

# An assessment of population size and demographic drivers of the Bearded Vulture using integrated population models

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*Abstract.* Conventional approaches for the assessment of population abundance or trends are usually based on a single source of information, such as counts or changes in demographic parameters. However, these approaches usually neglect some of the information needed to properly understand the population as a whole, such as assessments of the non-breeding proportion of the population and the drivers of population change. The Bearded Vulture Gypaetus barbatus is a threatened species and its Pyrenean population (the largest in Europe) inhabits parts of Spain, Andorra, and France. We developed an Integrated Population Model (IPM) using data from a long-term study (1987-2016) in the three countries, including capturemark-recapture of 150 marked individuals, to assess population size and age structure at the whole population scale, and obtain estimates of survival and breeding parameters of this population. The breeding population experienced a geometric mean population increase of 3.3% annually, falling to 2.3% during the last 10 yr. The adult proportion of the population increased with time, from 61% to 73%. There were 365 (95% Bayesian credible interval [BCI]: 354–373) adult breeding birds in 2016, representing 49% of the adult population and 36% of the total population (estimated at 1,026 individuals, 95% BCI: 937–1,119). The large number of non-breeding adults probably led to higher mean age of first reproduction than previously estimated, and to an estimated 30–35% of territories occupied by polyandrous trios. Population growth rate was positively and strongly correlated with adult survival, which had a much greater effect on population growth than productivity. The effects of subadult and juvenile survival on population growth were weaker. We found strong evidence for a density-dependent decrease in juvenile survival, productivity and adult survival, leading to reduced population growth with increased population size. Our approach allowed us to identify important conservation issues related to the management of supplementary feeding sites and geographic expansion of this population. Our study supports the use of IPMs as a tool to understand long-lived species, allowing simultaneous estimates of the non-breeding size of the population (which is critical for understanding population functioning), better estimates of population parameters, and assessment of demographic drivers.

Key words: age-class structure; Bearded Vulture; density dependence; integrated population model; non-breeders; polyandry; population growth rate; productivity; survival rate.

#### INTRODUCTION

Assessments of population size and trends lie at the core of any population ecology or conservation biology

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study. These are often inferred from indirect information such as abundance indices, or estimated extrapolating from density in certain sampled areas. However, detailed information on density or total population size is essential to address certain demographic and conservation management questions (MacKenzie et al. 2005, Ryan et al. 2019). Similarly, estimating a variety of demographic variables (e.g., productivity, survival, age of first breeding, likelihood of the different age groups entering the breeding population) is critical to properly understand population processes and diagnosing factors limiting population growth (Turchin 2003, Beissinger et al. 2008). However, some of these estimates are not always easily obtained from population monitoring programs, so in many cases they are not simultaneously estimated for a given population (or subpopulation), impairing their comprehensive interpretation.

In addition, monitoring is frequently fragmented in space by logistic, political or administrative barriers. Population parameters may differ locally, so the representativeness of population or demographic results obtained from projects limited in space or time should be carefully considered. Processes occurring across entire, continuous populations may not be interpreted correctly if only part of the population can be assessed, and this is particularly important for wide-ranging species, where assessments at the whole population level are most useful (Lambertucci et al. 2014, Margalida et al. 2018). Several examples of species distributed across administrative boundaries at low densities or in difficultto-study areas show that it can be challenging to anticipate the effects of management and conservation decisions when they are based on information from only one part of the population (Linnell et al. 2016, Vitkalova et al. 2018).

Some endangered species are monitored regularly, sometimes through intensive, resource-costly, long-term fieldwork programs (Birkhead 2014), both to assess their status and examine the effects and consequences of conservation management interventions. Conventional approaches are usually based on a single source of information, either counts (e.g., number of active nests) or changes in demographic parameters (e.g., productivity or survival rates, the latter usually based on capturerecapture models; Williams et al. 2002, MacKenzie et al. 2005, Kendall et al. 2009, Blakesley et al. 2010). However, these approaches usually lack part of the information necessary to understand the population as a whole. For example, for practical reasons population monitoring of territorial species such as raptors usually focuses on observations of occupied territories to assess changes in breeding population size and productivity (Sergio 2003, Saurola 2008, Ortega et al. 2009). This, however, ignores the non-breeding part of the population, which may strongly influence the overall population dynamics (Lande et al. 2003, Penteriani et al. 2008, Lee et al. 2017). Monitoring and quantifying non-territorial individuals or floaters is usually exceedingly difficult because of the frequent dispersive lifestyle and the cryptic nature of non-breeding animals, which may need to be detected through complex approximations, e.g., using molecular techniques (Katzner et al. 2011). An alternative way of estimating the size of non-breeding populations is to take into account their different detectability in models such as capture-mark-recapture/resighting (CMR; Sandercock et al. 2000).

Integrated population models (IPM) represent a methodological advancement for the estimation of population parameters (Kéry and Schaub 2012). IPMs can combine the analysis of CMR data, population counts and information on reproductive success into a single model to enhance estimates of population size and demographic parameters (Besbeas et al. 2002, Abadi et al. 2010b, Plard et al. 2019, Saunders et al. 2019). IPMs have proved useful in improving our ecological understanding of population processes, and in improving management decisions (Rushing et al. 2017, Bled et al. 2017).

