2016; therefore, values from 2004 were used for Bearded Vulture reproduction years prior to 2004, and values from 2016 were used for years after 2016.

Additionally, we calculated the proportion of each Bearded Vulture breeding territory included in a protected area (PA). PA were assigned to two categories according to their IUCN definition, as previous research has shown that IUCN categories influence PA effectiveness in terms of biodiversity conservation (Ferreira et al., 2020). The first category, designated as "strict protection", included category I protected areas (strict nature reserves) and category II protected areas (national parks). The second category, designated as "not strict protection", included categories IV and V protected areas and others not assigned to an IUCN category, referring to areas where human activities are less controlled. We also considered the year of creation of each protected area. This means that, for a given territory that included part of a protected area, the proportion of the buffer under protection was considered zero for the years prior to the creation of that protected area. The map of protected areas was downloaded from the European Environment Agency, using the dataset CDDA EuropeEPSG3035.

Weather conditions can be an important factor influencing Bearded Vulture breeding success. We calculated the total amount of winter (January to March) and spring (April to June) precipitation for each year and territory (buffer area around the nest). Maps of average precipitation per day were downloaded from Copernicus (https://cds.climate.copernicus.eu/cdsapp#!/dataset/insitu-gridded-observations-europe?tab=overview), providing daily data at 5 km^2 spatial resolution. A dataset covering 1995–2022 was used to extract rainfall data.

Finally, we calculated the number of occupied nests within the buffer around each territory and for each year ("Bearded Vulture neighbors") to obtain a proxy of conspecific density in each breeding territory.

2.5 | Statistical analyses

First, in order to assess potential temporal variations in population size between countries, we built a linear model with the number of breeding pairs as the response variable and country, year, and their interaction as explanatory variables.

To test variables explaining variations in breeding success (defined as the probability that a clutch led to a fledgling), we implemented Generalized Linear Mixed Models (GLMM), fitting the response variable to a binomial distribution with a logit link function and using 'year' and 'territory' as random effects. However, we found no variance associated with the random effect of 'territory'. Consequently, we reverted to a more parsimonious model that included only 'year' as a random term.

We had an initial set of 16 explanatory variables to be used in these analyses, 6 related to individual factors, and 10 related to environmental factors (see above and Table S1). Among individual variables, 'female age' and 'male age' were excluded because they were correlated to "Years Paired", which we chose to keep as this variable included indirect information about both male and female age characteristics. Among environmental variables, "% open area" was strongly negatively correlated to "road density"; we chose to keep "open area" for our analyses as this covariate is directly associated with Bearded Vulture optimal foraging habitat while road density may not be a good proxy for human disturbance in the mountains, because there was no distinction between road types and the access of mountain roads may depend on the topography. Regarding weather variables, and considering Bearded Vulture phenology, we included only the total amount of spring rainfall in our analysis as young nestlings are the most vulnerable to bad weather conditions. We tested for collinearity among the remainder variables by estimating the variance inflation factors (VIF). All of these variables had VIF values lower than 3, the threshold below which the variables are considered not collinear (Zuur et al., 2009). Therefore, 12 explanatory variables were finally considered in our models (see Table S1). All covariates were standardized to allow direct comparison of effect sizes.

In order to identify non-linear patterns between the response variable and the explanatory variables, before implementing the GLMM, we performed a Generalized Additive Mixed Model (GAMM) using restricted maximum likelihood including all environmental factors with 'year' as a random effect. Given the relationships highlighted by the GAMM plots between breeding success and 'Nest altitude', 'Cliff height', 'number of neighbors' and 'kinship', we also considered a quadratic term for all these variables in the initial GLMM.

For these analyses, we only considered breeding attempts where a clutch had been laid and for which we had information in all considered variables. Since information on individual variables was available for far fewer events compared to environmental variables, we ultimately used a dataset with 257 breeding events.

