

RESEARCH ARTICLE

Demographic assessment of reintroduced bearded vultures in the Alps: Success in the core, challenges in the periphery

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Abstract

1. Regular assessment of reintroduced populations is essential to guide management and provide lessons for other reintroduction projects. Bearded vulture *Gypaetus barbatus* reintroduction in the Alps began in 1986 with the release of the first fledglings, the first successful reproduction was recorded in 1997, and the population has grown steadily since. A previous assessment suggested that no further releases would be required to establish a self-sustaining population from a demographic point of view. However, this conclusion was based on a small sample size and spatially homogeneous demographic rates of released individuals, which may differ from and be spatially variable among wild-hatched individuals.
2. Using longitudinal data and breeding site survey data, we constructed an integrated population model to examine the demography of the entire Alpine population, spatially stratified into a core and a periphery. We performed retrospective population analyses to identify demographic reasons for spatial differences in population growth and conducted population viability analyses to assess the impact of future threats and reintroduction options.
3. In 2021, an estimated 172 (CRI: 147–198) females were present in the Alps, of which 65 (CRI: 63–67) were breeders. Adult survival and productivity were higher in the core than in the periphery, so the population grew more strongly in the core than in the periphery. Differences in adult survival contributed most to the differences in population growth between the two areas.
4. The population viability analysis predicts that the Alpine population will double in 10 years but that an increase in the mortality hazard above 0.055 will lead to a population decline. Unlike the population in the core, the population in the periphery is dependent on further releases at this stage.
5. Bearded vulture reintroductions in the Alps have succeeded in creating a self-sustaining population with higher reproductive success and similar survival probabilities to the autochthonous Pyrenean population. In general, management should focus on preventing further mortality risks. In the periphery, reducing current mortality and increasing reproductive success are essential to make the population independent of releases.

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KEYWORDS

additional mortality, bearded vulture, demography, density-dependence, integrated population model, population viability analysis, reintroduction

1 | INTRODUCTION

Reintroduction of individuals into a species' historical range is a common conservation practice that can successfully reestablish populations (Seddon et al., 2007). The aim is to establish a self-sustaining population capable of surviving in the medium and long term, even if new threats arise. Assessing the success of a reintroduction requires both thorough demographic and viability analyses and mitigation measures if the survival of the reintroduced population is in doubt. Evaluating the success of reintroduction programmes is therefore important for adjusting the management of an ongoing project and for learning from similar projects.

The bearded vulture *Gypaetus barbatus* is a large scavenging raptor that feeds mainly on the bones of wild and domestic ungulates and lives in mountainous areas. Bearded vultures became extinct in the Alps at the beginning of the 20th century (Mingozzi & Estève, 1997), mainly as a result of direct persecution by humans. In 1986, an international reintroduction programme was initiated, consisting of the annual release of 1–10 captive-bred young (total by 2021: 228) at various sites in the Alps (Figure 1). The first successful breeding in the wild occurred in 1997 and the population has grown steadily since then. In 2006, the population numbered 9 breeding pairs and a demographic study showed excellent demographic performance and predicted further population growth (Schaub et al., 2009). Although this study indicated a high sensitivity of the population to further threats, particularly to an increase in adult mortality, it was suggested that further releases were not necessary from a demographic perspective. Nevertheless, annual releases of captive-bred bearded vultures have continued, mainly to improve the genetic diversity of the population, to establish a link between the Alpine and Pyrenean populations, and to strengthen the eastern subpopulation.

As there were few wild-hatched individuals at the time of the previous assessment (Schaub et al., 2009), only released individuals were included. However, for a more thorough assessment, it is crucial to understand the dynamics of the wild-hatched population as well, as at some point the population will be dominated by wild-hatched individuals and their demographic performance will become the most dominant part of the population dynamics. Moreover, the sample size of the previous assessment was small, leading to large uncertainties in the estimates of demographic rates and preventing the inclusion of temporal variation in most of them. Thus, despite the fairly bright future predicted 15 years ago, a more thorough population assessment that is based on less restrictive assumptions is needed.

Breeding pairs tended to establish in the vicinity of release sites, but only in the central Alps did the population increase strongly (Jenny et al., 2018). In the more peripheral areas of the eastern and southern Alps, only a few breeding pairs were able to establish around the release sites. The reason for the spatial heterogeneity in population recovery

has been hypothesised to be related to food availability and habitat structure, in particular the presence of dense populations of ibex *Capra ibex* and of a limestone substrate (Hirzel et al., 2004; Vignali et al., 2021). However, anthropogenic pressures may also be contributing to this pattern, with several deaths due to poaching, illegal poisoning from bait used to kill large carnivores, lead poisoning, collisions with cables and power lines (Loercher & Hegglin, 2021), and possibly also with the blades of wind turbines, which are increasingly being installed in the Alps (Vignali et al., 2022). In order to effectively manage the Alpine bearded vulture population, it is essential to understand the reasons for the spatial variation in population growth and to assess the sensitivity of the population to future threats that may increase mortality.

The bearded vulture population in the Alps has been closely monitored and longitudinal data collected on individuals since the start of the reintroduction programme. While at the beginning of the reintroduction, longitudinal data were limited to released juveniles, which were ringed and their wing and tail feathers individually marked, genetic sampling and satellite tracking have been increasingly used over the last 15 years. We analyse these data using an integrated population model (Schaub & Kéry, 2022), which provides estimates of demographic parameters, population age structure and population size. We spatially stratified the population into a core and a periphery. We tested for evidence of density-dependent population regulation and performed retrospective analyses to assess the extent to which core and periphery populations were driven by variation in demographic rates and population age structure. We also determined the contributions of demographic rates and age structure to the difference in population growth between the core and periphery. We then carried out a population viability analysis (PVA) to predict population sizes up to 2031. We assessed how much the growth and population size of the core and periphery would be affected if releases stopped and mortality increased.

2 | MATERIALS AND METHODS

2.1 | Study area

The study area covers the entire European Alpine arc, including parts of France, Italy, Switzerland, Germany, Austria, Liechtenstein and Slovenia (Figure 1). Topographic and geological conditions vary across the massif, with the highest peaks located in the west and in the centre, and limestone zones mostly in the north (Hirzel et al., 2004). We lack spatially explicit data on the density of large ungulates, which provide the main carcasses for bearded vultures, but ibex, a key resource (Hirzel et al., 2004; Vignali et al., 2021), occur mostly in the higher elevation zones.

Bearded vulture monitoring is organised by the International Bearded Vulture Monitoring Network IBM (www.gyp-monitoring).

