Man-induced activities modify demographic parameters in a long-lived species: effects of poisoning and health policies

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Abstract. Recent changes in sanitary policies within the European Union (EU) concerning disposal of carcasses of domestic animals and the increase of non-natural mortality factors, such as illegal poisoning, are threatening European vultures. However, the effects of anthropogenic activities on demographic parameters are poorly studied. Using a long-term study (1994–2011) of the threatened Pyrenean Bearded Vulture *Gypaetus barbatus* population, we assess the variation in the proportion of breeding pairs, egg-laying dates, clutch size, breeding success, and survival following a sharp reduction in food availability in 2005 due to the application of restrictive sanitary policies decreasing livestock carcass availability. We found a delay in laying dates and a regressive trend in clutch size, breeding success, and survival following policy change. The maintenance of specific supplementary feeding stations for Bearded Vultures probably reduced the negative effects of illegal poisoning and food shortages, which mainly affected subadult survival. A drop in food availability may have produced changes in demographic parameters and an increase in mortality due to an increased exposure to contaminated food. As a result, supplementary feeding as a precautionary measure can be a useful tool to reduce illegal poisoning and declines in demographic parameters until previous food availability scenarios are achieved. This study shows how anthropogenic activities through human health regulations that affect habitat quality can suddenly modify demographic parameters in long-lived species, including those, such as survival, with high sensitivity to population growth rate.

Key words: Bearded Vulture; breeding parameters; European sanitation policies; Gypaetus barbatus; *health regulations; life history; poisoning; Pyrenees, Catalonia, Spain; supplementary feeding; survival.*

Introduction

Increasing, negative anthropogenic effects on ecosystem dynamics are provoking biodiversity losses, with ecological consequences for ecosystem function (Loreau et al. 2002, Naeem et al. 2009). Species with "slow life styles" (Sæther and Bakke 2000) are especially sensitive to anthropogenic effects as they are of large size, high adult survival, and low fecundity (Bennett and Owens 1997), three traits that characterize species with slow life styles. Thus, any factor that disturbs the balance between fecundity and survival will be particularly hazardous for these taxa (Owens and Bennett 2000, Cardillo et al. 2004). For example, the recent and sudden appearance of non-natural mortality factors related to the ingestion of veterinary drugs or the increase in the use of illegal poison baits severely

affected populations of Old World vultures (Green et al. 2004, 2006, Virani et al. 2011, Margalida 2012). In parallel, a recent change in European health policy may be exacerbating the precarious status of these large species. Coinciding with the outbreak of bovine spongiform encephalopathy in 2001, scavenger food resources have been reduced because farmers were forbidden to retain certain dead livestock (Donázar et al. 2009*b*, Margalida et al. 2010). In situations such as this, policy decisions can have important consequences for biodiversity conservation (Meffe and Viederman 1995). The need to provide timely and meaningful information to policy makers can depend on the existence of large data sets (Clutton-Brock and Sheldon 2010). We illustrate the ability of long-term data to inform policy decisions by considering one European vulture species affected by new mortality sources and changes in livestock handling policy.

The Bearded Vulture *Gypaetus barbatus* is a long-lived threatened species with a European population of only 170 territories. The Spanish population, with 117 territories, is considered the most important in the Palaearctic, and conservation measures applied to this population are critical for the maintenance of a

European metapopulation. However, in recent years this population has been characterized by high adult mortality as a result of the increased use of illegal poisoning (Margalida et al. 2008b, Oro et al. 2008). In contrast, other causes such as collision and hunting practices diminished progressively during this time (Margalida et al. 2008b, Martínez-Abraín et al. 2009). Thus, taking into account that this illegal practice increased during the last years and can be considered as the main non-natural cause of mortality of wildlife in Spain (Margalida 2012), we consider this to be the most plausible factor affecting Bearded Vulture population dynamics (see Oro et al. 2008). In addition, geographical range expansion is very low because supplementary feeding sites are keeping pre-adult individuals in the core area (Margalida et al. 2008a), where there is density-dependent depression in fecundity (Carrete et al. 2006a) and an increase in the proportion of polyandrous territories with lower productivity (Carrete et al. 2006b).