Models including one or various of the explanatory variables were compared by ranking them according to their AICc using the function dredge from the MuMIn package (version 1.46.00) (Burnham & Anderson, 2002). When using Akaike's Information Criterion for model selection, AICc will sometimes support the inclusion of uninformative variables in the "best" models if a variable with poor explanatory power is added to an otherwise good model and the result is a model with $\Delta AIC < 2$ (Arnold, 2010). Although there is no universal solution to this problem, various potential solutions have been proposed, including model averaging (which potentially minimizes the effect of uninformative parameters) and identifying uninformative parameters through determining 95% confidence intervals of the parameter estimates and assessing whether they include zero (Arnold, 2010). Model averaging was thus performed on the candidate set of models showing a $\Delta AIC < 2$, and we also computed the 95% confidence intervals of the model-averaged parameter estimates and discussed only informative parameters identified in our approach. All statistical analyses were performed using the lme4, MuMIn, and ggeffects packages in R statistical software version 4.1.2 (Bates et al., 2015; Burnham & Anderson, 2002; Lüdecke, 2018). We checked for normality and homogeneity of variance by using residual diagnostics following the procedures described in the DHARMa package for the initial model (Hartig, 2022).

3 | RESULTS

3.1 | Trends in population size

The number of territorial pairs increased regularly during the study period, from 1 in 1995 to 65 in 2021 (Figure 2). The total number of young produced per year in the population increased with increasing numbers of breeding pairs, from 0 in 1995 to 42 in 2021 (Figure 2). Results from the linear model showed that there were significant differences in population trends between countries, with the strongest increase recorded in Switzerland and the weakest in Austria (see Table S2 and Figure S1). In France, the first pair settled in 1995, and the breeding population grew steadily until 2021, reaching 19 pairs (Figure 2). The first successful reproduction was recorded in 1997. Although the number of fledged young generally

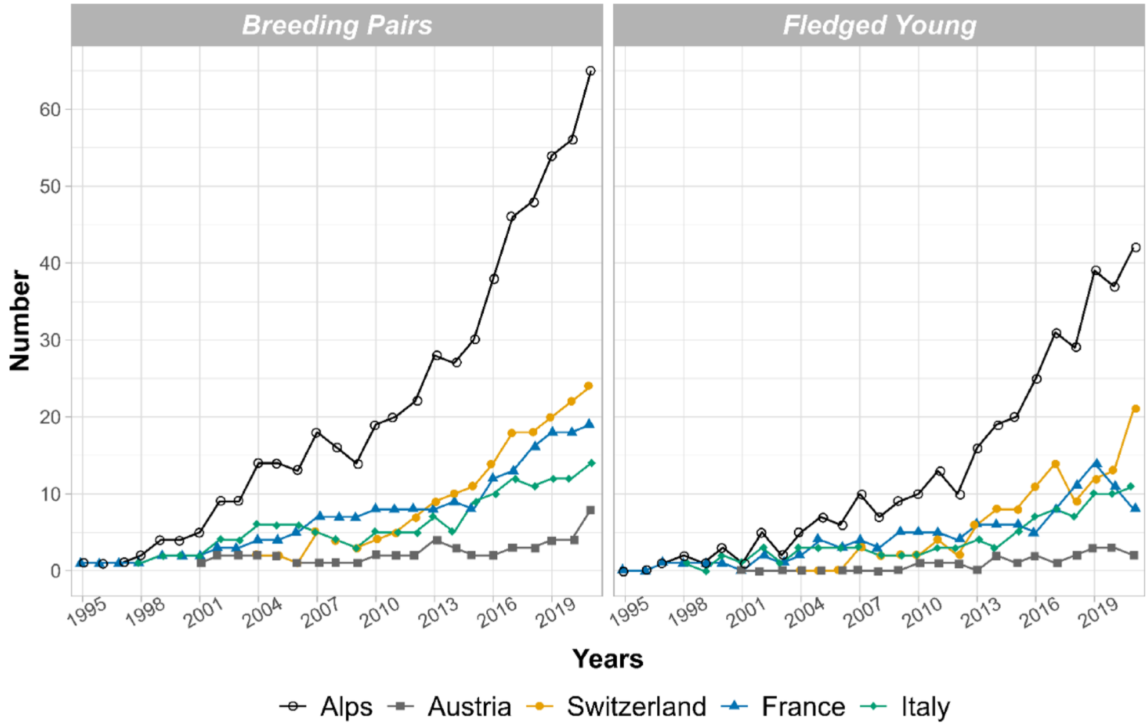

FIGURE 2 Temporal trends of the number of breeding pairs and number of fledglings in the whole Alpine range and in each country.