We exemplify their usefulness for the Bearded Vulture (Gypaetus barbatus), a threatened species with the majority of its European population in the Pyrenees. The Pyrenean population is shared between Spain, France, and Andorra. Numbers of breeding birds there have increased progressively from the 1970s due to various conservation programs, including protected status, protection of breeding sites and the creation of supplementary feeding stations (SFS) at various locations. Conventional surveys include monitoring of breeding sites and counts at SFS, regularly performed to estimate variations in population size and productivity. Additionally, some studies focused in part of the Spanish fraction of the population have estimated survival rates and agestructure of the population using CMR data from marked individuals (Oro et al. 2008, Gómez de Segura et al. 2012, Margalida et al. 2014). Results from previous studies indicate density-dependent processes occurring in at least certain areas (Carrete et al. 2006a), possibly as a result of increased survival of juveniles using SFS (Oro et al. 2008), although differences between the Spanish and French watersheds have been suggested (Arroyo et al. 2020). No studies have quantified the entire population size for the whole of the Pyrenees, including estimates of the non-breeding fraction of the population, or have estimated demographic parameters (including survival of different age groups, age of first breeding and productivity) at that scale. The latter may allow assessing whether the increase in population has led to any density-dependent processes in these parameters, and thus understand current or future population limitation. Additionally, all this information is key to assess conservation status of the species, both in the Pyrenees and in nearby areas, as well as to forecast impacts of current and future conservation management programs on the species.

Here, we take advantage of the long-term study (1987–2016) of the Pyrenean Bearded Vulture population, including survey data on territory numbers, observed productivity and CMR data on marked individuals, and use an IPM approach to assess the population size (both breeding and non-breeding parts), age structure, survival and breeding parameters at the population level throughout the study period. Additionally, we assess the relationships between the different demographic parameters and population growth rates, and test density-dependent relationships on population growth rate or demographic parameters. We discuss our results in relation to population processes in this increasing population, and the conservation implications for this threatened and managed species.

#### MATERIALS AND METHODS

# Study species and population

The Bearded Vulture is a large, solitary, territorial scavenger with a diet largely consisting of the bones of domestic and wild ungulates (see review in Margalida 2010).

The European range of the Bearded Vulture comprises the Pyrenees, Andalusia (southern Spain), Asturias (northern Spain), the Alps, Corsica (France), and Crete. Uniquely, the Pyrenean population has been intensively monitored within the framework of the Species' Recovery Plan in the Autonomous Communities of the Basque Country, Navarra, Aragon, and Catalonia in Spain, particularly with regard to population trends, breeding parameters and survival rates (including a regional CMR program). Intensive monitoring of population trends and breeding output has also been performed on the French side of the Pyrenees within the framework of a National Action Plan (Arroyo et al. 2020), although CMR programs are less intensive there.

The Bearded Vulture is a long-lived species that, in general, reaches adult plumage at 5-6 yr of age. Based on plumage characteristics, we defined juvenile or immature birds as those <2 yr old, subadults as birds 2-5 yr old, and adults as those >6 yr old. Studies in the wild and in captivity have indicated that birds first pair and become territorial at an average age of 6.5 yr (Antor et al. 2007).

Territorial individuals display defensive behavior against both conspecifics and heterospecifics, most of which occurs at a distance of <300 m from the nest (Bertran and Margalida 2002, Margalida et al. 2015). Clutch size is usually two eggs, but only one chick survives due to inter-sibling aggression (Margalida et al. 2004). After fledging, young Bearded Vultures may disperse large distances from their natal territories until they enter the breeding population (usually relatively close to their natal area). Radio tracking and satellite telemetry studies have shown that juvenile, subadult and non-territorial adults in the Pyrenees move across the whole mountain range and generally aggregate at SFS, mainly on the southern side of the Pyrenees (Margalida et al. 2013, 2016, 2017a). Non-territorial birds use areas of around 11,000 km<sup>2</sup>, while territorial birds exploit home ranges (Kernel 90) of about 60 km<sup>2</sup>, with daily movements of 46.1 and 23.8 km, respectively (Margalida et al. 2016).

The species is usually monogamous, but polyandrous trios have been described in the Spanish part of the Pyrenean population (Carrete et al. 2006*b*, Bertran et al. 2009), where their frequency seems to be density-dependent, increasing with increasing population size (forming up to 20-25% of all occupied territories, Carrete et al. 2006*b*) in response to increasing scarcity of empty territories of sufficient quality (Carrete et al. 2006*a*).

# Data collection

We collected three types of data from 1987 to 2016: CMR data, observed data on breeding output (productivity and breeding success of monitored nests) and breeding population counts (individuals in pairs and polyandrous groups).

Regarding the observations on breeding counts and output, all known occupied territories in the Pyrenees (in Spain, France and Andorra) were regularly visited (2-4 visits/month) to record reproductive parameters. In addition, potential suitable territories were also visited each year searching for signs of occupancy (territorial and/or courtship behavior, nest arrangement/building) to detect new occupied territories. Observations began in September-October, coinciding with the start of nestbuilding and sexual activity (Bertran and Margalida 1999, Margalida and Bertran 2000) and ended during fledging (June-August, Margalida et al. 2003). Nests were observed from a distance using  $20-60 \times$  telescopes, and using video cameras in some cases. Egg-laying was confirmed when an incubation shift between parents was observed or when the nest content was visible. We defined productivity as the number of chicks fledged per nesting pair (i.e., those territorial pairs that had at least built a nest).

With respect to CMR data, 150 birds of known age were captured between 1987 and 2016, ringed, marked with bands and wing tags and safely released in the trapping area (for details on capture and marking procedures, see Oro et al. 2008, Margalida et al. 2014). Each individual was marked with two wing tags with the same alphanumeric code (one per wing) to reduce the probability of misidentification if one tag was lost. In this sense, tag loss was not a problem for the estimates because only 2.3% cases were documented. We aimed to obtain observations of marked individuals through our monitoring of breeding territories, as well as by visiting weekly SFS (mainly the larger ones) located within the study area (Sesé et al. 2005, Margalida et al. 2011a, b). Only resightings carried out during the first period of each year (from early January to late April) were taken into account to meet the assumption of capture-recapture models that resightings shall be obtained within a short period of time.

# Integrated population model implementation

We used IPM methods to estimate demographic parameters (Schaub and Abadi 2011) and population sizes using a Bayesian approach that integrates CMR multi-state data and counts to improve the precision of the estimates (Besbeas et al. 2002, Brooks et al. 2004, Abadi et al. 2010a,b, Cave et al. 2010).