Considering the importance of such information for managers and conservationists, our purpose is to test if two human-induced activities (i.e., illegal use of poison baits and regulations in the availability of domestic carcasses) can modify life-history traits in a threatened vulture population. Some assessment of food resources and their relationship to population dynamics (Colomer et al. 2011, Margalida et al. 2011b, Margalida and Colomer 2012, Martínez-Abraín et al. 2012) and behavioral changes (Zuberogoitia et al. 2010, Margalida et al. 2011a) has been documented. In this sense, although food availability can also influence life-history traits and the scientific literature in birds is abundant (Lack 1968, Western and Ssemakula 1982, Oro et al. 1999, 2004, Sibly et al. 2012), to our knowledge, few studies have attempted to relate the effects of human-induced activities on life-history traits in long-lived raptor species (Martínez-Abraín et al. 2012). Here we analyze breeding parameters (during 1994–2011) and survival probabilities (during 1987–2011) to determine whether changes in the availability of food supply and/ or the effects of illegal poisoning are important anthropogenic mortality factors affecting this population, and whether they can modify life-history traits in a long-lived species. In particular, we assess whether food or mortality affects the proportion of breeding pairs, egg-laying dates, clutch size, productivity, and survival in the Pyrenean Bearded Vulture population.

METHODS

Study area

The study was mainly carried out from 1994 to 2011 in an 8450-km^2 area in the central Pyrenees (Catalonia, northeastern Spain). This area is inhabited by a Bearded Vulture population that has increased from 17 territories in 1994 to 37 in 2011. It supports an important wild and domestic ungulate population, and 16 supplementary feeding sites (see Margalida et al. 2011b, Margalida and Colomer 2012). However, since 2005, coinciding with

the application of restrictive sanitary policies, livestock carcass availability has decreased progressively in the study area. A monitoring program marking adult and pre-adult individuals was carried out in the Pyrenees from 1987 to 2011, which allowed modeling of the resighting and survival probabilities in 106 marked Bearded Vultures.

Data collection

The southern face of the Pyrenees has been intensively monitored within the framework of the Species' Recovery Plan in the Autonomous Communities of the Basque Country, Navarra, Aragón, and Catalonia. Here, programs to monitor population trends, breeding parameters, and survival rates (including a specific capture–mark–resighting subprogram) have been performed.

Between 1994 and 2011, all known territories were visited (2–3 visits/month) to search for signs of occupancy (territorial and/or courtship activity, nest arrangement/building), and to record reproductive parameters. Observations began in September–October, coinciding with the start of nest-building and sexual activity (Bertran and Margalida 1999, Margalida and Bertran 2000), and ended during fledging (June–August). Nests were observed with the help of 20–60× telescopes and video cameras (Margalida et al. 2006). During the egg-laying period, 14–20 focal pairs per year were monitored daily until the dates of egg-laying were determined. Egg-laying was confirmed when an incubation shift between parents was observed or when the nest interior was visible. When the previously mentioned methods failed, clutch size (a one-egg simple clutch vs. a two-egg double clutch) was determined after confirming a breeding failure and visiting the nest to recover the remains. In this case, we only included data when entire eggs were found or when the nest inspection was carried out one or two days after breeding failure, to avoid possible biases due to predation by Common Ravens (*Corvus corax*) (Bertran and Margalida 2004). For the analyses of breeding parameters, we defined productivity as the number of chicks fledged per nesting pair and fledging rate as the number of chicks fledged per pair that successfully laid eggs.

During the study period, all dead Bearded Vultures were recovered and their cause of death was determined (see Margalida et al. 2008b, Margalida 2012). Samples from Bearded Vultures found dead or injured were analyzed by the Wildlife Forensics Laboratory in Madrid, Spain. Poisoning was recorded when intentional exposure to a toxic substance was confirmed (Margalida et al. 2008b). In order to analyze variations in mortality, we used survival estimates by age classes obtained through resighting and recoveries. From 1987 to 2011, a total of 106 individuals were monitored (Oro et al. 2008; R. Heredia [Fundacíon para la Conservacíon del Quebrantahuesos], *unpublished data*; A. Margalida, *unpublished data*). Finally, in order to assess food

availability, we calculated the food resources (bone biomass) provided by wild and domestic ungulates, taking into account Bearded Vulture dietary habits and the presence and population trend of ungulate species in the study area (Colomer et al. 2011, Margalida et al. 2011b). Considering that >70% of the diet of the species is based on livestock (Margalida et al. 2009), we obtained the biomass available (bone remains expressed in megajoules) as a surrogate of food potentially available. To assess food shortages related to carcass disposal policies, we obtained data from the agricultural insurance Spanish government agency Enesa (*available online*)[5] to calculate the proportion of domestic ungulate carcasses that were destroyed (e.g., by incineration) and thus not available to scavenging birds. Using these official data, which can be considered a reliable picture to assess the potential food available in the field, we inferred the proportion of such destroyed domestic carcasses collected from farms from those hypothetically available to scavenging birds at feeding sites obtained through censuses and mortality rates (for more details, see Margalida and Colomer 2012).

