

POPULATION SIZE OF THE ENDANGERED  
BEARDED VULTURE *GYPÆTUS BARBATUS*  
IN ARAGON (SPAIN): AN APPROXIMATION  
TO THE PYRENEAN POPULATION

TAMAÑO POBLACIONAL DEL QUEBRANTAHUESOS  
*GYPÆTUS BARBATUS* EN ARAGÓN (ESPAÑA):  
UNA APROXIMACIÓN A LA POBLACIÓN PIRENAICA

Amaia GÓMEZ DE SEGURA<sup>1</sup> \*, José María MARTÍNEZ<sup>1</sup> and Manuel ALCÁNTARA<sup>1</sup>

**SUMMARY.**—The population size of the Pyrenean population of the bearded vulture *Gypaetus barbatus*, the most important viable wild population in Europe, remains poorly known, despite its status as endangered in Europe. In this study, the abundance of immature vultures and adults (both territorial and floaters) was estimated in the Aragón region, the core area of the Pyrenean population, to provide an indicator of the total Pyrenean population. Using artificial feeding stations specifically designed for bearded vultures as survey points, 25 censuses were conducted during March 2010 in which 873 sightings (106 of individually marked birds and 767 of unmarked birds) were recorded. By applying the mark-recapture method, the total population of bearded vultures in the study area during the winter period was estimated to be 328 individuals (95% CI: 279-391 individuals). Separate estimates by age groups suggested a population of 129 immature individuals (95% CI: 107-160) and 227 adults (95% CI: 173-311). The adult floating population was estimated at 49 individuals and the adult non-breeding fraction was 93 individuals. Compared to previous censuses, the results suggest that although the reproductive fraction is increasing, the total population still has some problems: the immature fraction is not increasing, as predicted in previous studies, and a high proportion of adults are not contributing effectively to the breeding process. Conservation measures should focus on these two issues to increase the viability of the Pyrenean population.

**Key words:** Population estimation, bearded vulture, mark-resighting, population changes.

**RESUMEN.**—A pesar del delicado estado de conservación que presenta el quebrantahuesos *Gypaetus barbatus* en Europa, el tamaño de la población pirenaica, la más importante población silvestre viable en Europa, es desconocido. En este estudio se ha estimado la abundancia de la fracción inmadura y adulta (tanto individuos territoriales como flotantes) de quebrantahuesos en la Comunidad Autónoma de Aragón, el área principal de la población pirenaica, como un indicador de la población total. Usando los puntos de alimentación suplementaria específicos para quebrantahuesos como puntos de muestreo, se han realizado 25 censos durante marzo 2010 en los que se obtuvieron 873 avistamientos (106 indi-

---

<sup>1</sup> Dirección General de Desarrollo Sostenible y Biodiversidad, Departamento Medio Ambiente, Gobierno de Aragón, Paseo María Agustín 36, 50071 Zaragoza, Spain.

\* Corresponding author: amaiago@gmail.com

viduos marcados y 767 no marcados). Por medio de la metodología de marcaje y recaptura se estimó que la población total de quebrantahuesos en invierno en el área de estudio sería de 328 individuos (95% IC: 279-391 individuos), de los que 129 (95% IC: 107-160) serían inmaduros y 227 (95% IC: 173-311) serían adultos. La población adulta flotante fue estimada en 49 individuos y la fracción adulta no reproductora la compondrían 93 individuos. Al comparar con censos previos, nuestros resultados sugieren que, aunque la fracción reproductora está aumentando, la población total todavía presenta algunos problemas; por un lado, la fracción inmadura no está aumentando, como se estimaba en estudios previos; por otro lado, existe una gran fracción de adultos que no están contribuyendo de forma efectiva al proceso reproductor. Las medidas de conservación de la especie deberían centrarse en estos dos problemas para incrementar la viabilidad de la población pirenaica.

*Palabras clave:* cambios poblacionales, estimas poblacionales, marcaje-reavistamiento, quebrantahuesos.

## INTRODUCTION

The bearded vulture *Gypaetus barbatus* is a large territorial raptor that once occupied all the mountainous regions of the Old World. In Europe, this once widespread species has undergone a dramatic decline, becoming extinct in the Alps, the Balkans, the Carpathians, Cyprus and Sicily (Tucker and Heath, 1994). It is been classified as endangered in Europe since 2000.