Based on our long-term study of Bearded Vultures (Margalida 2010), we constructed our IPM using the structure described by Szostek et al. (2014).

The first element of the IPM is a population model that links the demographic rates with changes in population size, consistent with life history parameters and available data, using an age-classified matrix population model (Caswell 2001). The second element expresses the likelihood of all the data sets used in the model: (1) counts of breeding pairs, polyandrous groups and fledg-lings, and (2) CMR data in a multistate Cormack-Jolly-Seber (CJS) model. In a last step, we constructed the joint likelihood and made statistical inferences (Kéry and Schaub 2012).

In our IPM, transitions between states were defined as occurring between year t and t + 1. The states were defined based on a combination of the breeding status of an individual and its age. We defined 16 states for individuals that had never bred, 10 states for first-time breeders and 11 states for experienced breeders (Fig. 1, Appendix S1, Data S1). The number of individuals in a certain state in year t + 1 is a function of the number of individuals in other states in year t and their demographic

rates (survival and fecundity). Fecundity (f) was defined, following Kéry and Schaub (2012), as fledglings per breeding female. Although fecundity is likely to change with age, we do not have quantitative information to parameterize this adequately for the IPM so we used the average value for all ages. Our model estimated parameters on age-specific probabilities of survival (3 age classes: 0-2 yr  $\phi_1$ , 2-6 yr  $\phi_2$ , older than 6 yr  $\phi_3$ ), first time breeders ( $\alpha_t$ , 15 age classes, but we defined 1–5 as zero), fecundity (equal in all reproductive age classes), first-time breeders *i* at the age of *t* ( $F_{i,t}$ ), and yearly breeding propensity  $(\delta_t)$  of adults *i* of age *t*  $(B_{i,t})$  that had bred before. The sex ratio at fledging was assumed to be equal. The life cycle graph is shown in Fig. 1, and a graphical depiction of the integrated population model showing the different data sources in Fig. 2.

Mean age of first reproduction (AFR) was calculated (following Arlettaz et al. 2017) as follows:

$$AFR = \alpha_6 + \sum_{n=7}^{15} \left( n * \alpha_n \prod_{i=6}^{n-1} (1 - \alpha_i) \right).$$

Non-breeding individuals from ages 1-5 (2–6 calendar years, cy) in year t + 1 were modeled as a function of survival and the population in the previous year.



FIG. 1. Life cycle graph of Bearded Vultures used in the integrated population model. We assume neither emigration nor immigration. See states and demographic rates descriptions in the section *Integrated population model implementation* 



FIG. 2. Graphical depiction of the Bearded Vulture integrated population model (IPM) showing the different data sources to contribute to shared inference on demographic parameters and population abundance. Demographic parameters are represented with green circles, observation parameters with white, and data are symbolized with blue. Arrows demonstrate the dependences between nodes. Sub-models are represented by yellow rectangles and titled with the data type and model structure. Node notations:  $n_n$ , number of nests;  $n_j$ , number of juveniles produced; f, per-capita recruitment rate;  $s_{juv}$  juvenile survival probability;  $s_{sub}$ , subadult survival probability;  $n_{pain}$  number of individuals in breeding polyandrous groups;  $\sigma^2$ , observation error on count data; N, true population abundance; d, recovery rate of dead individuals; M, capture-recapture data;  $p_m$ , capture probability for marked individuals. Figure adapted from Zipkin and Saunders (2018).

$$N_{2...6,t+1}$$
: Binomial( $\phi_{2,t}, N_{1...5,t}$ )

Environmental stochasticity was included by allowing annual variation in all demographic rates. To estimate the number of 1-yr-old individuals, we used the Poisson distribution, and used the Binomial distribution to describe the link between state-specific numbers in year t + 1 and t (Kéry and Schaub 2012, Szostek et al. 2014) as follows:

$$N_{1,t+1}$$
: Poisson $\left(\frac{P_t}{2}\phi_{1,t}\left(\sum_{i=7}^{i=17}F_{i,t}+\delta\sum_{i=8}^{i=18}B_{i,t}\right)\right)$ .

From the age 6–15 (7–16 cy) the number of individuals that never bred was modeled as a function of adult survival, the probability ( $\alpha_{6...15,t}$ ) that a bird that has not reproduced before starts to reproduce at year *t*, and the population during the previous year

$$N_{7\dots 16,t+1}$$
: Binomial  $(\phi_{3,t}(1-\alpha_{6\dots 15,t}), N_{6\dots 15,t})$ .

Whereas first breeders were modeled as

$$F_{7\dots 16,t+1}$$
: Binomial $(\phi_{3,t} \cdot \alpha_{6\dots 15,t}, N_{6\dots 15,t})$ .

From the age of 7–15 (8–16 cy), experienced breeders in year t + 1 were modeled as a function of adult survival and individuals that bred previously

$$B_{8\dots 16,t+1}$$
: Binomial $(\phi_{3,t}, F_{7\dots 15,t} + B_{7\dots 15,t})$ .

And older individuals

$$B_{17...,t+1}$$
: Binomial  $(\phi_{3.t}, B_{16...,t})$ .

We assumed that all individuals commenced breeding by age 15 yr (16 cy) at the latest, and thus all birds aged 16 yr (17 cy) or older were considered potential breeders (although some could skip reproduction; life stage matrix: Appendix S2; see also Data S1).

The second element of the IPM expresses the likelihood for each data set. We used a state-space model to model population counts (number of individuals in breeding pairs and polyandrous individuals). For the number of individuals in breeding pairs (NT), data for counts were modeled as follows:

CountsPairs : Normal 
$$\left(NT \times \left[1 - \beta_{[l]}\right], \sigma_{obs}^2\right)$$

where  $\beta_{(t)}$  is the proportion of polyandrous groups in year *t* and  $\sigma_{obs}^2$  is the observation error. Data for counts of breeding individuals in polyandrous groups were modeled as

CountsPoly:Normal 
$$(NT \times \beta_{[t]}, \sigma_{obs}^2)$$
.