Scenarios considered

Although the outbreak of bovine spongiform encephalopathy began in 2001, the restrictive legislation forced the closure of 80% of feeding stations (Donázar et al. 2009a, Cortés-Avizanda et al. 2010) and obliged the collection of domestic ungulates to be destroyed. These measures were not implemented effectively until 2005 (Donázar et al. 2009b, 2010, Margalida et al. 2010, 2012), when dead livestock were collected from farms and most feeding stations (80%) were closed. Thus, we considered the period 1994–2004 as the "before policy implementation period" (noted as BPI) and 2005–2011 the "after policy implementation period" (noted as API). During the BPI, remains of domestic ungulates were present in the field and food availability was considered sufficient to cover the energy requirements of avian scavengers (Margalida et al. 2011b). However, during API, the carcasses of domestic animals progressively had to be collected from farms and destroyed in authorized plants (Donázar et al. 2009b). The monitoring of several regions suggested that >80% of remains of *Ovis/Capra* were collected, and nearly 100% for the remains of *Bos/Equus*.

Modeling resighting and survival probabilities

Marked birds at release (including radio-tracked and not radio-tracked birds, i.e., birds with wing marks only) were grouped considering their true age (for fledglings, which represented 65% of marked individuals) and plumage characteristics into seven age classes (from 1-year-olds to older than 7 years; see details in Oro et al. 2008). In other words, each bird entered the database with different ages, so time-since-marking equaled different ages for each bird, depending on the age at marking. To improve the reliability of our estimates compared to the unistate modeling carried out by Oro et al. (2008), we used a multi-event probabilistic framework by combining the information obtained from resights and recoveries (i.e., dead marked animals). During the study, 36 recoveries of dead individuals were obtained and this information was added to the capture–recapture histories to inform the estimation of survival, with probabilities of resighting and recoveries. Furthermore, the multi-event approach allowed us to consider the capture heterogeneity resulting from young birds visiting the supplementary feeding stations more frequently than older birds (see Oro et al. 2008, Margalida et al. 2011c). We did not model population-wide survival, but because we covered most of the distribution range of the species in Spain and because the nearest breeding areas are far away and have very small breeding populations (e.g., the Alps), we can assume that our local survival approached true survival. All models were fitted using E-Surge software (Choquet et al. 2009).

We tested the hypothesis that the reduction in the availability of food resources in the ecosystem (as consequence of a sudden reduction of domestic carcasses in the field from 2005 and the closure of several feeding stations) should decrease survival probabilities, especially those of juveniles and subadults, which are more dependent on this food resource than are older birds (Oro et al. 2008). Thus, we introduced age to test for variations in survival, first with no specific trend, and second following a trend but only for adults (as recorded in a previous study from the same population; see Oro et al. 2008), or having two categorical values: before and after the application of the restrictive sanitary policy in 2005. This last model tested the hypothesis that survival decreased due to reduced food availability. Models testing potential effects of age (not necessarily showing a trend, as in the previous models) grouped individuals based on ecological knowledge of the species: youngest age class (juveniles, noted as 1 in models), immature birds (2- and 3-yr-old birds, noted as 2_3 in models), subadults (birds 4–5 yr old, noted as 4_5 in models), and older, territorial age classes (i.e., birds at least 6 yr old, noted as 6 in models). Other combinations of age classes were also considered, for instance by grouping immature and subadult age classes. Thus, we took the unconstrained model for survival as the starting model, which considered time and age variations for this parameter, whereas recapture and recovery probabilities varied only with age, as recorded in a previous study on the same population (Oro et al. 2008).

Field observations suggested that adults and subadults were increasing their numbers at the remaining supplementary feeding stations relative to the numbers of juveniles, so we also tested whether the survival of adult Bearded Vultures increased after food shortages.