increased, it declined recently from 14 in 2019 to 8 in 2021 (Figure 2). In Switzerland, the first three pairs settled in 2004 and then the number of breeding pairs increased very rapidly, with 24 pairs in 2021 (Figure 2). The first young successfully fledged in 2007 and this number increased to 21 fledglings in 2021 (Figure 2). In Italy, the first pair settled and bred successfully in 1998 (Figure 2). With an overall slower increasing trend, the breeding population in Italy was 14 breeding pairs in 2021, producing 11 fledglings (Figure 2). Finally, in Austria, the first pair settled in 2001. The number of breeding pairs increased slowly to four by 2020, then doubled to eight in 2021 (Figure 2). The first successful breeding was recorded in 2010, but fledgling numbers have remained low, with two fledged in 2021 and a maximum of three in 2019 and 2020 (Figure 2). No breeding attempts have been observed in Germany yet. These differences in trends do not appear to be related to the intensity of releases (see Table S2) nor to the starting year of the reintroduction program (which may be related to the availability of breeding-age birds). In fact, more birds have been released in the Austrian part of the Alps while a higher productivity (in terms of wild hatched birds) was observed in Switzerland and France (Figure 1). Indeed, a low number of wild fledglings was observed in the Southern Alps (Italy and France) and in the Eastern Alps (Austria) (Figure 1).

3.2 | Variations in breeding success across the Alps

Laying rate was 88% (509 clutches for 578 monitored breeding attempts), hatching rate was 81% (413 out of 509 clutches), fledging success was 84% (350 fledglings out of 413 hatches) and overall success rate (proportion of occupied territories, $n = 578$, in which a fledgling was produced) was 60%. Overall success rate was similar among countries: 60% in France ($n = 195$), 64% in Italy ($n = 152$) and 65% in Switzerland ($n = 179$). Only the Austrian sub-population had a lower success rate, with 36% ($n = 52$) (pairwise prop. test, p-value$_{\text{AUT-CHE}} = .002$; p-value$_{\text{AUT-FRA}} = .016$ and p-value$_{\text{AUT-ITA}} = .005$). Overall breeding success (proportion of clutches leading to fledging) was 68%.

3.3 | Factors affecting breeding success

The global model (including eight environmental and four individual explanatory variables and their quadratic terms when appropriate) explained 31% of the variation in the data. The 54 models with ΔAIC < 2 (Table S3) were used to produce model-averaged parameter estimates.

The model-averaged parameter estimates (Table 1) indicated that breeding success was significantly explained only by five variables (three environmental and two individual). Breeding success significantly increased with nest elevation, with a quadratic relationship, with reproductive success rising from low to medium elevations and then plateauing above a certain threshold (Table 1; Figure 3). Additionally, it declined with the proportion of open areas in the territory and increased with the proportion of not strictly protected areas in the territory (Table 1; Figure 4). Among individual factors, pair constitution had a significant effect on Bearded Vulture breeding success: pairs formed by two wild-hatched individuals had higher breeding success (ca. 30% higher) compared to mixed pairs with one released individual or pairs where both members were released (Table 1; Figure 5). Additionally, pair bond length positively influenced breeding success as Bearded Vultures paired for more years had higher breeding output (Table 1).

4 | DISCUSSION

4.1 | Success of the reintroduction program

Our results showed a marked and continuous increase in the number of territorial pairs and fledglings produced in the Alps over the years, after the start of the reintroduction program. This indicates that the program has been a success in terms of the establishment and expansion of a breeding population of Bearded Vultures at the Alpine arc scale (Schaub et al., 2024), supporting the value of this conservation action in at least certain contexts (Morandini & Ferrer, 2017).

However, our results also indicate spatial variation in population trends between countries that are apparently unrelated to the intensity of releases. For example, despite a larger number of birds being released in Austria over an extended period since 1986, the Austrian subpopulation is growing at a slower rate compared to the core areas in the Central and North-Western Alps. A possible explanation for the lower success in Austria could be higher mortality in the Eastern Alps due to various factors, including anthropogenic sources, like illegal shooting, lead intoxications, or collisions with transport cables or energy infrastructure (Loercher et al., 2021). Recent findings support this hypothesis, as Schaub et al. (2024) have highlighted that adult survival is lower in the peripheral Alpine areas compared to the core regions. Additionally, the core areas of the Alps offer better conditions for Bearded Vultures in terms of food resources and nesting habitat (Bassi et al., 2017; Margalida et al., 2016). Consequently, this suggests that the establishment of new Bearded Vulture territories is more likely in these

TABLE 1 Model-averaged parameter estimates (considering the set of models with ΔAICc < 2) describing the effect of environmental, anthropogenic, and individual variables on breeding success.