For CMR data, we used the likelihood of the multistate model (Hestbeck et al. 1991, Nichols et al. 1992) that provide a natural framework for estimating the state-transition and apparent survival parameters needed to parameterize stage-structured population models (Nichols et al. 1992). We had 21 observation states (1, juvenile; 2–17, not yet breeding at age 2–17; 18, breeder; 19, experienced breeder that skips reproduction; 20, dead recently and recovered; and 21, dead or dead recently and not recovered; Data S1). We modeled the succession of states over time with a categorical distribution

$$z_{i,t+1}|z_{i,t}$$
: Categorical( $\Omega_{z_i,1,2,\dots,21,t}$ )

where  $\Omega$  is the state-transition matrix (Appendix S3; see also Data S1):

The observation process links the true states with the observed states

$$y_{i,t}|z_{i,t}: \operatorname{cat}(\boldsymbol{\theta}_{z_{i,t}1,2,\ldots,2,t})$$

where  $\theta$  is the matrix of detection probabilities for individual *i* in year *t* 

	0	0	0		0	0	0	0	1 ]
	0	$p_1$	0		0	0	0	0	$1 - p_1$
	0	0	$p_2$		0	0	0	0	$1 - p_2$
	:	÷	÷	·.	÷	÷	÷	÷	:
$\theta =$	0	0	0		$p_2$	0	0	0	$1 - p_2$
	0	0	0		0	$p_3$	0	0	$1 - p_3$
	0	0	0		0	0	$p_4$	0	$1 - p_4$
	0	0	0		0	0	0	1	0
	0	0	0		0	0	0	0	1

 $p_1$  is the probability of an encounter of an individual in this first year of age, which according to Margalida et al. (2011*a*, *b*), is higher than other age-classes,  $p_2$  is the probability of an encounter with individuals that had never bred before,  $p_3$  is the probability of an encounter with breeding individuals, and  $p_4$  is the probability of an encounter with breeding individuals that skipped reproduction.

The probabilities of survival  $(\phi_t)$  and first reproduction were modeled with random year effects. Thus, e.g., for parameter  $\phi_t$  we used

$$logit(\phi_{t,s}) : Normal(\overline{\phi}_{t,s}, \sigma_{\phi_s}^2)$$

wwhere  $\overline{\phi}_{t,s}$  is the mean survival in the period 1988–2016 in state *s*, and  $\sigma_{\phi_s}^2$  is the temporal variability of  $\phi$  in state *s*.

We used a binomial regression to model productivity. For each year t, we counted the total number of fledglings (J) that were produced. We also counted the number of females R that raised these fledglings

## J: binomial(f, R)

where *f* is the productivity.

The last elements of the IPM are the joint likelihood and Bayesian computations (Data S1). If we assume independence, the joint likelihood of the complete model is the product of the likelihoods of the different data sets (Besbeas et al. 2002). There were some violations of this assumption, because several birds occurred in all of the data sets, but these violations are expected to have a negligible effect on the accuracy of parameter estimates (Abadi et al. 2010a). We specified vague priors, uniform distribution (0,1), for the parameters to be estimated (except for the part of the population that commences reproduction at age 15, where we specified a gamma distribution (1,10) to facilitate the convergence, because of the scarcity of data).

An issue not considered in our study is the potential for immigration (i.e., individuals born outside the Pyrenees that arrive to breed in this area). Although some individuals released in Andalusia (southern Spain) and the Massif Central (central France) have occasionally been observed in the Pyrenean range, these observations were mostly made during the pre-breeding phase. The closest breeding populations are situated in Andalusia (550 km from the Pyrenees, comprising three territorial pairs with the first breeding attempt in 2016) and in the Picos de Europa (360 km from the Pyrenees, currently with a single unsuccessful breeding pair). No evidence exists that any of these reintroduced individuals have settled into the wild Pyrenean population. We are therefore confident that ignoring immigration in our model is justified.

Methods for checking overall goodness of fit of IPMs are still under development. Several authors (Besbeas and Morgan 2014) propose exploring separately each different sub-model to inform about the origin of a potential lack of fit in the overall model. Count models (individuals in breeding pairs, polyandrous groups, and fledglings) were evaluated using the chi-square discrepancy measure, simulating expected data from the model and then comparing expected to observed data (see Appendix S4). We tested as well the CMR model outside of the IPM using the R package R2ucare (Gimenez et al. 2017).

We used Markov chain Monte Carlo methods to simulate observations from the posterior distributions using the JAGS software (Plummer 2003), run using R (R Core Team 2019) and the jagsUI package (Kellner 2018). We specified a burn-in of 75,000 and simulated 1,500,000 samples with 20,000 adaptations. These were then thinned by a factor of 10 and run as three chains with different starting values. Our inferences were therefore obtained from 427,500 samples from the posterior distributions. Convergence of the Markov chain was evaluated using the Brooks-Rubin-Gelman diagnostics (Brooks and Gelman 1998). Results (<1.1 for all parameters) and visual inspections of the trace plots indicated that the Markov chains successfully converged.

We used the posterior means and Bayesian credible interval (BCI) for point estimates and uncertainty assessments, except where mentioned otherwise.