TABLE 1. List of the 15 models explaining Bearded Vulture (*Gypaetus barbatus*) survival with lowest QAIC$_c$ values.

No.	Np	Deviance	QAIC$_c$	Δ_i	w_i	Hypothesis tested on survival by time and age
1	28	921.148	979.148	0	0.41	Only two values: before and after 2005 different for juveniles (1y) and immatures and subadults (2y_5y); for adults, trend with time.
2	28	922.572	980.636	1.488	0.19	Temporal trend in survival only for adults (>5y old); the two other age classes considered have constant survival and differ for juveniles (1y) and immatures and subadults (2y_5y).
3	28	923.76	981.823	2.675	0.11	Only two values: before and after 2005, but different for juveniles, immatures, and subadults (2y_5y) and adults.
4	28	924.045	982.109	2.961	0.09	Two values: before and after 2005, but only for adults; other age classes had constant survival but different for juveniles (1y) and immatures and subadults (2y_5y).
5	28	924.561	982.624	3.476	0.07	Two values: before and after 2005, but only for adults; other age classes had constant survival for juveniles (1y_5y).
6	25	931.319	982.965	3.817	0.06	Constant (all age classes had the same survival).
7	27	928.733	984.625	5.477	0.03	Two values: before and after 2005, but only for adults; other age classes had the same constant survival.
8	27	928.757	984.675	5.527	0.03	Only two values: before and after 2005, but different for juveniles, immatures, and subadults (1y_5y) and adults.
9	31	921.023	985.553	6.405	0.01	Only survival of old-subadults and adults (>5y old) had a temporal trend; other age classes had constant survival and differed for each age.
10	29	930.044	990.258	11.11	0.00	Only two values: before and after 2005; different for juveniles (1y) and immatures and subadults (2y_5y); for adults, a temporal trend before 2005 and another temporal trend (different slope) after 2005.
11	41	904.715	991.165	12.017	0.00	Change only with age.
12	29	931.077	991.291	12.143	0.00	Only two values: before and after 2005, but different for juveniles (1y) and immatures and subadults (2y_5y); for adults, survival had a temporal trend until 2006 and then remained constant.
13	30	929.903	992.272	13.124	0.00	Only adult survival changes with time; other age classes have constant survival; grouped differently for juveniles (1y), immatures (2y_3y), and subadults (4y_5y).
14	84	810.319	997.854	18.706	0.00	Change with time and age, but recapture equal for all ages except for juveniles.
15	94	797.367	1010.411	31.263	0.00	Change with time and age.

Notes: Age of individuals was grouped into eight age classes, the last grouping 6-yr-old birds and older (see *Methods*). Models referring to 2005 deal with a tipping point in that year, after which API were in short supply, probably affecting survival. Models considering different groupings of age classes were noted by their first age class considered; for instance, a model grouping 2- and 3-yr-old birds was noted as 2y_3y. Model structures were decided following methods described in Genovart et al. (2012). Np is the number of identifiable parameters; Δ_i is the QAIC$_c$ difference value between the best model and model i; w_i is the weight of model i. A complete list of models is shown in the Appendix: Table A1.

Taking into account the study by Oro et al. (2008) and the previous results obtained, we assessed the effects of poisoning and food availability on adult and pre-adult survival before and after 2005. We started by constraining the number of age classes for recapture probabilities from the unconstrained model (model 15 in Table 1); none of those models performed better, even considering separately the recapture for juveniles and for the rest of age classes grouped (model 14, Table 1; see also Table A1 in the Appendix). We then kept recapture probabilities changing for each age class separately when modeling changes in survival. When we tested how a model without time variations in survival performed (i.e., survival changing only with age; see model 11), the QAIC$_c$ value showed that this type of model behaved better and that the influence of time, if it existed, was small (see also model 6, Table 1). We then tested whether adult survival decreased with time due to an increase in poison exposure, as found previously, whereas the younger age classes had constant survival (see, e.g., models 2, 9, and 13). One of those models (model 2) performed very well and suggested that the environmental conditions did not change in the last years. Finally, we tested a set of models in which survival changed categorically, taking two values (before and after 2005, when most feeding stations were closed), and differently for each age class. Some (but not all) of those models performed well; for instance, model 3 suggested that the closure of feeding stations affected not only adults but also younger age classes.