Its situation in Europe has slightly improved since the 1980s. The main European population, located in the Pyrenean Mountains, has increased in terms of breeding pairs. However, the other two natural populations, in Corsica and Crete, are thought to be stable and decreasing, respectively, and are prone to extinction due to their very small size (Bretagnolle *et al.*, 2004; Heredia, 2005; Xirouchakis and Tsiakiris, 2009; Razin *et al.*, 2009). Reintroduction projects have been carried out successfully in the Alps (Schaub *et al.*, 2009) and have recently been initiated in Spain in Andalucía and the Picos de Europa (Simón *et al.*, 2005; Báguena *et al.*, 2007). There were about 150 breeding territories in the European Union in 2006 (Margalida *et al.*, 2008a). Most of the European breeding bearded vulture population is found in the Pyrenees, particularly in the Spanish Pyrenees: which hold over 60% of the European

Union breeding population (Margalida and García, 2011). Here, the species reached its lowest population levels in the 1980s, when the first specific census of breeding birds began, and fewer than 40 occupied breeding territories remained in the Spanish Pyrenees. The breeding population has greatly increased in recent years, largely due to the nationwide prohibition of killing raptors and of using poison to control predators, as well as to the application of management actions as part of the species Recovery Plans. In 2009 the Spanish Pyrenean population comprised 110 territories (Margalida and García, 2011). One of the most significant management actions was the creation of a network of feeding sites, which has reduced immature mortality (Oro *et al.*, 2008) and has allowed the monitoring of marked individuals, although its conservation efficacy has been questioned (Carrete *et al.*, 2006a).

The recovery of the Pyrenean population is not guaranteed despite the increase in the breeding population. Productivity has decreased recently, possibly due to density-dependent factors (Carrete *et al.*, 2006a) and/or human disturbance around the nesting areas (Arroyo and Razin, 2006). Also, increased human-induced mortality through illegal poisoning and other activities also affects the birds' survival (Margalida *et al.*, 2008a).

Information on the status or population trends of the non-breeding elements of the population, i.e. the immature ( $\leq 5$  years) and non-territorial adult floater fractions, has been lacking. The last estimate of the Pyrenean immature population was made in 2002 but the results were not accurate (Antor *et al.*, 2005). The Pyrenean adult floating population has never been evaluated or estimated

despite the important role that floaters play in the population dynamics of raptor species (Hunt, 1998). Information on population size is indispensable to predict population trends and to assess the conservation status of the species and the efficiency of the conservation measures applied. The mark-recapture method (Amstrup *et al.*, 2006) is widely used to estimate population abundances. A



FIG. 1.—Study area (Huesca province) and location of artificial feeding stations (spots), the survey points of this research. The most important artificial feeding stations are represented with open circles. The dashed area shows the actual Pyrenean distribution area of the bearded vulture.

[Área de estudio (provincia de Huesca) y localización de sitios artificiales de alimentación (puntos), utilizados como lugares de censo en este estudio. Los sitios artificiales de alimentación más importantes se representan con círculos blancos. El área rayada muestra la distribución actual del quebrantahuesos en los Pirineos.]

mark-resighting method is a less invasive alternative to traditional mark-recapture, and it is more convenient to use when working with sensitive species. This method has been applied successfully to many taxa, including birds (McClintock and White, 2011).

The initial aim of this study was to estimate the total bearded vulture abundance of the Pyrenean population to compare it with previous information. However, the study was conducted only in the core area, Aragón region (fig. 1), since it was difficult to coordinate the survey across all the administrative regions. Aragón holds most of the Spanish Pyrenean population, both immatures and adults: 67% of the Spanish breeding population (Heredia, 2005) and 78% of the sightings of immatures made during the Spanish simultaneous censuses (unpublished data, Aragón Government, GA). Hence, the results obtained in this study may be regarded as an indicator of the situation of the entire Pyrenean population.

## MATERIAL AND METHODS

### *Study area*

The study area, the Aragón region (Spain), occupies some 12,000 km<sup>2</sup> in the central sector of the Pyrenean chain (fig. 1). It includes the three types of biogeographical zone present in the range: the axial Pyrenees: the central zone with the highest altitudes; the internal ranges: closer to the axial Pyrenees but of lower altitudes; and the external ranges or Pre-Pyrenees: isolated mountain massifs running parallel to the *axial Pyrenees*. The study area represents approximately 50% of the existing Pyrenean distribution area of the bearded vulture (fig. 1).