Variables	Parameter estimates ± SE	*Z*	2.5% CI	97.5% CI	*p*
Intercept	0.585 ± 0.527	1.107	−0.451	1.620	0.268
Nest elevation	0.971 ± 0.279	3.463	**0.421**	**1.520**	**0.000**
(Nest elevation)^2	−0.285 ± 0.135	2.106	**−0.556**	**0.000**	**0.035**
Cliff height	0.505 ± 0.353	1.422	−0.441	0.969	0.155
(Cliff height)^2	0.294 ± 0.442	0.663	−0.166	0.183	0.508
Lay date	0.228 ± 0.183	1.242	−0.313	0.204	0.214
Nb Neighbors	0.703 ± 0.459	1.523	−0.542	0.822	0.128
(Nb Neighbors)^2	−0.237 ± 0.133	1.766	−0.266	0.172	0.077
Ibex density	0.294 ± 0.255	1.146	−0.383	0.264	0.252
Spring rainfall	−0.234 ± 0.180	1.293	−0.373	0.219	0.196
% Open habitat	−0.458 ± 0.220	2.067	**−0.892**	**−0.023**	**0.039**
PA no strict	0. 068 ± 0.300	2.253	**0.088**	**1.272**	**0.024**
PA strict	0.290 ± 0.203	1.427	−0.260	0.511	0.154
PC.real.wild	0.562 ± 0.377	1.483	−0.181	1.304	0.138
PC wild-wild	2.744 ± 0.740	3.692	**1.287**	**4.200**	**0.000**
Years paired	0.083 ± 0.038	2.164	**0.004**	**0.159**	**0.030**
kinship	0.955 ± 0.515	1.846	−0.740	1.456	0.065
(kinship)^2	−0.494 ± 0.260	1.892	−0.737	0.379	0.058

Note: The values highlighted in bold are statistically significant ($p < .05$). PC.real.wild = Pair Constitution_released-wildhatched; PC.wild.wild = Pair Constitution wildhatched-wildhatched.

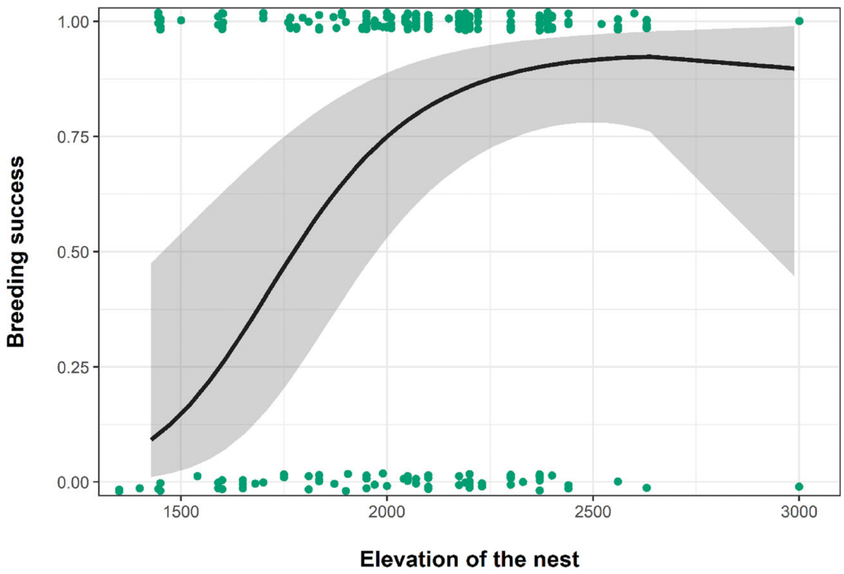

FIGURE 3 Model estimates and 95% confidence intervals, describing the effect of nest elevation on breeding success. Points show the raw data for breeding events and are vertically jittered to improve visualization.