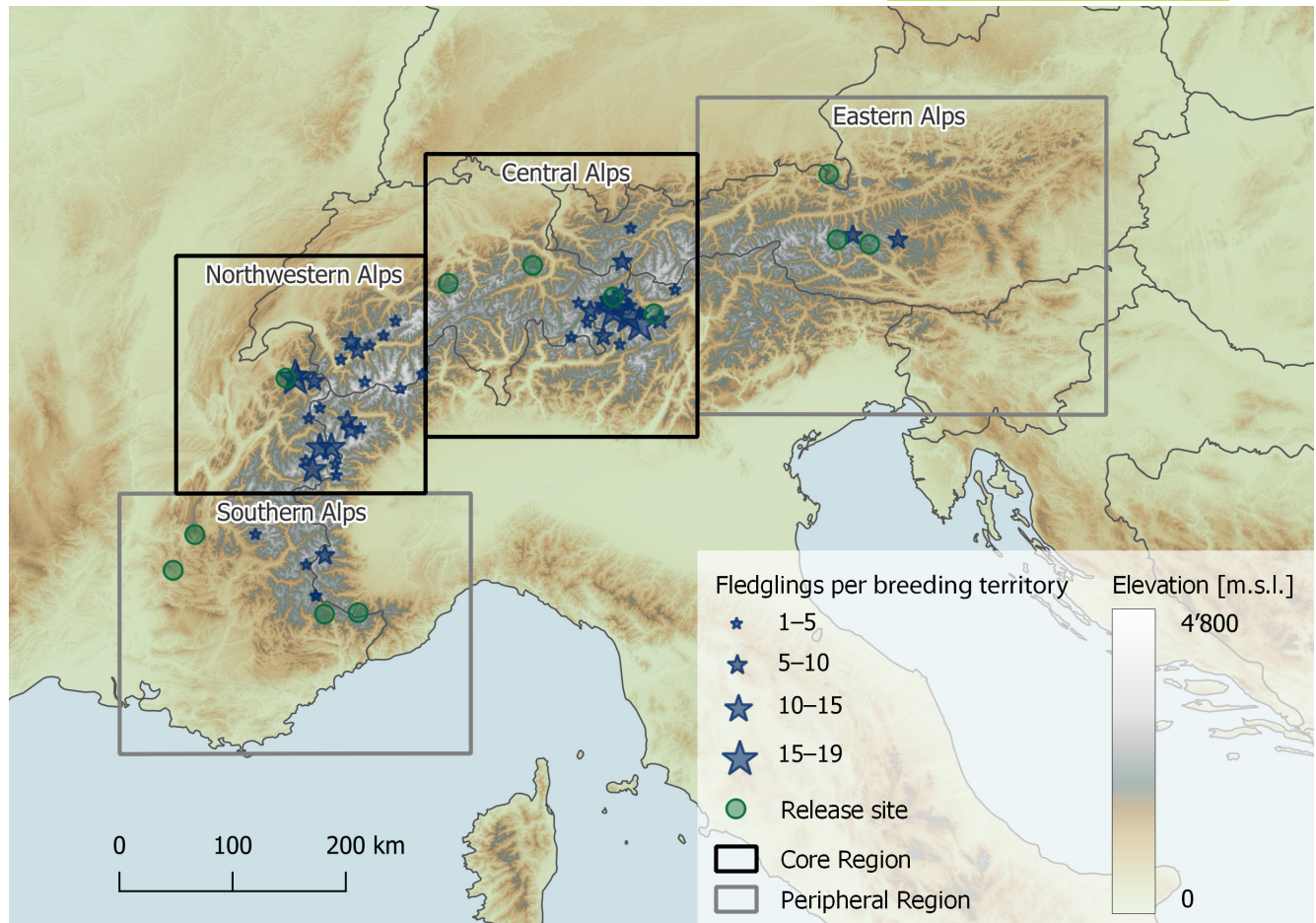


FIGURE 1 Geographical representation of the Alpine Arc with country borders. Circles show release sites, and squares show the four different IBM regions (see text for explanation) that we used to assign each marked individual and territory to either the core (black boxes: north-western and central Alps) or the periphery (grey boxes: southern and eastern Alps). The stars represent breeding territories and their size is proportional to the cumulative number of fledglings per territory.

com) and started in 1986 with the release of the first individuals. Within this network, partners from all over the Alpine region cooperate and coordinate their monitoring activities. The IBM validates the collected monitoring data, enters them into a central database and makes them available for analysis.

Reintroductions have taken place at several sites throughout the Alps. For a rough spatial stratification of the monitoring data, IBM defined four areas (eastern, central, north-western and southern Alps), to which all spatial data were assigned (Figure 1). For our analyses, we defined a core area (central and north-western Alps) with a high proportion of high altitude and therefore attractive to bearded vultures and a periphery area (eastern and southern Alps) with a lower proportion of high altitude.

2.2 | Breeding site survey

Since the establishment of the first breeding pair, the occupancy of bearded vulture territories has been monitored, with a focus on finding new pairs and recording breeding activity and reproductive

output. As new breeders usually establish a territory a few years before their first reproduction, the chances of finding them are high. It is therefore safe to assume that the breeding survey was very accurate, despite the vast area that had to be covered. Known territories were visited several times during the breeding season and it was recorded whether (1) the territory was unoccupied, (2) the territory was occupied but the birds did not attempt to breed, (3) the territory was occupied, a brood was started but failed and (4) the territory was occupied, a brood was started and successfully fledged. The definition of a breeding attempt was the presence of eggs, which could usually be inferred from the distinct incubation behaviour of the adults when the clutch remained invisible.

2.3 | Individual sighting and tracking data

Between 1986 and 2020, a total of 379 individuals (228 released and 151 wild-hatched) were marked using different methods or genetically identified, subsequently re-encountered and could therefore be used for estimating survival and age at first reproduction. All

released individuals were marked with colour or alphanumeric rings, some wing and tail feathers were bleached to create an individual pattern and they were genotyped prior to release. Forty-eight of them were also fitted with a satellite tag (data available since 2008). Over time, different satellite tags have been used. In the early years, the tags were battery-powered, but since 2011, only solar-powered tags have been used, which have a longer lifespan. Of the 309 wild hatchlings, 151 were marked (14 with satellite tags and 137 genetically identified) and could be used in the current study. A feather or blood sample was taken from 79 wild hatchlings in or below the nest, the sample was genotyped and the individual identified. From a further 58 wild hatchlings, a feather sample was collected after they had left the territory of their parents, so the age of these individuals was not known exactly (see Appendix S5: Table S5-1 for sample sizes).

Re-encounters of individuals without satellite tags were visual observations but also included genetic identifications. Visual identifications through bleached feathers (immatures prior to first moult) or colour ring readings were possible throughout the year, with a peak during chick rearing and during the coordinated bearded vulture surveys organised each autumn. To meet the instantaneous sampling assumption of capture-recapture models, we only included visual observations from June to October in each year. Feathers for genetic identification were mostly collected near nests, but randomly found feathers were also included. Genetic samples from January to May were assigned to the previous year and samples from June to December were assigned to the current year based on their date of discovery. Some marked individuals were also found dead. All unmarked individuals found dead were genetically identified.

