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Abstract

Conservation strategies for long-lived vertebrates require accurate estimates of parameters relative to the populations’ size, numbers of non-breeding individuals (the “cryptic” fraction of the population) and the age structure. Frequently, visual survey techniques are used to make these estimates but the accuracy of these approaches is questionable, mainly because of the existence of numerous potential biases. Here we compare data on population trends and age structure in a bearded vulture (Gypaetus barbatus) population from visual surveys performed at supplementary feeding stations with data derived from population matrix-modelling approximations. Our results suggest that visual surveys overestimate the number of immature (<2 years old) birds, whereas subadults (3–5 y.o.) and adults (>6 y.o.) were underestimated in comparison with the predictions of a population model using a stable-age distribution. In addition, we found that visual surveys did not provide conclusive information on true variations in the size of the focal population. Our results suggest that although long-term studies (i.e. population matrix modelling based on capture-recapture procedures) are a more time-consuming method, they provide more reliable and robust estimates of population parameters needed in designing and applying conservation strategies. The findings shown here are likely transferable to the management and conservation of other long-lived vertebrate populations that share similar life-history traits and ecological requirements.


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Introduction

The estimation of the non-breeding fraction of wild vertebrate populations is of great interest to ecologists and conservationists because these individuals represent a buffer that can allow populations to survive stochastic environmental and demographic phenomena [1–5]. In addition, changes in the non-breeding population’s size and age structure may serve as accurate early-warning signals previous to the decline of the breeding population [6,7].

Thus, for conservation purposes, it is essential to take into account the existing relationship between settlement-breeding areas as a consequence of the influence of the dynamics within entire populations [8–11]. Estimates of the non-breeding fraction are difficult to ascertain because they are often “cryptic” in nature and are generally not detectable other than via long-term monitoring programmes or complex approximations based on molecular techniques [12]. This question is accentuated in the case of long-lived vertebrates characterized by delayed reproduction, which ensures that individuals are not recruited into the breeding population until they are a few years old. In the meantime, these individuals often lead dispersive life-styles not necessarily linked to their main breeding areas (i.e. the spatial segregation of non-breeding birds) [13,14]. Although in raptors it is assumed that the non-breeding fraction of populations is mainly composed of juvenile individuals [15,16], information regarding their age structure remains scarcely explored in the literature [11,17].

The application of the results of direct observations and individual counts (hereafter, visual surveys) in determining population age structures and demographic trends is frequently used as a basis for conservation proposals to aid in the recovery of threatened vertebrates [18–21]. Particularly, the aggregation of individuals at migratory stopovers, roosting sites and at sites with an abundance of trophic resources (e.g., the so-called vulture restaurants) [22] has been used to determine the age structure of populations of birds with large but scattered populations that are difficult to monitor [23,25]. Nevertheless, the probability of detecting individuals by means of visual surveys may be asymmetrical due to both the individual’s behaviour and/or environmental variability [26]. To assess these potential biases it is necessary to compare results obtained from visual surveys with precise estimates derived from matrix population models. To date, very few such analyses have been performed, probably due to the inherent difficulty in obtaining long-term monitoring data for long-lived vertebrate populations [27–30].

The bearded vulture (Gypaetus barbatus) is a long-lived territorial vulture species that is under threat in Europe (170 pairs in the European Union in 2010). Owing to its specialized diet based on...
the bones of wild and domestic ungulates [31], the conservation methods employed to ensure the recovery of the Pyrenean sub-population (145 pairs), the largest in Europe, are based on supplementary feeding (i.e. provision of sheep limbs and other bone matter in winter). As a result, almost all of the non-breeding population is concentrated around this network of feeding stations [32,33]. These large aggregations of dozens of non-breeding birds make visual surveys feasible and the information thus obtained is one of the basic tools used by regional and state governments to draw up conservation strategies [34]. Apart from this, since the end of the 1980s, the Pyrenean bearded vulture population has also been monitored using individual tagging, which has enabled demographic models based on capture-recapture and stochastic population modelling [35].

Taking advantage of this scenario, our main objective is to compare the population trend and age structure estimated on the basis of visual surveys with data derived from approximations reached via matrix population models. As a corollary, we examined the existence of age-related asymmetries in the use of supplementary feeding stations by bearded vultures.

Materials and Methods

Field procedures

During 1990–2006, between 9 and 13 (mean±sd: 11.5±1.5) supplementary feeding stations were surveyed annually. The annual visual surveys (mean±sd: 3.53±1.28) were carried out simultaneously at the end of winter (February-April), coinciding with the beginning of the breeding period (incubation and first weeks of chick-rearing) [36] and with the maximum numbers of birds at feeding stations owing to food shortages in the field [32,33]. A minimum of two experienced observers equipped with 20–60× telescopes and binoculars monitored each supplementary feeding station between 09:00–16:00 h from dominant vantage points. Birds were identified individually on the basis of plumage characteristics and patterns recorded on standardized data sheets.