Notation and selection of models followed common procedures in capture–recapture studies: the corrected Akaike Information Criterion for small sample sizes (QAIC$_c$) was calculated for each model and the model with the lowest QAIC$_c$ was considered to be the most parsimonious, i.e., the model with the lowest number of parameters necessary to explain the highest percentage of the variance. Models differing in less than two points in QAIC$_c$ were considered statistically equivalent (e.g., Lebreton et al. 1992, Williams et al. 2001).

Statistical analysis

Statistical tests were performed in R2.15.2 (R Development Core Team 2012). To assess if egg-laying
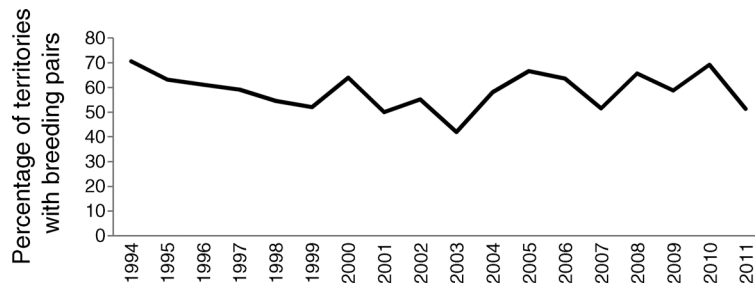
Fig. 1. Interannual variation (from 1994 to 2011) in the percentage of Bearded Vulture (*Gypaetus barbatus*) territories that had breeding pairs.

dates varied among years, we used GLMs (general linear models) with Gaussian error distribution and identity link function. The correlations between the different variables were carried out using the Spearman rank coefficient. We used nonparametric tests such as the Mann-Whitney U test for independent samples and the Wilcoxon test for matched pairs to compare the values of variables before (BPI) and after policy implementation (API) periods.

RESULTS

Percentage of breeding pairs

Between 1994 and 2011, we monitored 510 breeding attempts with a total of 298 clutches being laid. The average percentage of pairs that annually began breeding was $58.7\% \pm 11.6\%$ (mean $\pm$ SD, range 41.9–70.6%, $n = 18$) with a similar trend between years ($r_S = -0.094$, $P > 0.05$, $n = 18$; Fig. 1). The percentage of pairs that started breeding before and after policy change were not statistically different (for BPI, $57.2\% \pm 14.9\%$, range 41.9–70.6%, $n = 11$; for API, $61\% \pm 18.4\%$, range 51.5–69.2%, $n = 7$; Wilcoxon test, $W = 28$, $P > 0.05$).

Laying dates

We documented egg-laying dates on 258 occasions, without significant differences between years (GLM, $t = 1.36$, $P = 0.174$; Fig. 2). However, when we compared egg-laying dates before and after policy change, we found a significant delay following reduction in food supplies (for BPI, average 8 January, range 8 December–1 March, $n = 135$; for API, average 12 January, range 11 December–26 February, $n = 127$; $t = 2.44$, $P = 0.016$).
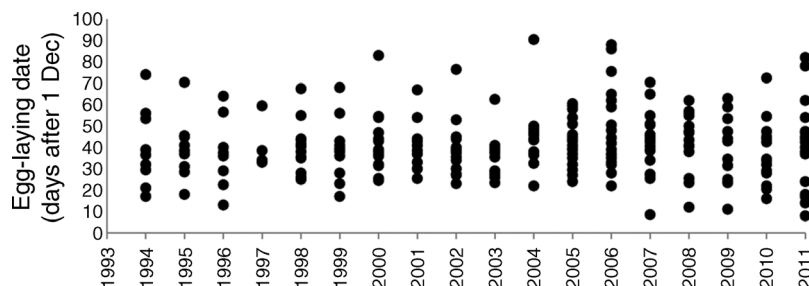
Clutch size

We observed a total of 104 clutches of which 59 (56.7%) consisted of a single egg (the remainder were two-egg clutches). The percentage of single-egg clutches increased through time ($r_S = 0.564$, $P = 0.018$; Fig. 3), and differed before and after policy change (single-egg clutches, for BPI, 39.37%, $n = 46$; for API, 69.59%, $n = 58$; $\chi^2 = 5.99$, df $= 1$, $P = 0.014$).