Individuals with a satellite tag could be re-encountered either by remote geolocation, visual observation or genetic identification. However, we only used information from the satellite tag and excluded all other observations from the analysis unless the information was unclear (see below). All satellite tags transmitted position, temperature and accelerometer data at intervals ranging from a few hours to every few days. These data told us whether the bird was alive or dead, whether the tag was working or had fallen off. Individuals could either be alive at the end of the current study (December 2021), they could have died earlier and their death was confirmed, their tag could be confirmed as broken (no longer working or fallen off), or the fate of the individual and the tag was unknown. Data from individuals with a broken tag were censored at the last time the tag was functioning. Satellite data from birds with a tag but unknown fate were excluded, but in this case, we used re-encounters by visual observation and genetic information.

The collection of data was in accordance with the legal requirements of the countries in which it was carried out (Appendix 7).

2.4 | Data analysis

We jointly analysed the different data sets with an integrated population model (IPM; Besbeas et al., 2002; Schaub & Abadi, 2011; Schaub & Kéry, 2022) to estimate population sizes and demographic

rates and to perform a PVA. The IPM has the advantage of providing estimates with increased precision, which is important for small data sets, of the ability to estimate latent demographic rates, and its streamlined use as a PVA (Abadi et al., 2010; Schaub & Kéry, 2022). The estimated demographic rates and population sizes were used to test for evidence of density dependence, to identify the demographic drivers of the dynamics of each of the two spatial units of the Alpine population and to assess which demographic drivers contributed to the differential population dynamics between the two areas (Koons et al., 2016, 2017). Below we briefly describe the underlying stage-structured population model which is the main part of the IPM, the density dependence test, and finally the prospective (PVA) and retrospective population analyses. A full description of the IPM including the component likelihoods and the JAGS code can be found in Appendices S1 and S6, respectively.

2.5 | Integrated population model

The core of the IPM is a stage-structured population model (Caswell, 2001), whose underlying demographic rates and stage-structured numbers are estimated jointly from the breeding site survey data and the individual sighting and tracking data. We defined a post-breeding survey, female-based, stochastic model with a total of 10 stages for each of the wild-hatched and released individuals and the two areas (Appendix S1: Figure S1-1). These 10 stages refer to non-breeding females aged 0 to 8 years, and to breeding females aged at least 5 years. We assume that recruitment to the breeding stage begins at age 5 and is completed at age 10 and that the demographic rates of released and wild-hatched females are identical. The number of released female fledglings ($N_{1,t,m}^R$) in each area m and year t is known and given by the release management, while the number of wild-hatched female fledglings ($N_{1,t,m}^W$) is estimated and a function of productivity and breeding population size,

$$N_{1,t,m}^W \sim \text{Pois} \left(\frac{\rho_{t,m}}{2} \left(\left(N_{5,t-1,m}^W + N_{5,t-1,m}^R \right) \alpha_m s_{3,t-1} + \sum_{a=6}^8 \left(N_{a,t-1,m}^W + N_{a,t-1,m}^R \right) \alpha_m s_{4,t-1,m} + \left(N_{9,t-1,m}^W + N_{9,t-1,m}^R \right) s_{4,t-1,m} + \left(N_{10,t-1,m}^W + N_{10,t-1,m}^R \right) s_{4,t-1,m} b_{t,m} \right) \right)$$

where $\rho_{t,m}$ is the number of fledglings produced per breeding female in year t and area m , α_m is the probability that an as yet not reproducing female in area m starts to reproduce, $b_{t,m}$ is breeding propensity of experienced breeders in year t of area m , and s are annual survival probabilities (see Appendix S1: Table S1-1 for notation of parameters). For the latter, we used a specific age structure inspired by the behaviour of the vultures. s_1 is survival during the first year of life (0–1 year survival), which is area-specific because individuals do not move much yet. s_2 is annual survival during the second and third years of life (1–3 years survival), and s_3 is annual survival during the fourth and fifth years of life (3–5 years survival). At these ages, bearded vultures are highly mobile and therefore survival is assumed to be the same in both areas. s_4 is annual survival from the fifth year of life onwards. At this age, the

vultures have established a territory and are no longer mobile, so survival is again area-specific. Since dispersal between the two areas is rare (only 15% of individuals breed in a different area than where they fledged or were released, see also Jenny et al., 2018), we assume that the area where an individual fledged or was released is the area where it eventually breeds, which is equivalent to assuming that there was no dispersal between areas.

The number of females belonging to group G (with levels R [released] and W [wild-hatched]) in the remaining stage classes a (with $a=2 \dots 10$) in year t and area m ($N_{a,t,m}^G$) is a function of survival s and recruitment probability α , hence:

$$\begin{aligned} N_{2,t,m}^G &\sim \text{Bin}(N_{1,t-1,m}^G, s_{1,t-1,m}) \\ N_{3,t,m}^G &\sim \text{Bin}(N_{2,t-1,m}^G, s_{2,t-1,m}) \\ N_{4,t,m}^G &\sim \text{Bin}(N_{3,t-1,m}^G, s_{3,t-1,m}) \\ N_{5,t,m}^G &\sim \text{Bin}(N_{4,t-1,m}^G, s_{4,t-1,m}) \\ N_{6,t,m}^G &\sim \text{Bin}(N_{5,t-1,m}^G, (1-\alpha_m)s_{5,t-1,m}) \\ N_{7,t,m}^G &\sim \text{Bin}(N_{6,t-1,m}^G, (1-\alpha_m)s_{6,t-1,m}) \\ N_{8,t,m}^G &\sim \text{Bin}(N_{7,t-1,m}^G, (1-\alpha_m)s_{7,t-1,m}) \\ N_{9,t,m}^G &\sim \text{Bin}(N_{8,t-1,m}^G, (1-\alpha_m)s_{8,t-1,m}) \\ N_{10,t,m}^G &\sim \left(\text{Bin}(N_{5,t-1,m}^G, \alpha_m s_{3,t-1,m}) + \text{Bin}\left(\sum_{a=6}^8 N_{a,t-1,m}^G, \alpha_m s_{4,t-1,m}\right) + \text{Bin}(N_{9,t-1,m}^G + N_{10,t-1,m}^G, s_{4,t-1,m}) \right) \end{aligned}$$

As the entire Alpine population is modelled, we assume the absence of immigration and emigration. The model also assumes exponential growth, so no density-dependent feedback is included. We applied independent temporal random effects to most of the demographic parameters, the only exception being the probability of starting reproduction, which we assumed to be constant. We omitted temporal effects because our data were poorly informative for this parameter.

The IPM jointly analyses the different data sets, that is, the individual sighting and tracking data with capture-recapture models and the breeding site survey data with multinomial and state-space models. Each of the data sets is informative about some of the parameters of the developed population model. The results of the IPM are estimates of the stage-specific population sizes and of the demographic rates.

We fitted the IPM using the Bayesian framework (Kéry & Schaub, 2012; Schaub & Kéry, 2022) and used JAGS (Plummer, 2003) that was run from R with the package jagsUI (Kellner, 2019). We specified vague priors for all parameters (see Appendix S6) and ran 3 Monte Carlo Markov chains (MCMC) for 210,000 iterations, discarding the first 10,000 as burn-in and keeping every 200th value. This specification resulted in 3000 samples of the posterior distribution for each parameter. Model testing results are presented in Appendix S2.