Accordingly, we considered the following age categories [32,37]: i): <2 years (immature): robust silhouette in flight, head and shoulders black, but back, chest, belly and legs brown. ii): 3–5 years (subadult): more stylized flight silhouette than immature birds, with moulded primary and/or secondary flight feathers; feathers on face, head and neck beginning to turn white; the back is still brown and the chest, belly and legs are also still brownish, although the orange tones are beginning to appear. iii): >6 years (adult): stylized, svelte silhouette in flight; head, chest and belly colour vary from white to orange; the back is now slate grey or black with an obvious contrast with the head.

In addition, the existence of wing-tags or rings was also recorded [35]. On the basis of all of this information and for each day of census the maximum number of birds belonging to the three age categories was estimated.

Parameter estimations

We built an age-structured model that was initially used for projecting the evolution of the bearded vulture population in the Pyrenees [35] on the basis of tagged individuals. Demographic and environmental stochasticities were introduced into the model, as well as density-dependence on fertility [38]. We assumed that recruitment started at the age of six and was completed at 12 (i.e. a total of 12 age-classes were considered [see also 35]); survival probabilities decreased with time in line with capture-recapture estimates [35]. The 12 age-classes considered by the model were easily accommodated to the three age classes obtained from the counts. The model considered a post-breeding census and was a one-sex (female) model, because we had no evidences for sex-dependent parameters [33]. Initial conditions in year $t=1$ (1990 in our case) were set to include the number of females in each age class.

This number was estimated as follows: a deterministic model using average demographic estimates was run and to start such run the total number of females (breeders and non-breeders) was divided by the number of age-classes and such number was assigned equally to each age class. The resulting scaled right eigenvector of the matrix (i.e. the stable stage distribution, see below) was used to multiply the estimated number of females for each age-class in the population in $t=1$ to set the initial conditions of the stochastic simulations. Given that the model had an age structure we were able to calculate the mean scaled population structure, i.e. the abundances of each age class relative to the abundance of the first age-class [39], once the model converged and the population tended asymptotically to that age-structure and growth rate [40]. The right eigenvector of the population matrix $W$ is the stable stage distribution; the proportion of individuals in ages $[1, 2, …, 12]$ at time $t$ is:

$$W(t) = \frac{\begin{bmatrix} n_1(t) \\ n_2(t) \\ \vdots \\ n_{12}(t) \end{bmatrix}}{n(t)} \cdot \begin{bmatrix} \hat{n}(t) \\ \hat{n}(t) \\ \vdots \\ \hat{n}(t) \end{bmatrix},$$

with $n_i(t)$ being the abundance of the oldest age class at time $t$ and $n$ the total population size. After a few generations (i.e. at demographic equilibrium) $W(t) \rightarrow W^*$, i.e. the stable age distribution. Monte Carlo simulations were run for 23 years to cover the study period (1986–2006), and yearly estimation of population sizes obtained were compared it with the counts from visual surveys. Note that such estimates of population size for each age-class were multiplied by two because the model yielded only the number of females, and counts included females and males.

Data analyses

We used Generalized Linear Mixed Models (GLMM) [41,42] to explore the relationship between the maximum observed abundance of bearded vultures and that predicted by the model (link function: logarithmic, error distribution: Poisson). Age was included as a factor with three levels corresponding to the above-described categories. ‘Year’ was fixed in the models as the random term to account for inter-annual variability [43,44].

Results

The maximum number of bearded vultures observed during the simultaneous visual surveys was significantly related to both the abundance predicted by the model ($F_{1,31} = 13.48, \ p = 0.0009$) and the age of the individuals ($F_{2,31} = 19.75, \ p<0.0001$: adult<subadult<immature). These results initially seem to indicate that visual surveys reflected the real population trend (a progressive increase, Fig. 1). However, this relationship was only approximate: inter-annual variability was strong and visual surveys were not good at detecting finely tuned trends such as the slowing down of the population growth observed during the final years of the study (2004–2006, Fig. 1). In addition, visual surveys also overestimated the number of immature birds, but underestimated the numbers of subadults and adults with respect to the predictions of the population model using stable-age distribution (Fig. 1), being the mismatch for the adult age class extremely large.

Discussion

Visual surveys at supplementary feeding stations did not reflect the structure of the bearded vulture population. Compared to
Our findings are likely transferable to the management and conservation of other long-lived vertebrate populations that share common life-history traits and ecological requirements. Thus, estimations of the size of “cryptic” fraction of the populations [12] may be misleading in those scenarios leading to the spatial concentration of individuals. Despite being a more time-consum-
References