This area includes most of the Spanish Pyrenean breeding population and contains most of the artificial feeding stations designed for bearded vultures. These supply

bones and lambs' legs and tend to congregate birds, especially the immature population (Sesé *et al.*, 2005).

Although the area of influence of our survey points (artificial feeding stations) has not been studied in detail, it probably extends far beyond the regional and state limits (see Discussion).

### *Marking method and marked animals*

Bearded vultures have been marked in the Pyrenees since 1987 (Heredia and Sunyer, 1989). An intensive marking program was set up in Aragón in 1994, marking six birds annually on average, and is still on-going. Birds were marked either as chicks in the nest (at an age of approximately three months) or when caught at an artificial feeding station (birds of any age). In both cases, birds were marked with tarsus rings and two wing tags (one per wing) of different colours to identify them individually. They were also fitted with radio-transmitters in nearly all cases (Heredia and Sunyer, 1989; Gil *et al.*, 2010).

Since 1987 and until the date of the present surveys, 114 birds have been marked with wing tags in the Pyrenees: one in France, 3 in Catalonia, 5 in Navarra and 105 in Aragón. Wing tags can be lost over time and given that this study is based on visual censuses, only animals that retained at least one of the wing tags were considered as marked. In order to estimate population size it is necessary to know the number of marked individuals still alive and within the study area during the sampling period. For this study, we considered an individual to be alive when it had been observed (at an artificial feeding station, in territorial areas, incidentally, etc...) or radio-detected in Aragón during 2009 or 2010. However, a marked animal not detected in Aragón since 2008 need not necessarily be dead, since it may have lost its two marks or have settled outside the study area.

In March 2010, we estimated that 39 birds (17 immatures,  $\leq 5$  years old, and 22 adults,  $\geq 6$  years old) were alive and marked (with at least one wing tag) in the study area. Nineteen had been marked in their nests, two were raised in captivity and released into the wild, and 18 were captured and marked at an artificial feeding station. The value of the number of marked individuals alive in the study area is critical for the estimation of population size. Therefore, this value was also estimated using a different method to compare the results. The number of marked animals observed at an artificial feeding station or in territorial areas in Aragón between January and March 2010 was divided by the recapture rate estimated by Oro *et al.* (2008): 17 marked adults were observed at artificial feeding stations and territories in Aragón and the recapture rate of adults was 0.751 (Oro *et al.*, 2008). All 17 of the immatures individually marked in the Pyrenees were detected in Aragón between January and March 2010, so it was not necessary to estimate the number of surviving marked immatures.

### Resighting method

All six of the artificial feeding stations for bearded vultures in the Aragon Pyrenees were used as survey points. These are distributed across the Pyrenees and Pre-Pyrenees (fig. 1), although 86% of the observations in the central Pyrenees were concentrated at two of them.

Surveys were conducted during a single month, March 2010, with the aim of maximising the number of sightings (maximum number of birds at artificial feeding stations, especially of immatures, Sesé *et al.*, 2005) and minimising a bias assumed by the method (lower adult dispersal at the beginning of the breeding period. See Discussion). Both sexes contribute equally to incubation and chick care (Margalida and Bertran, 2000),

so no sex bias was expected at artificial feeding stations. Surveys were conducted twice weekly, on Thursdays and Fridays, over four weeks. Three censuses were carried out on each day at the same times: 10:30, 12:00 and 13:30 hrs. On each occasion the numbers of marked ( $m_i$ ) and unmarked individuals ( $u_i$ ) observed at that precise time were counted, distinguishing between age groups. The observed marked individuals were also identified if possible, although this information was not used for estimating abundance (see below). If there were too many birds to count accurately (more than 30), only settled birds were counted.

Surveys were conducted by at least two experienced observers from a point situated 200-300m from the artificial feeding stations, to minimise disturbance while ensuring mark resightings.