2.6 | Tests for density dependence

We tested whether the annual population growth rate decreases with increasing population size and followed the simulation approach outlined in Schaub and Kéry (2022) which accounts for the

negative correlation between population growth rate and population size due to the mathematical dependence of them (Lebreton & Gimenez, 2013). We compared the observed relationship between population growth rate and population size with a simulated relationship between the two that would arise in the absence of density dependence. If the observed and simulated relationships do not differ, there is no evidence for density dependence. We have performed these tests for the entire Alpine population, and for the core and the periphery separately. In each case, we excluded the first 3 years after the first brood because of the large fluctuations in population growth at very low population sizes.

2.7 | Prospective and retrospective population analyses

We first calculated elasticities of realised population growth rates to temporal changes in demographic rates and in population structure (Koons et al., 2016, 2017) separately for each area, and also for the entire Alpine population. These prospective analyses show how much population growth would change if a demographic rate or population structure changed.

Second, we performed retrospective population analyses to identify the drivers of growth rates in each area. We used temporal decomposition to quantify the contribution of temporal variability and covariability of demographic rates and population structure to the temporal variability of population growth rates.

Thirdly, we compared population growth in the two areas over the period 2006–2021 and assessed how much each demographic rate and through which mechanism (i.e. differences in mean and/or temporal variability) contributed to the different dynamics (Koons et al., 2017).

2.8 | Population viability analyses

Using the IPM, we predicted the population size for the next 10 years after 2021 under different scenarios. The scenarios related to whether releases would continue as in the past or whether they would stop. We only considered releases of females because the model is female-based. In a scenario where releases continue

into the future, we assumed that one female is released in the core and two females in the periphery, which is the average of the last 10 years. Another scenario concerns the potential increase in mortality. We assumed increasing mortality hazards (instantaneous mortality intensity) from 0.01 (equivalent to 1 additional death per 100 individuals per year) to 0.10, which is additive to the current level of mortality. We also assumed that these additional mortality risks were the same for all age classes.

We calculated predicted population trends (2021–2031) from the predicted population sizes by linear regressions of log population sizes against time. From the posterior means of these growth rates, we calculated the probability that they would be negative, that is, that the population would decline, for the different scenarios. We quantified the effects on population growth rates in each area separately as well as for the Alpine population as a whole.

We generally present posterior means and 95% credible intervals (CRI). Data files and R code for all analyses performed are available on the [vogelwarte.ch](https://www.vogelwarte.ch) Open Repository and Archive (Schaub et al., 2024).

3 | RESULTS

The number of free-ranging bearded vultures in the Alps has increased significantly since the start of the reintroduction programme (Figure 2). By 2021, an estimated 172 (CRI: 147–198) females were alive, of which 65 (CRI: 63–67) were breeders, giving a total population size of 344 (CRI: 294–396) individuals, assuming an equal sex ratio. The mean annual population growth rate from 2002 to 2021, calculated from a linear regression as the logarithm of the total population size (i.e. the sum of released and wild-hatched individuals of all age classes) versus time, was 0.083 (CRI: 0.071–0.095). Although the number of individuals released was lower in the core (96: 54 females and 42 males) than in the periphery (130: 66 females and 64 males), the population grew faster in the core (mean growth rate: 0.093; CRI: 0.079–0.108) than in the periphery (0.051; CRI: 0.030–0.073), and the probability that the mean growth rates were different was 1.00. Since the appearance of the first wild-hatched individuals, their numbers have grown faster than the number of released individuals (Figure 2), and in the core area, the former exceeded the latter in 2009, or 2016 if only breeders were considered. In the periphery, however, the number of released individuals was still greater than the number of wild-hatched individuals by 2021.

Annual survival probabilities were high for all age classes and annual variation was low (Figure 3). Mean juvenile survival did not differ between birds from the two areas, but adult survival was higher in the core than in the periphery (Table 1). The breeding propensity of individuals from the periphery was temporally variable and tended to increase over time (Figure 3), while the other parameters related to reproduction were remarkably constant over time. Breeding propensity, probability of successful breeding

and probability of starting reproduction were all higher on average for birds from the core compared to those from the periphery. Thus, individuals from the core reproduced at younger ages (mean age at first reproduction, core: 8.1 [CRI: 6.0–9.7] years, periphery: 9.1 [CRI: 7.0–10.0] years), more regularly and more successfully than individuals from the periphery. Estimates of the nuisance parameters are presented in Appendix S3.

3.1 | Tests for density dependence

In the core, there was a tendency for annual population growth rates to be higher when the population size was less than about 30 females, but there was little change in the growth rate as the population increased beyond 30 females, and the probability that density dependence was operating was 0.92. There was no evidence of density dependence in the periphery or when considering the entire alpine population (Appendix S4).

3.2 | Prospective and retrospective population analyses

Population growth rates in both areas were more sensitive to changes in demographic rates than to changes in population structure (Figure 4). Adult survival was the demographic parameter with the highest growth rate elasticity and the probability of starting reproduction was the parameter with the lowest elasticity. Juvenile and immature survival, breeding propensity and breeding success had similar elasticities in the core, whereas in the periphery the elasticities of breeding propensity and success were lower than those of survival. As expected for a long-lived species (Sæther & Bakke, 2000), these results show that bearded vulture population growth is highly sensitive to changes in survival, much more so than to changes in reproductive parameters.

The retrospective analyses quantify how much temporal variation in demographic rates and relative population structure have contributed to the temporal variation in population growth rate. In the core, variation in survival and the proportion of breeders contributed more to the variation in population growth than variation in breeding parameters and the proportion of non-breeding individuals (Figure 4). In the periphery, variation in juvenile survival contributed the most. Compared to the core, the contribution of variation in breeding propensity was stronger in the periphery and the contribution of the relative proportion of breeders was lower. The uncertainties of all estimated contributions were pronounced, making conclusions difficult.

Over the last 16 years (2006–2021), the core population grew faster than the periphery population, mainly as a result of differences in adult survival between the two areas (Table 2). Differences in breeding success also contributed, while the effects of differences in breeding propensity and juvenile survival were smaller. Interestingly, the contribution of the difference in means was similar for adult