# Influence of demographic rates on population growth rate and density dependence

To assess the differential influence of the various demographic rates on population dynamics, we compared temporal variation of vital rates (fecundity, and adult, subadult, and juvenile survival) with the variation in population growth rate (population size in the year t divided by population size in t - 1). For this purpose, we used a sensitivity analysis to study the contributions of different population parameters to the growth rate (Robinson et al. 2014). The sensitivity analysis was conducted using the function vitalsens in the R package popbio (Stubben and Milligan 2007). We used the matrix population model and all vital rates calculated in the IPM model to calculate the sensitivity and elasticity of eigenvalues to changes in the projection of matrix elements. A life stage simulation analysis (LSA) was used to explore the importance of vital rates under variation. By regressing  $\lambda$  on each vital rate, the analysis provides an estimate of the amount of variation in  $\lambda$  explained by each vital rate  $(r^2)$  and the rate of change in  $\lambda$  as a function of each vital rate (slope regression  $\beta_1$ ; Beissinger et al. 2008, Eacker et al. 2017). One thousand matrices were constructed by randomly sampling vital rates from a lognormal statistical distribution (Mills and Lindbert 2002) and  $\lambda$  was calculated in a Bayesian approach for each matrix (Wisdom et al. 2000) using JAGS (Plummer 2003) and retained the most likely parameter values based on the data. We used 3 MCMC chains and at least 20,000 iterations to retain 15,000 samples of each vital rate.

In order to assess the strength of any density dependence on demographic parameters, we used a formal IPM approach as described by Abadi et al. (2012). We modeled inside of our IPM the effect of density on both survival probabilities ( $\phi$ ) and fecundity (f) as follows:

$$\begin{split} & \log \operatorname{it}\left(\varphi_{1,t}\right) = \beta_{0} + \beta_{1}N_{t}^{*} + \varepsilon_{\varphi_{\operatorname{juv},t}} \quad \varepsilon_{\varphi_{\operatorname{juv},t}} \sim N\left(0, \sigma_{\varphi_{\operatorname{juv},t}}^{2}\right) \\ & \log \operatorname{it}\left(\varphi_{2,t}\right) = \beta_{2} + \beta_{3}N_{t}^{*} + \varepsilon_{\varphi_{\operatorname{sub},t}} \quad \varepsilon_{\varphi_{\operatorname{sub},t}} \sim N\left(0, \sigma_{\varphi_{\operatorname{sub},t}}^{2}\right) \\ & \log \operatorname{it}\left(\varphi_{3,t}\right) = \beta_{4} + \beta_{5}N_{t}^{*} + \varepsilon_{\varphi_{\operatorname{ad},t}} \quad \varepsilon_{\varphi_{\operatorname{ad},t}} \sim N\left(0, \sigma_{\varphi_{\operatorname{ad},t}}^{2}\right) \\ & \log \operatorname{it}\left(f_{t}\right) = \beta_{6} + \beta_{7}N_{t}^{*} + \varepsilon_{f_{t}} \quad \varepsilon_{f_{t}} \sim N\left(0, \sigma_{f_{t}}^{2}\right) \end{split}$$

where  $N_t^*$  is the standardized (i.e.,  $N_t^* = (N_t - \text{mean}(N_t))/\text{SD}(N_t))$  population size. The slope coefficients  $\beta_1$ ,  $\beta_3$ ,  $\beta_5$ , and  $\beta_7$  estimate the strength of

density dependence on juvenile survival, subadult, and adult survival and fecundity, respectively. We also regressed the population growth rate ( $\lambda$ ) on population size; we calculated this regression outside of our IPM in order not to induce constraints on the density dependence at the population level (Abadi et al. 2012):

$$\log(\lambda) = \beta_8 + \beta_9 N_t^* + \varepsilon_{\lambda_t} \quad \varepsilon_{\lambda_t} \sim N(0, \sigma_{\lambda}^2).$$

#### RESULTS

#### Population size

Estimated breeding population size increased progressively from 45 (42–50, 95% Bayesian credible interval) territorial pairs/trios in 1987 to 164 (160–168) in 2016 (Fig. 3), an annual population increase of 4.3 territories/yr. The breeding population experienced a geometric mean population increase of 3.3% annually.

As Fig. 4 shows, population growth rate was irregular at the beginning of the study period, reached a maximum in 2000, after which it showed a steady decline (although being still above 1 in 2016).

The estimated total population size reached 1,026 individuals (937–1,119, 95% BCI) in 2016 (Fig. 5): 57 juveniles (39–77), 220 subadults (179–282) and 748 adults (677–826). Within the adult age-class, only 365 (354–373) were breeding individuals (48.8% of the adult population, and 35.6% of the total population). The latter figure excludes birds >17 yr old (thus potential breeders) skipping reproduction.



FIG. 3. Breeding territories of Bearded Vultures in the Pyrenees from 1987 to 2016. Open circles are the raw count data of breeding territories and solid circles are posterior means from the integrated population model with 95% credible intervals.



FIG. 4. Interannual population growth rates of Bearded Vultures in the Pyrenees from 1987 to 2016. Solid line links the posterior means from the integrated population model. Shaded polygon is the 95% credible interval.

With respect to the population age structure, we found an increase in the adult proportion with time (Fig. 6), in parallel with a decrease in the percentage of adult birds in the breeding population. Non-breeding adults showed the greatest proportional increase with time.

## Demographic parameters

Mean age of first breeding was estimated at 10.31 yr (6.57–15.69, Fig. 7). Mean breeding propensity (or probability that an experienced breeder reproduced) was estimated at 0.62 (0.56–0.69), with no significant temporal trends. Mean fecundity was estimated at 0.41 (0.37–0.46) fledglings per nesting pair, showing an overall declining trend over from 0.56 (0.44–0.68) in 1987 to 0.28 (0.22–0.35) in 2016 (Fig. 8).

Juvenile survival was estimated at 0.947 (0.903–0.982), subadult survival at 0.966 (0.952–0.978) and adult survival at 0.968 (0.958–0.978). We found almost no temporal trends in adult and subadult survival over the study period, but juvenile survival showed a decline in the last years (Fig. 9). Estimated ratio of breeders that were in polyandrous groups increased from 0.21 (0.17–0.27) in 1987 to 0.30 (0.28–0.31) in 2016 (Fig. 10).