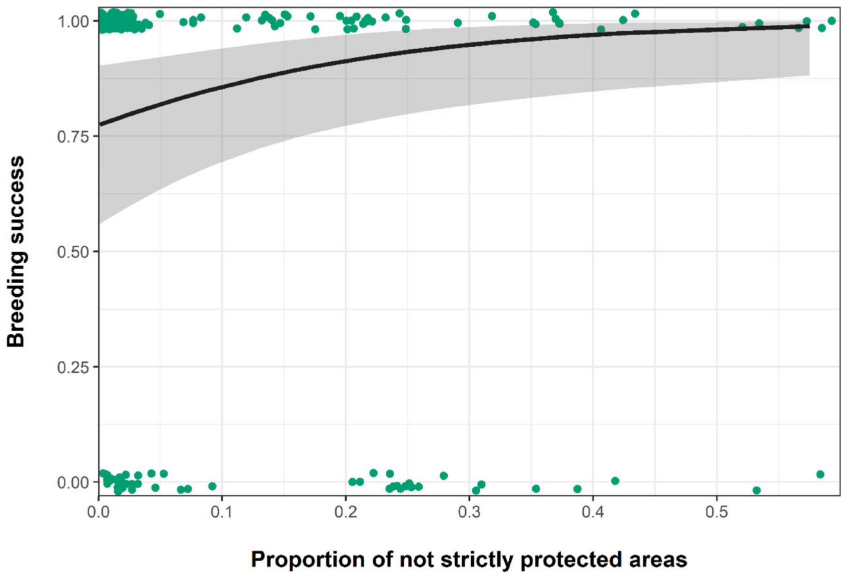

FIGURE 4 Model estimates and 95% confidence intervals, describing the effect of the proportion of not strictly protected areas on breeding success. Points show the raw data for breeding events and are vertically jittered to improve visualization.

high-quality habitats, regardless of the release site location. Conspecific attraction may also influence these patterns. Despite strong philopatry, some individuals do not stay in their natal area but disperse and settle in more distant places where breeding densities are high (Margalida et al. 2013; Jenny et al., 2018). Such natal dispersal patterns driven by conspecific attraction have been highlighted recently in a reintroduced population of Cinereous Vultures *Aegypius monachus* (Rousteau et al., 2022). Overall, the subpopulation in the Central Alps contributes substantially to the resettled and growing Alpine population of the Bearded Vulture and appears to be self-sustaining (Schaub et al., 2024). The difference in population trends between countries highlights the importance of conducting large-scale studies and of transboundary conservation actions for wide-ranging species.

4.2 | Factors affecting breeding success

The lay rate (proportion of breeding attempts resulting in a clutch) in the Alps was high at 88%, surpassing the 83% lay rate observed in the French Pyrenees (Arroyo et al., 2021) and significantly higher than the 59% recorded in the Spanish Pyrenees (Margalida et al., 2014). Overall breeding success (proportion of clutches leading to fledging) was 68.7%, which is also higher than the rates observed in both the French and Spanish Pyrenees (44% and 56%, Arroyo et al., 2021; Margalida et al., 2003). In

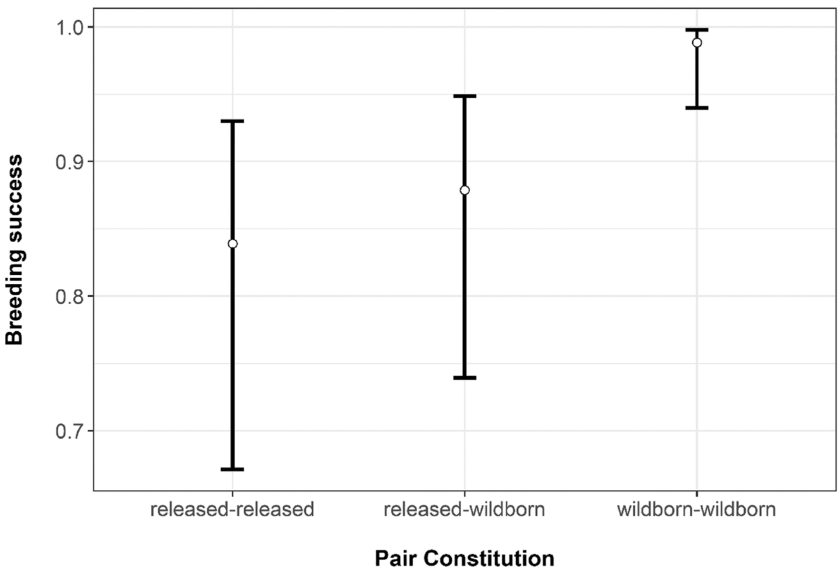

FIGURE 5 Model estimates and 95% confidence intervals describing the effect of pair constitution on breeding success.