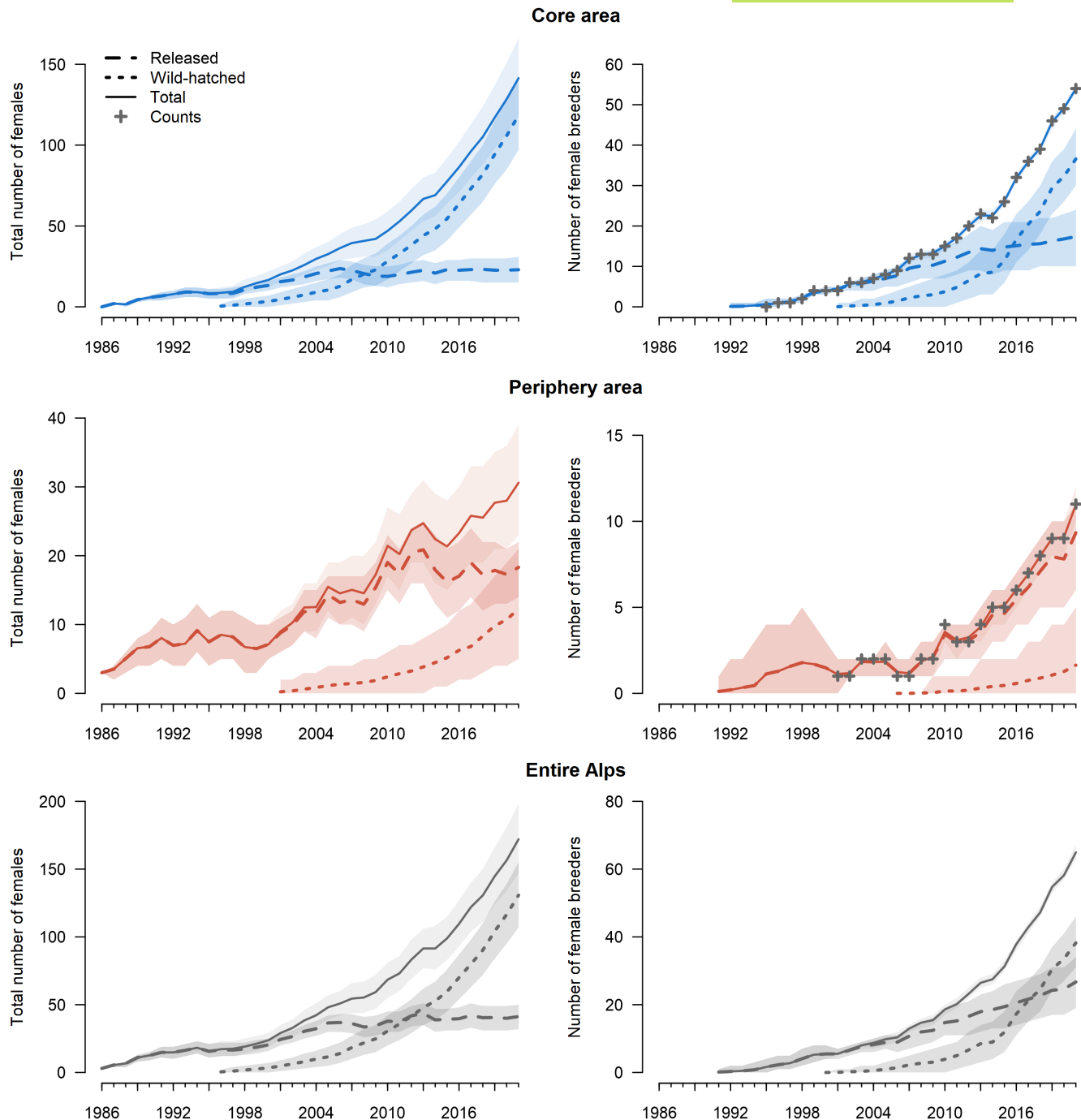


FIGURE 2 Estimated number of female bearded vultures by area (core, periphery) and origin (released, wild-hatched, plus the sum of them [total]). The panels in the left column show the total number of females (all age classes), the panels in the right column show the number of female breeders. The lines show the posterior means, the areas the limits of the 95% credible intervals. The number of breeding pairs counted for each area is also shown (counts).

survival and breeding success, but the indirect effects mediated by the change in population structure were opposite: improved adult survival in the core resulted in a relative increase in older age classes, which had a positive effect on population growth, whereas improved breeding success resulted in a relative increase in the youngest age class, which had a negative effect on population growth (see also Figure 4). Differences in the temporal variability of the demographic rates hardly contributed to differences in population growth rates.

Because the probability of starting reproduction was assumed to be constant over time, we have not evaluated the effect of it.

3.3 | Population viability analyses

The entire Alpine population of bearded vultures is predicted to double by 2031 (mean: 353 females; CRI: 248–458) if the current