### Data analysis

Population abundance ( $N$ ) was estimated using the mark-resighting method, which is a generalisation for more than two sampling occasions of the classic two-sample Lincoln-Petersen estimator:

$$\hat{N} = \frac{M n_i}{m_i}$$

where  $M$  is the total number of marked animals alive in the area surveyed and  $n_i$  is the total number of animals seen during the  $i_{th}$  sighting survey, consisting of  $m_i$  marked animals and  $u_i$  unmarked animals, so that  $n_i = m_i + u_i$ .

We calculated separate abundance estimates for two easily distinguishable age classes: immatures ( $\leq 5$  years) and adults ( $\geq 6$  years). The division into these two groups was done bearing in mind their biological interest (breeders or territorial birds *vs* the immature population, Antor *et al.*, 2007) and

because it is very difficult to determine the age of birds more than six years old in the field. We calculated population estimates for each age class and for the total population using the NOREMARK program with the joint hypergeometric maximum likelihood estimator (JHE). JHE is the value of  $N$  which maximises the following likelihood ( $N$ ):

$$\mathcal{L}(N | M, n_i, m_i) = \prod_{i=1}^k \frac{\binom{M}{m_i} \binom{N-M}{n_i - m_i}}{\binom{N}{n_i}}$$

The terms are defined for all  $i = 1$  to  $k$  sighting occasions. Confidence intervals are determined with the profile likelihood method (White, 1996).

We also generated population estimates using another estimator provided by the program, the Minta-Mangel estimator (Minta and Mangel, 1989), for comparing and testing the robustness of the estimations. Contrary to the previous one, this estimator does not require the assumption that each animal in the population has the same probability of resighting on a particular occasion, since estimate and confidence intervals are based on a bootstrap procedure. Finally, since three of the marked immature birds were observed outside the area during the study period, we also estimated the immature population using the immigration-emigration joint hypergeometric estimator (Neal *et al.*, 1993) extended to incorporate animals moving into and out of the study area. In addition, the adult population was estimated using the  $M$  value calculated with the recapture rate ( $M_1$ ) in order to check the robustness of the results.

Once the size of the adult population in the study area was estimated, we calculated the adult floating population (non-territorial adults) by subtracting the number of individuals that had showed reproductive behaviour during the 2010 season.

## RESULTS

In total 25 simultaneous censuses ( $k$ ) were conducted in the study area during March 2010, resulting in 103 sightings of marked individuals (66 of immatures and 37 of adults) and 767 sightings of unmarked individuals (419 of immatures and 348 of adults). During the surveys, 14 individually marked immatures and 12 individually marked adults were observed. During 2009 and 2010 a total of 22 individually marked adults were detected in Aragon and this value was taken to be the number of marked adults alive in the study area ( $M$ ). The total population of bearded vultures in the study area during the winter period was estimated to be 328 individuals (95% CI: 279-391 individuals; table 1). The estimated immature population was 129 individuals (95% CI: 107-160 individuals). The adult population was estimated at 227 individuals (95% CI: 173-311 individuals). Results obtained with the other models (Minta-Mangel and immigration-emigration) were also very similar although the confidence intervals of the abundances estimated with the bootstrap procedure were smaller (table 1).

The number of marked adults alive in the study area was also calculated using the recapture rate and the sightings of 2010, and was estimated to be 23 adult individuals ( $M_1$ ). The abundance obtained using this value was also very similar to the previous ones (table 1). Therefore, all estimations for the different models and  $M$  values were very similar, indicating that the population size estimate is quite robust (table 1).

Data from the annual breeding census in Aragon show that during the 2009-2010 breeding season 67 reproductive units (46 pairs, 20 trios and one group of 4 individuals) and 10 territorial units (8 pairs and 2 trios) initiated the breeding process in the study area (GA, unpublished data): at least copulations and territory defence were observed in these cases. Therefore, there were 178

TABLE 1

Estimations of the number of individuals ( $N$ ) of the immature fraction, adult fraction and total population of bearded vulture in the Aragon region during March 2011 and the 95% confidence interval using different models of the NOREMARK program, and of the number of adults with the  $M_i$  value (number of marked and alive adults calculated using the recapture rate).