# Relationships between demographic parameters and population size or growth rate

Posterior correlations of demographic parameters with the population growth rate were slightly skewed, so we used the mode instead of posterior means. The modes of the correlation coefficients of productivity, juvenile, subadult, and adult survival with the population growth rate were all positive: adult survival (mode and 95% CRI: 0.341, -0.169 to 0.650), productivity (0.559, 0.253–0.731), juvenile survival (0.139, -0.230 to



FIG. 5. Bearded Vulture estimated population size for the Pyrenees from 1987 to 2016. Dots represent the posterior means in each year for total population size (black solid circles), and numbers of adults (gray open circles), subadults (gray solid circles), and juveniles (black open circles), with 95% credible intervals.



FIG. 6. Age structure variations of the Bearded Vultures estimated in the Pyrenees from 1987 to 2016.



FIG. 7. Probability that a bird that has not reproduced before starts to reproduce in a given year (6–15th). Values are means and 50% and 95% credible intervals around the mean.

0.478), and subadult survival (0.072, -0.263 to 0.397). A formal sensitivity analysis also found a very high contribution of adult survival rate (0.82) to the population growth rate, and weaker contributions of subadult survival (0.16), productivity (0.09), and juvenile survival (0.08; Fig. 11; Appendix S5). We obtained similar results in the LSA (Fig. 12). The vital rate that accounts for greatest variation in population growth rate ( $\lambda$ ) was adult survival, having the greatest impact on population dynamics.

Posterior means of the strengths of density dependence were negative for juvenile survival, fecundity,



FIG. 8. Annual variation of productivity in Pyrenean Bearded Vultures between 1987 and 2016. Dots are the posterior means in each year. Thick gray lines are the 50% credible intervals, and thin black lines are the 95% credible intervals.



FIG. 9. Interannual variation of mean annual survival rates for juvenile, subadult, and adult Bearded Vultures in the Pyrenees from 1987 to 2016. The annual survival for adults refers to individuals that were more than six years old, the minimum age at first reproduction. Shown are the means (dots and line) and 95% credible interval around the means (shading).

and adult survival, in this order, but not so clearly negative for subadult survival (Fig. 13; Appendix S6). The posterior distributions of the strength of density-dependent relationships had a wide shape for juvenile, adult and immature survival, and peaked shape for fecundity (Fig. 13). Probabilities of negative effects of increased



FIG. 10. Annual variation in the proportion of territories including polyandrous trios for Bearded Vultures in Pyrenees from 1987 to 2016. Shown are the means (black dots) and 95% credible intervals around the mean.



FIG. 11. Sensitivity and elasticity of the population growth rate to main vital rates in the bearded vulture IPM model. $\phi_1$ , juvenile survival;  $\phi_2$ , subadult survival;  $\phi_3$ , adult survival; f, fecundity;  $\delta$ , propensity for reproduction (probability that experienced breeders do not skip reproduction).

population size were very high (P[r0 < 0] > 0.96) for juvenile survival, fecundity and adult survival. In contrast, the probability that increased population size has a negative effect on subadult survival was lower (probability = 0.254). Those effects on vital rates have an impact on population growth rate, which declined significantly with increasing total population size (Fig. 14).

#### Resighting rates

Resighting rate for individuals from age  $\leq 1$  yr was 0.978 (0.938–0.997). From age >1 and non-breeders, 0.925 (0.902–0.945). For breeders was 0.825 (0.731–0.945), and for breeders that skip reproduction, 0.956 (0.858–0.999). Probability of recovery of a dead animal was estimated as 0.418 (0.318–0.521).

We did not find evidence for lack of fit of the count models (Appendix S4). In the multistate model, we analyzed separately the groups according to the age when individuals were marked (juveniles, age  $\leq 1$  yr, and others, age >1 yr), to avoid the heterogeneity induced by the high probability of detection and variable survival in the individuals from the first group (Margalida et al. 2011b). We found no lack of fit for either group ( $\chi^2$  (61) = 56.40, P = 0.64, and  $\chi^2$  (38) = 22.32, P = 0.98, respectively).

#### DISCUSSION

The application of IPMs has led to substantial advances in studies of population dynamics and greater understanding of the drivers of population change in various species (Koons et al. 2017, Zipkin et al. 2019). We developed an IPM to assess the demographic parameters and population size of threatened Bearded Vultures in the Pyrenees at the whole massif scale. Using this approach we were able to provide an estimate of the non-breeding proportion of the population, in a significant improvement over previous estimates based on simultaneous counts at SFS, which did not take account of imperfect detection (Guillera-Arroita et al. 2014). Additionally, the IPM method, through data integration can provide better estimates of demographic parameters (Zipkin et al. 2019), allowing for a better understanding of population processes in this species and providing improved predictive models as key tools for adaptive conservation management decisions (Morris and Doak 2002, McGowan and Ryan 2009, McGowan et al. 2017). We develop these ideas in the two following subsections.

## Bearded Vulture population ecology

Our results show a strong population increase in all age-classes during our study period, reaching a total of around 937–1,119 individuals for the entire Pyrenean Bearded Vulture population in 2016, of which 64% were non-breeders (i.e., birds that had not yet entered the breeding population or breeders in previous years that skipped reproduction). Partial data using a CMR in the Aragonese Pyrenees had also provided a high estimated proportion of non-breeding birds (Gómez de Segura et al. 2012). In contrast, another previous study indicated that visual surveys overestimated the number of juvenile birds, whereas subadults and adults were underestimated in comparison with the predictions of a population model using a stable-age distribution (Margalida



FIG. 12. Results of the life-stage simulation analysis (LSA) based on creation of 1,000 matrices drawn from adult survival, subadult survival, juvenile survival, and fecundity.  $\beta_1$  are the slopes of the regressions and  $r^2$  the coefficients of determination between each vital rates and lambda ( $\lambda$ ).





FIG. 13. Posterior distributions of the estimated strength of density dependence on juvenile survival (black line), subadult survival (blue line), adult survival (green line), and productivity (red line) in the Pyrenean Bearded Vulture population.