these regions, observed density-dependent productivity depression in recent years indicates that the population may be approaching its carrying capacity (Margalida et al., 2020). Our results suggest that breeding conditions for Bearded Vultures in the Alps are generally favorable and that the population has not yet reached its carrying capacity (see also Schaub et al., 2024). Hatching rate was 81% and fledging success was 84%, indicating that breeding failure occurred at a similar rate during the incubation and the chick rearing periods.

Our study demonstrated that both individual and environmental factors influence Bearded Vulture breeding success. Regarding individual factors, our findings indicate that longer pair bonds positively impact breeding success, whereas newly formed pairs are less productive, consistent with observations by Sánchez-Macouzet et al. (2014) and Arroyo et al. (2021). In this long-lived monogamous species with slow maturation, several years typically pass between the first mating, first egg laying, and first successful reproduction (Antor et al., 2007). Consequently, the duration of the pair bond is likely linked to age-related improvements in reproductive performance, which may be attributed to increased experience.

Additionally, and interestingly, our study showed that breeding success is related to birds' origin, with wild-hatched pairs having higher reproductive success than pairs including released birds. This could suggest that wild-hatched birds may be better adapted to their environment than captive-raised birds, which experience different conditions during the period in captivity and the releasing period (Farquharson et al., 2018). However, these results should be interpreted cautiously, as a potential sampling bias favoring the identification of successful wild-hatched pairs might have contributed to the observed higher reproductive success in pairs formed by wild-hatched birds. Wild-hatched individuals are identified solely through genetic analysis of collected feathers, while released birds can also be identified by their rings. Feathers were collected at the nest site after each breeding event. Given that adults may leave the nest area after a failure, adult feathers are more readily found after successful breeding events, facilitating identification. Thus, during failed breeding events, pairs with at least one released bird are likely to be more easily identified than pairs composed entirely of wild-born individuals. Increasing feather sampling efforts, particularly targeting pairs consisting of un-ringed individuals early in their breeding cycle, would help confirm this finding.

In any case, even if the breeding success of reintroduced birds was lower than that of wild-hatched birds, it remained high (ca. 0.7 fledglings per initiated clutch, see Figure 4) as compared with the productivity observed in wild birds in the Pyrenean population (0.41, Margalida et al., 2020), and was sufficiently high to contribute to population growth, ultimately leading to a wild-hatched demographically self-sustainable population in the core areas as recently demonstrated by Schaub et al. (2024).

In relation to environmental variables, nest elevation positively affected breeding success, which improved from low to medium-high elevations. This finding supports earlier research on Bearded Vulture habitat selection and suitability (Margalida, Donazar, et al., 2008; Margalida, Heredia, et al., 2008; Vignali et al., 2021), which indicated that rugged high-elevation mountainous landscapes provide suitable breeding and foraging resources (such as limestone cliffs and ungulate carcasses), as well as reduced human disturbance. While higher-elevation breeding sites may also be associated with harsher climatic conditions during the breeding period that could potentially negatively influence breeding output (Arroyo et al., 2021), we did not detect an effect of spring rainfall on this parameter. Mountain ecosystems are highly vulnerable to the impacts of climate change, which are expected to intensify in the near future, with significant implications for bird populations (Scridel et al., 2018). For Bearded Vultures, climate change could influence breeding success through various mechanisms, such as direct effects of weather conditions during the breeding season or indirect effects on food availability caused by shifts in wild ungulate mortality patterns. Future research should focus on evaluating how climate change will affect habitat suitability for Bearded Vultures in the Alps.

Contrary to our expectations, we found a negative effect of the proportion of open area around the nest on breeding success. We had anticipated that this variable would indicate available foraging habitat, as Bearded Vultures primarily locate and access carcasses in open areas. Thus, a higher proportion of open areas should theoretically correlate with increased food availability (such as livestock carcasses in mountain grasslands) and, consequently, greater reproductive success. The observed negative effect may instead reflect other factors, such as accessibility, nest detectability, and increased vulnerability to anthropogenic disturbance (open areas were correlated with road density, see methods), rather than food availability as originally hypothesized.