[*Estimación del número de individuos (N) de las fracciones inmadura y adulta de la población total de quebrantahuesos en Aragón en marzo de 2011 y el intervalo de confianza al 95% utilizando diferentes modelos del programa NOREMARK y del número de adulto con el valor  $M_i$  (número de adultos marcados y vivos calculados utilizando la tasa de recapturas).*]

MODEL	TOTAL			IMMATURE			ADULT			ADULT (with $M_i$ )		
	$N$	95% CI		$N$	95% CI		$N$	95% CI		$N$	95% CI	
JHE	328	279	-391	129	107	-160	227	173	-311	238	181	-326
Minta-Mangel	327	298	-363	124	111	-141	230	201	-260	239	210	-273
Immigration- emigration				131	105	-168						

territorial adult individuals in the study area. Subtracting this number from the total estimated adult population, the number of adult floaters in the study area was 49 individuals (95% CI: 0-133 individuals), 22% of the adult population. Moreover, considering supplementary adult individuals from trios and territorial but non-breeding birds, no fewer than 93 adult individuals (95% CI: 39-177 individuals), 41% of the total adult population, do not contribute directly to the annual dynamics of the population.

## DISCUSSION

Estimating the population size of large raptors such as the bearded vulture is problematic, although critical for conservation purposes. The great mobility of individuals: over 100 km per day in this species (GPS unpublished data, Bearded Vulture Conservation Foundation, FCQ) and the difficulty

of observing non-territorial individuals can hinder the quality of results. The estimate of total population size (i.e. including all categories of birds: breeder and non-breeder, immature and adult) that we provide in this paper is the first of its kind for bearded vultures in the sector of the Pyrenees that holds containing most of the Spanish population.

### *Methodological assumptions*

Our population size estimates may suffer however from several biases, due to a failure to meet the methodological assumptions. The main one is the assumption of a closed population, which is related to the delimitation of the actual study area. Demographically speaking, closure is fulfilled since surveys were conducted over a very short period of time, but geographical closure was probably not achieved. Surveys were carried out early in the breeding season, during the incubation

or hatching periods. At this stage, territorial and reproductive adults show intense territory defence (Margalida and Beltran, 2005) and are not expected to move outside the study area. However, adult floaters and immature individuals could have moved beyond the study area when the census was conducted, in the same way as adult floaters and immatures from adjacent areas could have entered the study area. Data on sightings of marked individuals at artificial feeding stations in Aragon and adjacent regions/countries, as well as GPS data (unpublished, FCQ), corroborate this fact (see below). The mobility of the species thus makes it impossible to determine precisely how many marked animals were in the study area on a given survey day.

The principal problem involves establishing the actual demarcation of the study area. There are no precise studies of the extent of the areas of influence of artificial feeding stations, where censuses were conducted, and this area could vary according to the age class and reproductive status of individual birds. GPS data show that immatures and non-breeding adults can travel large distances to feed at a feeding station (unpublished data, FCQ), and adult floaters and immatures marked in other regions are frequently observed at the Aragón feeding stations (unpublished data, GA). These data indicate that the area of influence of an artificial feeding station can be quite large and can extend beyond the study area, to include part of contiguous areas (in France, Catalonia and Navarra), especially in the cases of the floating adult and immature population fractions. In fact, most of the immature Pyrenean population concentrates at the Aragon feeding stations, since they are the most reliable and most numerous of such feeding points (Heredia, 1991; Sesé *et al.*, 2005). It is therefore likely that the immature population size estimated in this study may be close to the actual Pyrenean immature bearded vulture population.

All this considered, the values presented here must be regarded with caution. The only way avoid all bias would be to coordinate a simultaneous survey across the entire Pyrenean area within all the relevant administrative regions in Spain and France.

Another assumption of the method is that the number of marked individuals that inhabit the study area during the census period is known. This figure cannot be known exactly since some were marked a long time ago. We estimated it on the basis of recent sightings (see Materials and methods) but this could introduce some bias into the population size estimate. In the case of the adult fraction, an individual that is considered to be 'alive' may be dead or may have lost its marks recently. In the same way, a territorial individual settled in an inaccessible area might be considered as 'dead' through not having been observed during the past year. We consider that these two sources of error had very limited significance since the Aragón Government makes an intensive monthly effort to monitor marked birds and to inspect all possible territory areas. In addition, the number of live marked adults within the study area was also estimated on the basis of 'recaptures' by using an alternative method. The population figures obtained by both methods were very similar, indicating that this estimate is not biased. The marked immature population did not require estimation since all the marked immature individuals in the Pyrenees were detected during the census period.