FIG. 14. Relationship between population growth rate and standardized population size obtained from an integrated population model with density dependence (solid line) with 95% Bayesian credible intervals (vertical gray line).

et al. 2011b). Our results further show that underestimation of non-breeding subadults and adults, despite their higher resighting rate, is even larger than previously thought. A possible explanation of the higher resighting rate of non-breeders is their regular presence in supplementary feeding sites that concentrate dozens of individuals, whereas experienced breeding adults visit less frequently these sites. This allows the identification of rings and marks more easily with respect to less conspicuous territorial (breeding) individuals.

Our results show that traditional monitoring provides a good estimate of the size of the breeding population, but significantly and markedly underestimates the number of non-breeders. The large number of adult nonbreeding birds in the Pyrenean Bearded Vulture population is particularly relevant when we consider the important effect of non-breeding birds on overall population dynamics, both as a buffer to maintain breeding populations by replacing adult losses in already occupied territories, and also as a source of intraspecific competition through either depletion or interference (Lande et al. 2003, Bretagnolle et al. 2008, Penteriani et al. 2008, Lee et al. 2017). In territorial birds such as Bearded Vultures, floaters depend on the availability of vacant territories to become breeders. The fact that the increase in the proportion of non-breeders is much higher than that of breeding birds strongly suggests that the breeding Pyrenean population could be very close to carrying capacity, probably through a scarcity of suitable nesting sites. Supporting this hypothesis, previous studies in the Spanish Pyrenees showed that the distance between occupied bearded vulture nests in the core of the distribution range has decreased with increasing breeding population size, suggesting that territory compression could occur without serious modification of nesting habitat quality, but that the relatively low quality of sites in adjacent mountains could be preventing the expansion of the breeding range (Margalida et al. 2008). A scarcity of high-quality breeding sites has also been suggested for the French versant of the Pyrenees (Arroyo et al. 2020). In contrast, and since the overall number of Bearded Vultures is still increasing, a scarcity of food resources currently limiting the population is unlikely. Concordantly, several studies have estimated that trophic resources available (natural food provided by wild and domestic ungulates and artificial resources provided through supplementary feeding stations) in the Pyrenees are largely sufficient to cover the energetic requirements of the current Bearded Vulture population (Margalida and Colomer 2012, Margalida et al. 2017b).

Associated with population growth, we found densitydependent relationships for most demographic parameters. The density-dependent variation in productivity observed at the whole population level mirrors that observed previously in the Spanish part of the population (Carrete et al. 2006*a*), including local effects. In that study, territories located at high-density situations became less productive and more unpredictable than territories located far away from conspecific pairs. The negative relationship between population size and productivity observed by Carrete et al. (2006a) was explained by the effects of behavioral interference on fecundity, both by nearby breeders (interacting with territory quality) as well as non-breeders gathering in SFS close to breeding areas, rather than by the effects of food depletion. In the northern versant of the Pyrenees no effects of local density have been found on productivity, and only weak non-significant relationships between population size and mean productivity (Arroyo et al. 2020); this may also point to interspecific interference as a driver of density-dependent reduced productivity, because non-breeders tend to gather in the southern versant of the Pyrenees (Sesé et al. 2005, Margalida et al. 2011a).

Our data at the whole population scale, which shows ongoing total population growth (including non-breeders), also disagrees with food depletion as the main mechanism behind density-dependent effects on productivity at that scale. However, the fact that we also found a decline in adult and, particularly, juvenile survival with increasing population size indicates that additive effects of competition for food cannot be excluded, although effects may be more related to food quality rather than food quantity. For example, sanitary regulations in Spain during 2005-2011 led to lower availability of livestock carcasses (i.e., food shortage for Bearded Vultures), which affected several breeding parameters (clutch size, lay date, breeding success, nestling condition, and adult survival; Margalida et al. 2014). Authors suggested that food quality rather than quantity may have been a limiting factor at that time; food shortages might have increased the risk of poisoning as an increase in the consumption of wild ungulates shot with lead ammunition increases adult mortality (Hernández and Margalida 2009, Berny et al. 2015). The decline in juvenile survival with increasing population size thus suggests that, with increasing competition, some individuals (particularly juvenile ones) take more risky foraging strategies. The fact that population growth rate decreased during the last years, and that we found density-dependent relationships for most demographic parameters suggests that the population as a whole may be approaching carrying capacity in the Pyrenees. Thus we should expect that population growth will no longer be linear in the future, maybe reaching asymptotic values in a few years.

# Utility of IPMs for understanding vulture population ecology

IPMs, integrating different types of data collected from multiple techniques and/or on different aspects of a study system, can yield better information about the demographic parameters of threatened and difficult-tostudy species than the use of a single data type (Zipkin et al. 2019). Indeed, we obtained estimates of all demographic parameters through our IPM. Mean age of first breeding estimated by our IPM is higher than that estimated in earlier studies (Antor et al. 2007, López-López et al. 2013, Margalida et al. 2014), suggesting that it has increased with time. Our estimate that the proportion of non-territorial adult individuals is increasing with time suggests that the high numbers of adults are reducing the number of new recruits to the breeding population (Sæther et al. 2002) and delaying this recruitment. Adult survival, as estimated by our IPM, is similar to that of other studies (based on a proportion of the same data set and classical CMR approaches), but our estimate of juvenile survival is lower than that in other studies for the same population (Oro et al. 2008). This may reflect the longer time span of our study, and the lower juvenile survival in more recent years, or could be related to the population increase and the density-dependent effects on juvenile survival. These results also highlight the added value of IPMs in improving assessments of demographic parameters for scarce and difficult-to-study species, for which only relatively small sample sizes are available.