Productivity and fledging rate at successful nests

Productivity and fledging rate decreased slightly through time (for productivity, $r_S = -0.389$, $P = 0.110$; for fledging rate, $r_S = -0.144$, $P = 0.568$; Fig. 4). When we compared differences for both variables between periods, both values decreased before policy changes, although the differences were not statistically significant for productivity (for BPI, 0.37 ± 0.09 chicks fledged by controlled pair [mean $\pm$ SD], range 0.33–0.42, $n = 11$; for API, 0.29 ± 0.08, range 0.26–0.31, $n = 7$; Wilcoxon test, $W = 58.5$, $P = 0.07$) or for fledging rate (for BPI, 0.54 ± 0.11 chicks fledged by a pair with clutches, range 0.49–0.61, $n = 11$; for API, 0.46 ± 0.10, range 0.41–0.52, $n = 7$; Wilcoxon test, $W = 56$, $P = 0.123$).

Mortality and food supplies

Between 1994 and 2011, we documented a total of 65 cases of mortality. Survival decreased with time in all age classes (adults, $r_S = -0.60$, $P = 0.0091$; subadults, $r_S = -0.56$, $P = 0.0147$; juveniles, $r_S = -0.48$, $P = 0.0418$, $n = 18$). Survival differences in juvenile and adult age classes did not coincide with policy change (for juveniles, BPI survival is 97.5% per year, $n = 11$; API survival is 98.1%

Fig. 2. Interannual variation (from 1994 to 2011) in egg-laying dates in the Bearded Vulture, where 0 = 1 December.
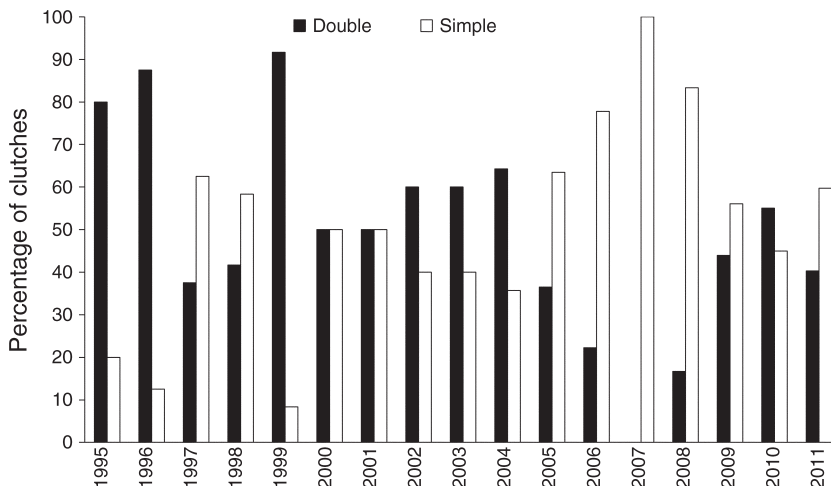
FIG. 3. Interannual variation (from 1995 to 2011) in the clutch size in the Bearded Vulture in the Pyrenees. Black columns are the percentage of clutches that are double (two-egg clutches); open columns are the percentage that are simple (one-egg clutches).

per year, $n = 7$; Wilcoxon test, $W = 52$, $P = 0.246$; for adults, BPI survival is 97.8% per year, $n = 11$; API survival is 94.6% per year, $n = 7$; Wilcoxon test, $W = 57$, $P = 0.104$), but did for subadults (BPI survival, 92.0% per year, $n = 11$; API survival, 90.2% per year, $n = 7$; Wilcoxon test, $W = 68$, $P = 0.0059$). This coincides with a progressive decrease in the number of carcasses provided by domestic ungulates from 2003 ($r_S = -0.909$, $P = 0.0001$, $n = 18$; Fig. 5).

Effects of illegal poisoning and reduced food supplies on adult and pre-adult survival

The model garnering the greatest support (model 1) showed that the closure of some feeding stations slightly changed survival and did so differently for juveniles (the age class exploiting feeding stations with higher frequency) and immature and subadults, whereas adults showed a temporal decline in survival over the study. Survival of juveniles decreased slightly from 97.5% (SE = 1.8%) to 95.7% (SE = 1.6%), that of immatures and subadults from 91.7% (SE = 1.3%) to 90.6% (SE = 1.8%), and adult survival decreased from 97.5% (SE = 1.4%) in

1987 to 90.1% (SE = 1.7%) in 2011 (adult estimates from model 14, Table 1).