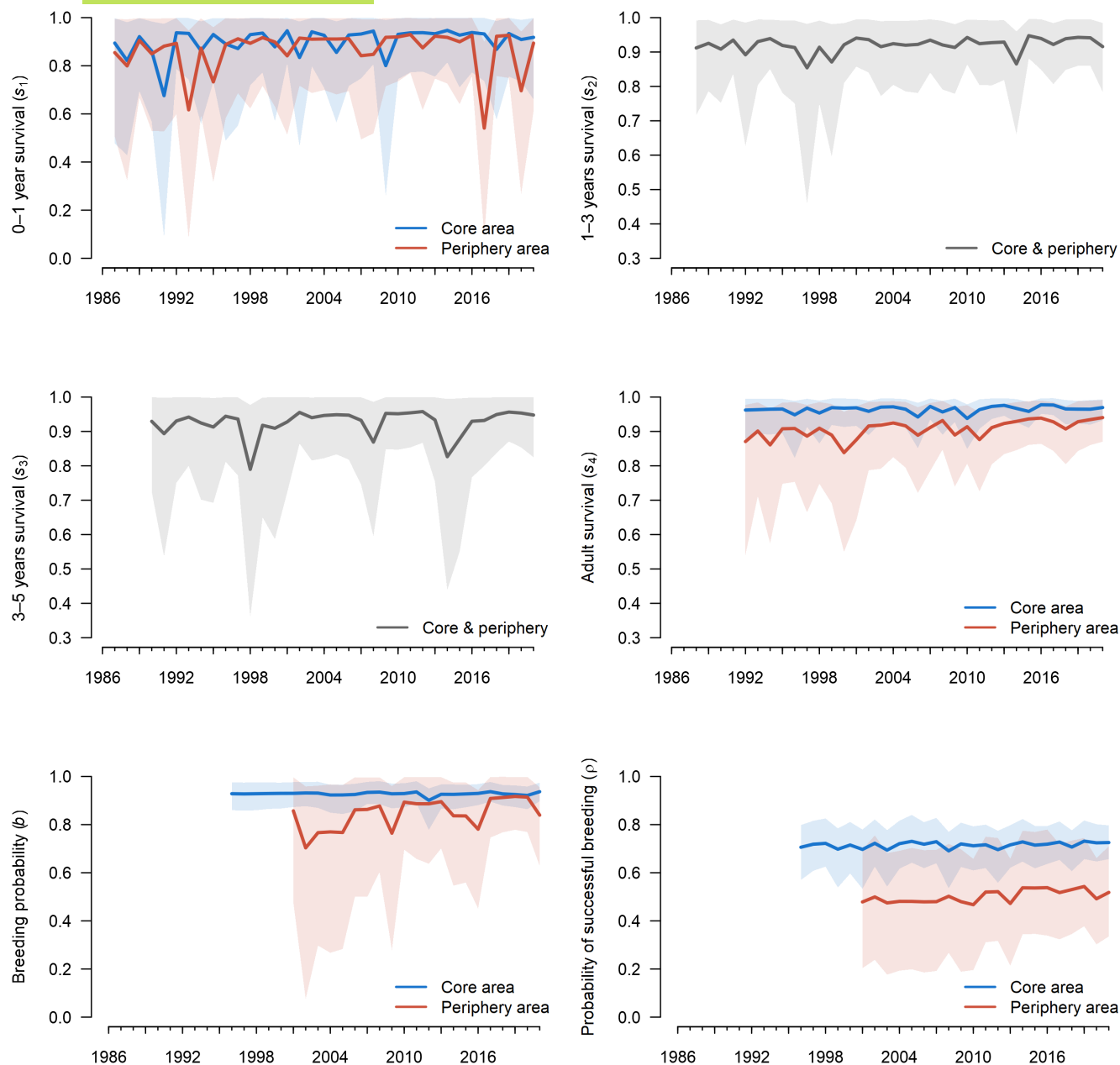


FIGURE 3 Estimated age-specific survival probabilities, breeding propensities and probabilities of successful reproduction of Alpine bearded vultures. Survival between 2 and 5 years is assumed not to differ according to the origin of the birds, all other parameters are assumed to differ. The solid lines refer to the posterior means, the coloured areas show the limits of the 95% credible intervals.

release practices continue and the demographic rates remain at current levels (Figure 5 and Appendix S5: Figure S5-1). Population growth is predicted to be stronger in the core than in the periphery area, and the probability of a population decline is 0 in the core and about 0.15 in the periphery. If the releases had stopped by 2022, the predicted size of the core and hence of the total population would grow to almost the same size, while in the periphery the growth would be much lower, and the probability of a population decline would increase to 0.6 (Figure 5).

The predicted population size in 2031 decreases with increasing additional mortality and the probability of a population decline increases (Figure 5 and Appendix S5: Figure S5-1). In the core area,

the probability of a population decline exceeds 0.05 once the mortality hazard becomes greater than about 0.025, equivalent to the additional death of 3–4 females per year at the current population size (Appendix S5: Figure S5-2). These values hardly change regardless of whether releases continue or cease. In the periphery area, the probability of a population decline already exceeds 0.05 at the current level of mortality. For the Alps as a whole, the probability of a population decline exceeds 0.05 when the mortality hazard becomes greater than 0.02, corresponding to the additional death of about 4 females per year at the current population size. An increase in the mortality hazard to 0.055, equivalent to an additional death of about 9 females per year, predicts a decline in the population in

TABLE 1 Estimated demographic rates of bearded vultures from the core and periphery. Posterior means with 95% credible intervals in brackets and probabilities that estimates in the core are greater than those from the periphery are given. For estimates of the entire Alpine population see Appendix S5: Table S5-2.

Parameter	Core	Periphery	p (core > periphery)
0–1 year survival (s_1)	0.935 (0.872, 0.981)	0.910 (0.822, 0.976)	0.726
1–3 years survival (s_2)	0.934 (0.890, 0.975)	0.934 (0.890, 0.975)	—
3–5 years survival (s_3)	0.950 (0.896, 0.992)	0.950 (0.896, 0.992)	—
Adult survival (s_4)	0.969 (0.953, 0.984)	0.919 (0.880, 0.953)	0.996
Breeding probability (b)	0.931 (0.904, 0.957)	0.872 (0.750, 0.956)	0.880
Probability of success (ρ)	0.716 (0.665, 0.762)	0.507 (0.376, 0.633)	0.999
Probability to start reproduction (α)	0.188 (0.023, 0.514)	0.082 (0.002, 0.316)	0.786

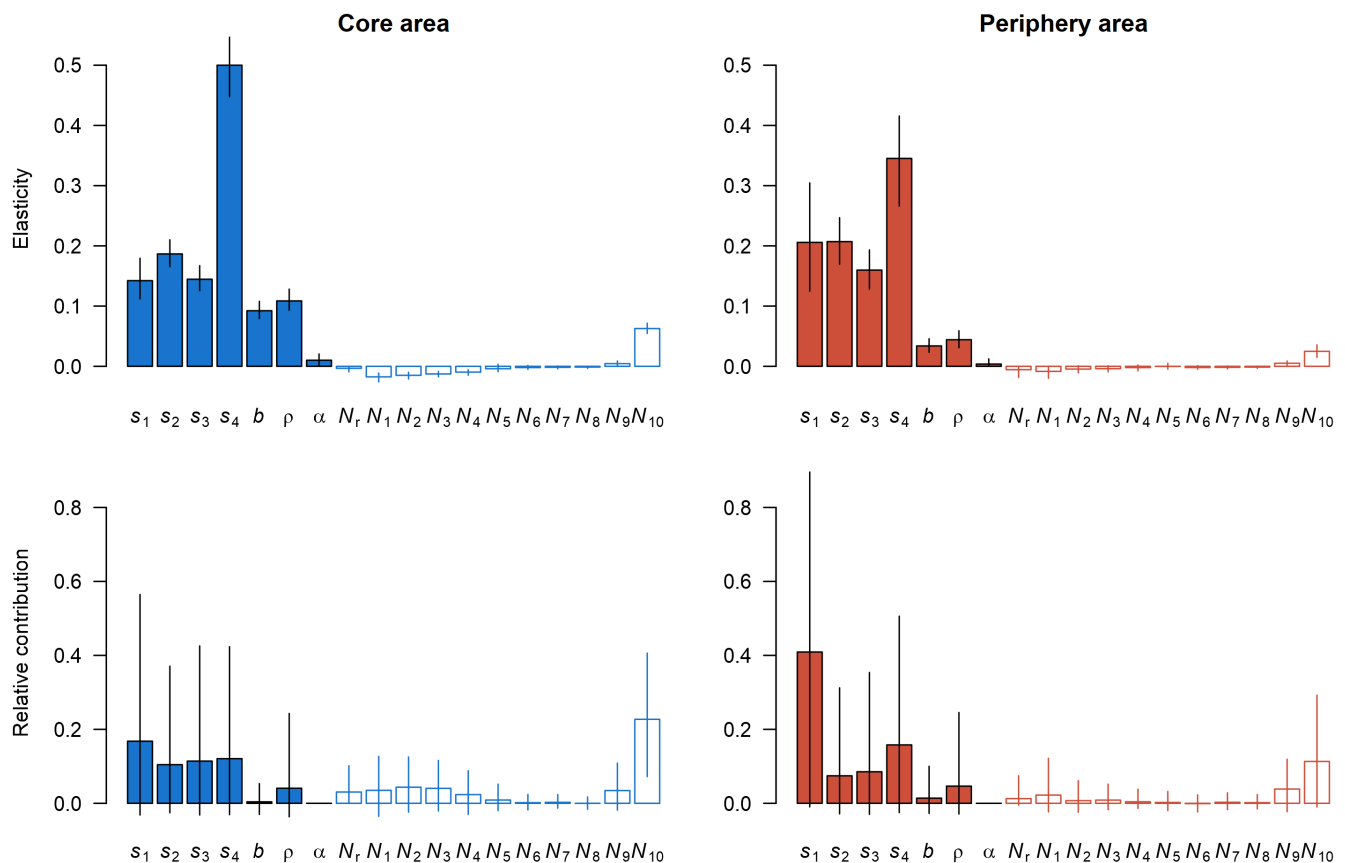


FIGURE 4 Growth rate elasticities and relative contribution of the temporal variability of demographic rates (closed bars) and of population structure (open bars) to the variability of the bearded vulture population growth rate in the core and the periphery area. The symbols for the demographic rates and population structure are shown in Table 1. N_r refers to the relative number of fledglings released.

the absence of further releases. If releases continue, the mortality hazard could increase to slightly higher values (0.063, equivalent to an additional death of 10.5 females per year) before the population is predicted to decline.