Our IPM also provided information about population parameters that reflect population functioning. Propensity to breed was estimated at 0.62, indicating that 38% of experienced breeders did not breed in any given year. This concurs with previous results obtained in a part of the southern side of the Pyrenees (41%; Margalida et al. 2014). This denotes birds that may take "gap years" in reproduction, for example after failures due to human disturbance (Arroyo et al. 2020) or due to intraspecific interactions during trio formation (Bertran et al. 2009), which sometimes leads individuals to change breeding sites or disrupts the pair/trio bond. The decision to start breeding could also be influenced by the physical condition of the individual (Jenouvrier et al. 2005). However, in this species regular "sabbatical years" are not known, as opposed to other long-lived species such as Albatrosses (Tickell 1968, Barbraud and Weimerskirch 2012). Thus, the relatively low estimated propensity to breed probably largely reflects the large proportion of birds over 16 yr of age (considered to be experienced breeders in our IPM) that never entered the breeding population, supporting again the hypothesis that suitable breeding territories are indeed limited in the Pyrenees.

Concordant with this, the proportion of polyandrous trios increased throughout the study period, reaching an estimate of 30–35% of all territories in recent years. The low values obtained between 1998 and 2006 are probably due to an underestimation in field data of territories occupied by polyandrous groups, as a result of lower effort for identifying trios during those years in the Spanish subpopulations (A. Margalida, *personal observation*). The fact that a third of the territories are currently occupied by trios further highlights the limitation of suitable breeding sites at the massif scale and that the breeding population has low perspectives of increasing

in the future. Given that polyandrous trios may suffer higher levels of intraspecific interference and lower productivity (Bertran and Margalida 2003, Carrete et al. 2006*a*, Bertran et al. 2009), these results also indicate and that further drops in productivity can be expected through higher interference with both breeders in polyandrous groups and non-breeders.

Our results on the impact of demographic parameters on population dynamics in this Bearded Vulture population are also relevant. According to the sensitivity analysis, the effect of adult survival variation on population growth was much greater than that of variations on productivity, something that could be expected given the life-history of Bearded Vultures (Oro et al. 2008, Schaub et al. 2009). Indeed, in long-lived species, adult survival is generally one of the main drivers of population dynamics (Schaub et al. 2006, Schorcht et al. 2009, Morris et al. 2011). The effect on population growth of subadult and juvenile survival variation was lower than that of adult survival. A possible explanation for this could be the buffering role of the increase in the numbers of non-breeders (Durell and Clarke 2004) because recruitment does not act as an additional buffer (Gaillard et al. 1998, Votier et al. 2008) in this population. The marked effect of adult survival on population growth, in our specific case, may also be related to the large fraction of the whole population being adult. In any case, the negative relationship between population size and adult survival indicates that despite the high values still observed, we could expect a reduction in adult survival in the future through density-dependent processes, which would have a disproportionate effect on overall population size. On the other hand, even if the effect of productivity on population growth was lower, our results also show that programs aimed at maintaining or enhancing productivity in this species (e.g., through protection of nesting areas, reduction of causes of breeding failure) will probably have a positive effect on population size. However, this effect may also be mitigated at the population level, because fecundity also varies in a density-dependent manner, and therefore decreases in impact as population size increases. At the beginning of the study period when the population size was smaller, fecundity was higher, before progressively declining as population size increased. The weaker population growth observed since 2000 (Fig. 4) may be the result of the declining productivity at that time, although population growth is still positive due to the additive effects of high survival rates in all age groups, particularly of adults, observed since the beginning of the study.

Finally, our study has also important applied inferences. As our IPM provides estimates of all demographic parameters, population size and age structure of the Pyrenean population of Bearded Vultures, our results will help to improve the design of population viability models (PVA), which will be essential to forecast the impact of different conservation management scenarios, e.g., different management plans for SFS or reintroduction projects. With respect to the usefulness of SFS as a conservation management tool, our findings on the size of the current Pyrenean Bearded Vulture population (~1,000 individuals) indicate the need of around 150,000 kg of food per year to cover its energetic requirements. Estimates of the food provided by carcasses of wild and domestic ungulates, the principal component of the species' diet (Margalida et al. 2009), allows an assessment of the usefulness of SFS for the species. This is especially relevant taking into account the limited geographic expansion of the population, and the density-dependent regulation of fecundity associated to interference by non-breeders gathering at SFS (Carrete et al. 2006a, Margalida et al. 2008). Accordingly, management and conservation actions focused on population growth (i.e., reintroductions, translocations, establishment of new SFS) should consider as a priority the spatial expansion of the population rather that an increase of K in the core area, which is likely to cause more density dependence. Attracting floaters to areas further away from breeding sites would reduce conspecific interference in the core area. Therefore, the management of SFS (in relation to their location to breeding areas, as well as on the amount of food available) could provide a useful tool to reduce presence of non-breeders in good quality breeding areas, or even promote geographic expansion of the species range, as has been shown to be helpful in the French subpopulation (Arroyo et al. 2020). Considering PVA and population dynamic models, forecasts of population trends based on demographic parameters could be improved by adding estimates of the energetic requirements for both the breeding and the floater populations. However, an important prerequisite is to consider temporal and spatial scales with respect to the distribution of resources, as well the demographic parameters of wild and domesticated ungulate food resources, in order to provide the accurate information necessary to maximize the robustness of the model outputs (Colomer et al. 2011, Margalida et al. 2018).

All this information is key for assessing the conservation status of Bearded Vultures, both in the Pyrenees and in nearby areas with much smaller breeding populations, (e.g., Corsica or Crete), as well as to underpin replenishment and reintroduction projects performed in these and other regions such as the Alps and other areas in Spain. For example, current reintroduction projects carried out in Spain are based on the removal of clutches and non-territorial adults from the Pyrenees (Ferrer et al. 2014), but this approach is highly controversial because of foreseen impacts on Pyrenean populations (Margalida et al. 2017a, Colomer et al. 2020). Researchers and practitioners need to evaluate the likely trade-offs among the management options available to improve reintroduction outcomes, for which an accurate estimate of population size and demographic parameters to forecast the impact of translocations on the source population will be vital (McCleery et al. 2014, Margalida et al. 2015, Colomer et al. 2020).

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