Finally, we also found that Bearded Vulture breeding success was higher in nest sites with a higher proportion of protected areas around the nest, highlighting the overall effectiveness of this conservation policy tool. Previous research has shown that human disturbance is significantly linked to reduced breeding success in Bearded Vultures (Arroyo et al., 2021; Arroyo & Razin, 2006; Donazar et al., 1993). Protected areas in the Alps usually have lower disturbance, implement targeted conservation measures for species within them, and are often located in high-quality habitats that offer important food resources, such as wild mountain ungulate carcasses, which could contribute to the higher breeding success observed. However, the relationship was only significant for not strictly protected areas, which potentially have fewer restrictions on human activities (and thus higher disturbance levels as compared with strictly protected areas). Further analysis is needed to fully understand how land protection impacts Bearded Vulture breeding success.

4.3 | Limitations of the study and future developments

Contrary to previous research indicating a positive effect of food availability on Bearded Vulture breeding parameters (Arroyo et al., 2021; Ferrer et al., 2018), we found no correlation between breeding success and ibex density. This suggests that ibex density may not accurately reflect the spatial variation in food conditions for the species in the Alps. To better capture food abundance, it would be beneficial to use more specific variables, such as a multispecies abundance index that accounts for the spatial and temporal variations in the populations of ibex, chamois, and red deer (*Cervus elaphus*). Unfortunately, such comprehensive data for all major Bearded Vulture food sources are not yet available on a large scale.

Collecting data on human disturbance, such as variations in visitation rates in protected versus unprotected Bearded Vulture territories, would be crucial for better understanding the primary drivers behind the observed positive effect of protected areas on breeding success, and the difference between strictly and not strictly protected areas. Additionally, our relatively small sample size for individual variables may have limited the statistical power needed to detect effects of certain factors, such as kinship or inbreeding. Finally, our study did not account for the density of immature non-breeding birds or examine variations in survival rates across the Alps or in relation to protected areas. The presence of immature birds near breeding territories could potentially increase intraspecific competition, thereby reducing reproductive success (Carrete et al., 2006; Margalida et al., 2020). Finally, given the critical importance of adult survival in driving Bearded Vulture population growth rates (Bretagnolle et al., 2004; Margalida et al., 2020; Schaub et al., 2009), it is crucial to expand our analysis to include other vital rates. Doing so would help identify the environmental and anthropogenic factors influencing survival across the Alpine Arc, which is essential for understanding the limitations to population growth in the Eastern Alps. This effort could greatly benefit from the recent development of an integrated population model by Schaub et al. (2024), which examines the demography of the entire Alpine Bearded Vulture population.

4.4 | Conservation management implications

Thirty-six years after its inception, the Bearded Vulture reintroduction program has resulted in the establishment of 65 breeding territories in the Alps, thanks to the continuous release of individuals and legal protection of the species. However, our results revealed spatial variations in population trends, pinpointing areas where conservation efforts should be prioritized. Bearded Vultures still face anthropogenic threats such as shooting, poisoning, and collisions with energy infrastructure. Ongoing conservation actions and environmental education programs should be intensified to mitigate these threats and help the species reclaim its historical distribution range. Furthermore, special attention should be given to the peripheral areas where breeding parameters are lower than in the core areas.

Our findings suggest that an effective network of protected areas supports the establishment and growth of reintroduced populations. Identifying factors driving high breeding success in certain protected areas can inform specific actions that could be replicated in other underperforming areas. Importantly, the study underscores the importance of long-term, internationally coordinated monitoring, which should continue in the future.

AUTHOR CONTRIBUTIONS

Conceptualization: Beatriz Arroyo, Franziska Loercher, Julien Terraube. Data collection and curation: Franziska Loercher, Alice Brambilla. Data analysis: Dorian Santos-Cottin, Julien Terraube. Writing and reviewing of manuscript: Dorian Santos-Cottin, Beatriz Arroyo, Franziska Loercher, Alice Brambilla, Julien Terraube. All authors approved the final version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available on request from the corresponding author for research purposes only. The data are not publicly available due to ethical considerations (dataset includes sensitive data, i.e., Bearded Vulture nest locations).

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SUPPORTING INFORMATION

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

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