4 | DISCUSSION

The number of wild-hatched bearded vultures in the Alps has increased significantly since the start of the reintroduction programme and the re-established population is currently self-sustaining from a demographic point of view and shows no signs of negative density dependence. Population growth was spatially heterogeneous,

with much slower growth at the edges of the Alpine distribution than in the central part, mainly due to differences in adult survival. Furthermore, our study shows that bearded vultures are very sensitive to changes in survival, especially of adults, and that a relatively small increase in mortality can turn the currently increasing population into a declining one.

Schaub et al. (2009) evaluated the reintroduction of bearded vultures in the Alps in the year 2006 when nine pairs were breeding, and it was already then concluded that the population was self-sustaining, that further releases were not necessary from a demographic point of view, and that bearded vultures were highly sensitive to changes in adult survival. The current study, which reassesses the population 15 years later, extends the previous work

TABLE 2 Estimated contributions (c) to the difference in the geometric mean population growth rate between the core and the periphery of the Alpine bearded vulture population from direct effects, denoted by (A) of a change in the mean (μ) or in the standard deviation (σ) of a demographic rate (s_1 : juvenile survival, s_4 : adult survival, b : breeding propensity, ρ : breeding success), and from indirect effects channelled through perturbations in the population structure over time, denoted by (n), again from changes in the mean or the standard deviation. Posterior means and 95% credible intervals (for the total contribution) are given.

Type of contribution	s_1	s_4	b	ρ
c_{μ}^A	0.0060	0.0272	0.0041	0.0225
c_{σ}^A	0.0001	0.0001	0.0000	0.0000
c_{μ}^n	-0.0033	0.0116	-0.0024	-0.0135
c_{σ}^n	0.0002	0.0005	0.0000	-0.0001
Total contribution	0.0030 (-0.0017; 0.0090)	0.0395 (0.0139; 0.0677)	0.0017 (-0.0004; 0.0056)	0.0089 (0.0029; 0.0170)

in several important ways. Larger sample sizes led to increased precision of the parameter estimates and more reliable inferences, as well as the ability to estimate breeding probability. We also included the demography of wild-hatched individuals, which is crucial for population assessment if the demographic performance of wild-hatched and released individuals differs, as has been observed in other reintroduction programmes (Armstrong et al., 2021; Sarrazin et al., 1994). We have also incorporated spatial structure and environmental stochasticity into the assessment to make it more realistic.

The prediction of Schaub et al. (2009) about the future population development turned out to be accurate, the predicted population growth rate under a scenario with releases and a breeding probability of 0.8 was about 0.09, only slightly higher than the now observed growth rate of 0.083. Estimated survival probabilities from the earlier analysis tended to be slightly lower than those now reported (Appendix S5: Table S5-2), but given the uncertainties, the most reasonable conclusion is that no major changes have occurred over time. Most of the demographic rates showed little temporal variation, with the exception of juvenile survival and the breeding probability in the periphery area (Figure 3).

Bearded vulture population growth was not spatially uniform, with growth in the core being almost twice that of the periphery, and the demographic reason for this difference was mainly differences in adult survival and secondarily differences in breeding success. The spatial heterogeneity in demographic performance may be related to spatial variation in the prevailing ecological conditions across the Alpine massif, which appear to be more favourable in the core than in the periphery due to limestone substrates and the high presence of ibex (Hirzel et al., 2004; Vignali et al., 2021). Dense populations of ibex provide an optimal food supply as they typically inhabit open rocky habitats, making it easier for bearded vultures to locate carcasses. Limestone substrates tend to form more mineralised landscapes, providing numerous screes with small stones, which are the most suitable bone-breaking surfaces for marrow extraction (Hirzel et al., 2004). In addition, human persecution appears to be higher in the periphery than in the core area, with several confirmed cases of bearded vulture poaching reported from the eastern and southern Alps (Loercher & Hegglin, 2021), which may have contributed to the differential survival.

The dynamics of the bearded vulture population in the Pyrenees have been studied using a similar IPM to ours (Margarida et al., 2020). This population has never gone extinct and is therefore suitable for comparison with the reintroduced population in the Alps. Currently, the Pyrenean population is about 3 times larger than the Alpine population. It has also been increasing steadily since the late 1980s, with an annual growth rate of 0.033, which is lower than the current growth rate of the Alpine population. The Pyrenean population is subject to density-dependent regulation, operating mainly through productivity and juvenile survival, while there is currently no evidence of density dependence in the Alpine population. Apart from density dependence, there are few demographic differences between the autochthonous population in the Pyrenees and the re-introduced population in the core of the Alps. The proportion of breeding females among all females (Pyrenees: 0.36, Alps: 0.38) and the survival probabilities are almost identical, and adult survival is almost exactly the same (Appendix S5: Table S5-2). However, productivity in the Pyrenees is about half that of the Alps, and the age at first reproduction is currently later in the Pyrenees than in the Alps, both of which are likely to be due to density dependence. As the population in the Alps continues to grow, it is expected that density-dependent regulatory mechanisms will eventually start to operate, probably affecting productivity as in the Pyrenees.

The dynamics of the Alpine bearded vulture population were mainly driven by the variation in the proportion of adults, the latter being a delayed consequence of several demographic processes. Variation in demographic rates contributed relatively little to the variation in population growth. Taken together, these results indicate that changes in demographic rates did not have an immediate strong effect on population growth, but were mostly delayed. The most sensitive parameter for population growth was adult survival, which did not vary much over time, presumably due to demographic buffering (Hilde et al., 2020), and therefore did not contribute strongly to short-term population fluctuations. Although the sensitivity of the growth rate to changes in juvenile survival was low, its temporal variation has contributed more to immediate population fluctuations than any other demographic parameter considered.