DISCUSSION

Recent changes in European health regulations provoked apparent contradictions between the application of sanitary and conservation policies (i.e., eliminating corpses to avoid the presence of carrion in the field vs. conserving a scavenger species; Donázar et al. 2009b, Margalida et al. 2010). Implementation of the sanitation policy appears to have undermined conservation goals, as evidenced by, for example, an annual decrease in breeding success, reduced population growth, increased mortality in young age classes, and changes in diet and behavior of Eurasian Griffon Vultures (Donázar et al. 2009a, 2010, Zuberogoitia et al. 2010, Margalida et al. 2011a). Our results confirm these observations with empirical, long-term data on another vulture species. After sanitation policies were enacted, the threatened Pyrenean Bearded Vulture population had reduced survival, especially of subadult individuals, and adults bred later and less successfully than prior to policy
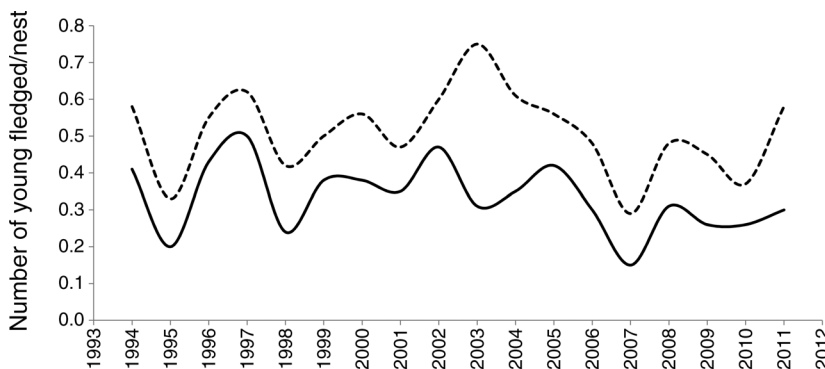

FIG. 4. Interannual variation (from 1994 to 2011) in the number of young fledged from all monitored nests (productivity, solid line) and number of young fledged from successful nests (fledging rate, dashed line) in the Bearded Vulture.
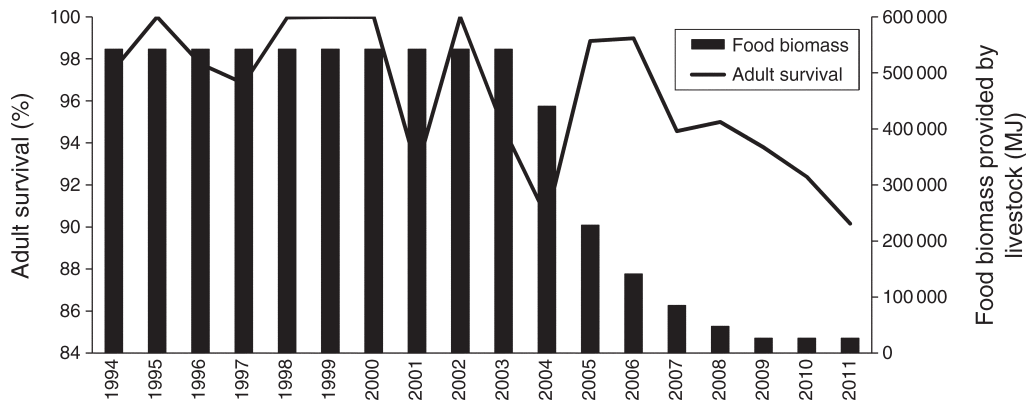
Fig. 5. Interannual variation (from 1994 to 2011) in the food biomass (bones) provided by domestic ungulates and adult survival of the Bearded Vulture. Biomass available was estimated through censuses and mortality rates of wild and domestic ungulates, taking into account the proportion of domestic ungulate carcasses that were destroyed and thus not available to scavenging birds (for more details, see *Methods*).

implementation. In this case, additional conservation actions, such as supplementary feeding, can buffer the negative effects of policy change on demographic parameters (Oro et al. 2008). However, because supplementary feeding can also have detrimental effects (Carrete et al. 2006a, Robb et al. 2008), this tool should only be used as a precautionary measure until the recovery of the previous scenario (i.e., availability of domestic carcasses in the field) is achieved.