The finding that bearded vulture populations are highly sensitive to increases in mortality is not new (Margarida et al., 2020; Schaub et al., 2009). We show that in the core area, an increase in mortality

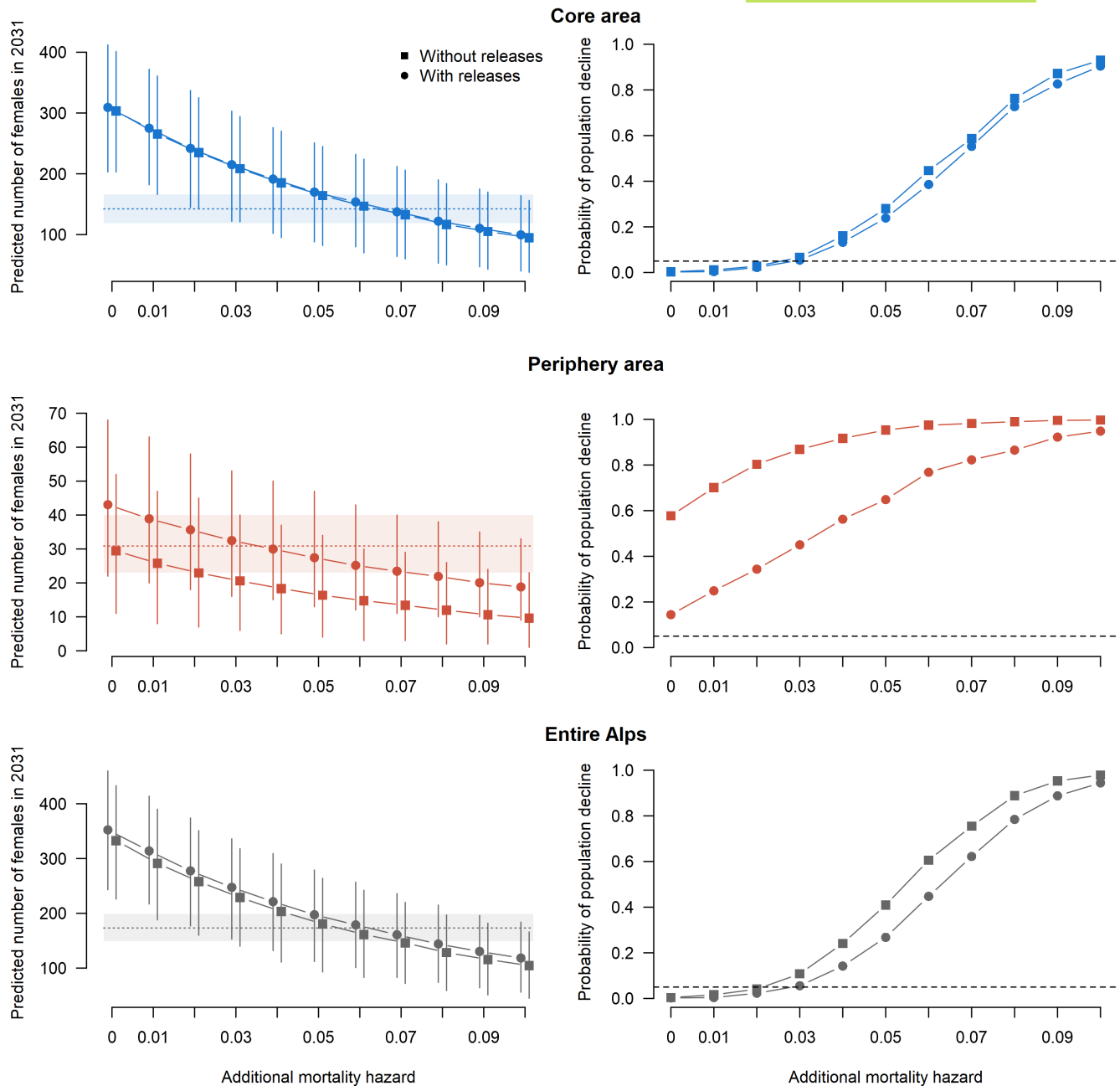


FIGURE 5 Predicted number of females in 2031 (left panels) and the probability of population decline in the next 10 years (right panels) as a function of additional mortality and release strategy. The estimated number of females in 2021 is shown in the left panels by dotted horizontal lines together with its 95% credible interval (light rectangle). The probability of population decline is calculated from 2021 to 2031 as a regression of log population size over time from which the probability of decline is derived. The dashed horizontal line corresponds to a probability of decline equal to 0.05, or conversely, when we are 95% certain that the population is not declining.

risk of 0.02, corresponding to an additional 6–8 individual deaths per year (calculated for the population size in 2021), is sufficient to lose the confidence in future population growth. Adding the current number of releases would not help to compensate for these losses. In the periphery, the probability that the population will continue to increase is much lower than in the core, even in the absence of additional mortality. If the mortality hazard were to increase to 0.02, the probability that the population would decline is already greater than 0.3 and would increase to about 0.8 if releases were stopped.

We conclude that the reintroduction of bearded vultures in the Alps has been very successful in establishing a demographically self-sustaining population. From a purely demographic perspective, further releases seem unnecessary. However, from a geographically explicit and genetic perspective, this conclusion should be dampened. In the periphery, further releases would help to drastically reduce the probability of a future population decline (Figure 5). Although the long-term goal of releasing captive-bred individuals cannot be to compensate for the demographic problems of bearded

vultures in the periphery, continuing releases will be beneficial in the short term. In the core, in contrast, further releases would have a negligible demographic effect (Figure 5) but could help to increase genetic diversity, which remains low (own unpublished data).

Due to the high sensitivity of bearded vulture populations to potential increases in mortality, efforts to avoid additional mortality should be given a high priority. New sources of mortality that may be of particular concern to the Alpine bearded vulture population are the installation of wind turbines in mountainous areas (Vignali et al., 2021, 2022), which may increase the probability of fatal collisions with rotor blades, and the spread of illegal poisoning of large carnivores, which may represent a new threat to all scavengers. It is therefore essential that monitoring of demographic rates continues to allow early detection of any demographic problems. The established sampling of feathers, which allows the genetic identification of individuals, is a particularly valuable source of information as the population is increasingly dominated by wild hatchlings, most of which are unmarked and therefore only genetically identifiable.

A downside of the otherwise successful reintroduction project is the higher adult mortality and the lower breeding success of the peripheral compared to the core population, which may reduce the capacity of bearded vultures to colonise the entire Alps. Identifying their causes is a high research priority and their subsequent mitigation is a key management target. Unless effective measures are taken, the peripheral population will remain dependent on further releases and/or immigration from the core.

AUTHOR CONTRIBUTIONS

Michael Schaub, Franziska Loercher, Daniel Hegglin and Raphaël Arlettaz conceived the ideas and designed the methodology; Franziska Loercher collated the data; Michael Schaub analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that there are no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data and code are available on the vogelwarte.ch Open Repository and Archive: <https://doi.org/10.5281/zenodo.11090787> (Schaub et al., 2024).

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SUPPORTING INFORMATION

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

Appendix S1. Detailed description of the integrated population model.

Appendix S2. Results of the assessment of the integrated population model.

Appendix S3. Results on the nuisance parameters of the integrated population model.

Appendix S4. Results of the density dependence tests.

Appendix S5. Additional tables and figures.

Appendix S6. JAGS code of the integrated population model.

Appendix S7. Statement on legal requirements for data collection.

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