According to our results, reduction of food supply does not affect the percentage of pairs that start breeding, so the decision to breed or not was not influenced by the change in carcass disposal legislation. Among the European scavenger guild, Bearded Vultures seem to be the least sensitive to the effects of food limitations (Margalida and Colomer 2012). Their specialized diet based on bone remains implies a foraging resource for which only conspecifics can compete; it lasts 10 times longer than meat remains and is very nutritious, having an advantage compared to a meat-based diet (Houston and Copsey 1994, Margalida 2008). Thus, although the percentage of pairs that do not start laying annually is important (range 29.4–58.1%), the decision to start breeding, which could be influenced by the physical condition of the individual (Jenouvrier et al. 2005), appears not to compromise the reproduction of Bearded Vultures. This suggests that, in this isolated population, several buffering mechanisms (e.g., changes in the structure of breeding age, low dispersal movements) may contribute to maintain stability in the percentage of pairs that start laying (Sergio et al. 2011, Oro et al. 2012, Margalida et al. 2013). In this sense, the carcass disposal policy does not seem to affect population movements because pre-adult individuals remained in the study area without greater pre-dispersal movements (Margalida et al. 2013). With respect to non-natural mortality, although mortality factors affect mostly adult age classes (Margalida et al. 2008b, Oro et al. 2008), they seem to play no role in the

start of breeding. Thus, buffering capacity through ecological and behavioral processes such as positive feedback from conspecific attraction could explain this regular pattern (Margalida et al. 2011b, Oro et al. 2012).

With respect to pre-adult and adult survival, although the closure of feeding stations and the widespread reduction of food resources suggest a decrease in both age class groups, their effects were not very pronounced. This could be explained because specific feeding stations for Bearded Vultures provided only with bone remains continued functioning after the application of health regulations; juveniles are the age class most dependent on these sites. Thus, the avian scavenger guild was limited by reduced food availability after the closure of several feeding stations and the destruction of domestic carcasses (Cortés-Avizanda et al. 2012), but their effects on Bearded Vultures were partially minimized with the specific, predictable feeding stations present.

During the last six years, the proportion of double clutches seemed to decrease in parallel with laying dates. Large avian species often show obligate brood reduction (two eggs laid, but only one chick survives) in which siblicide (when >90% of last-hatched chicks die; Simmons 1988) may occur, even when food supplies are abundant. The second egg thus serves as insurance against loss of the first egg from infertility, predation, or damage, rather than as a means of rearing two chicks (Stinson 1979, Anderson 1990, Mock et al. 1990). According to Winkler et al. (2002), there is a strong effect of laying date on clutch size, and earlier breeding may lead to larger clutch sizes. An increase of food resources could increase clutch size in facultative-fratricide species (Korpimaki and Wiehn 1998), but in obligate fratricide species such as Bearded Vultures, the second egg seems to be an adaptive mechanism serving as an insurance egg to avoid breeding failure if the first egg does not hatch (Stinson 1979, Margalida et al. 2004). Thus, if the second egg is a security egg, the reversed trend in two-egg clutches could, in part, explain the increase in breeding failures and, thus, the decline in breeding parameters

observed during this period. In several species, including the Bearded Vulture, it seems that single-egg clutches are related to old or young females (Frey et al. 1995). According to our results, the increase of single-egg clutches could be related to a reduction in food supply or the stress that changes in food availability could provoke in individuals (i.e., increasing foraging effort or agonistic interactions as a consequence of a greater competence for the resources) and the effects of mate loss with the incorporation of less experienced individuals.

The conservation implications of this work suggest that anthropogenic activities modifying habitat quality through human health regulations (i.e., a reduction in food availability) can alter demographic parameters and increase the probability of illegal poison bait consumption, thus increasing non-natural mortality. The shifts in demographic parameters can have important conservation consequences, being necessary to adopt preventive mitigation measures on targeted species. As a result, preventive management measures such as supplementary feeding can be effective until more flexible sanitary legislation allows increased trophic availability, minimizing the detrimental effects that food shortages and illegal poisoning can cause.

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SUPPLEMENTAL MATERIAL

Appendix

A list of the models explaining Bearded Vulture survival (*Ecological Archives* A024-026-A1).