#### *Population changes and conservation*

*Immature fraction:* From 1990 to 2006, simultaneous censuses were conducted in both French and Spanish Pyrenees to monitor the Pyrenean population and estimate its size. However, data from these censuses contain quite a lot of errors (Margalida *et al.*, 2011) and they were only used to estimate the im-



mature fraction from 1995 to 2004 (Antor *et al.*, 2005). The results of these estimates were not published in the scientific literature and therefore methods and confidence intervals are not available. Antor *et al.* (2005) estimated the Pyrenean immature population ( $\leq 5$  years) to have increased from 138 individuals in 1995 to 201 in 2002 (mean annual increase: 5.5%), and this increase was expected to continue given the conservation efforts. Had the Pyrenean immature population continued to grow as predicted, the 2010 population would have been 292 individuals. However, the results obtained in this study show much lower values than expected: an immature population of 129 individuals (with a maximum of 160 individuals). We cannot affirm that the immature population is decreasing, as we have not estimated the entire Pyrenean population, but we assert that the immature population at least did not continue to increase as predicted. Margalida *et al.* (2011), using matrix-modelling approximations, also observed a reduction in the growth of the immature population fraction during the final years of their study (2004-2006).

The number of reproductive units in the Spanish Pyrenees has increased during recent years (see Introduction), so the number of immatures was also expected to have grown. Furthermore, an estimate of the survival rate of the Pyrenean immature birds concluded that there was a slight increase recently (Oro *et al.*, 2008), and this would contribute to the numerical increase of that fraction of the population. However, the results of the present study reveal that the immature fraction is not increasing. A possible cause could be the recent decline in the productivity of the Pyrenean breeding units (Carrete *et al.*, 2006a; Margalida *et al.*, 2007; Woutersen *et al.*, 2009), which has reduced the incorporation of new individuals into the population. In Aragón particularly, the decline in productivity has been more pronounced since

2003, when Antor *et al.* (2005) had ended their studies (unpublished data, GA).

*Adult fraction:* The breeding of bearded vultures in the Aragón Pyrenees has been monitored since 1994 and has revealed a constant increase in the breeding fraction of the population, which has nearly doubled the number of reproductive units so far (unpublished data, GA). However, information on the adult floating fraction of the Pyrenees is very scarce and the result presented here is the first estimation of the population size of this fraction. Although we cannot confirm whether this number represents the adult floating population of Aragón alone or whether it is the population of a more extensive area, it is quite a significant number relative to the total population size (22%). Furthermore, if the number of adults that do not contribute directly to population growth (adult floaters plus territorials, plus the additional individuals within some reproductive units) is taken into account, the adult non-breeding fraction amounts to 41% of the adult population. Adult floaters play an important role in the population dynamics of raptor species. Whereas they may have a buffering effect through replacing breeding individuals that die, they can interfere with the breeding process by conflicting with nesting birds and causing reproductive output to decline (Hunt, 1998; Bretagnolle *et al.*, 2008). Carrete *et al.* (2006a) suggested that the current dynamics of the Pyrenean bearded vulture population may be explained in terms of a density-dependent hypothesis: as the population increases, average productivity decreases. The habitat saturation hypothesis could explain the large number of non-breeding adults observed, although nest-site selection studies (Donázar *et al.*, 2005; Margalida *et al.*, 2008b) have suggested that many potential breeding cliffs for bearded vultures in the Pyrenees are still unoccupied.

Finally, data from marked individuals also suggest the existence of a substantial fraction of adult floaters without breeding territories (Antor *et al.*, 2007) and the number of units formed by polyandrous trios has increased in the last few years (Carrete *et al.*, 2006b). Such data reinforce our finding that there is a large number of adult non-breeder individuals in the population, but more studies are required to establish the importance and implications of this.

### Conclusion

We here provide the first estimate of entire population, adults plus immatures, of the bearded vulture in the core area of the Pyrenees. Although we cannot be sure of the geographical range of the population censused here, due to the high mobility of non-territorial birds, our results provide new information on the status of Pyrenean population. In particular, the adult non-breeding fraction is quite large. Also, the immature fraction of the population is not increasing as expected.

Finally, this study also indicates the need to carry out coordinated and long-term surveys throughout the whole of the Pyrenees. The methodology used here could be a suitable basis for future surveys. This method is highly time-efficient and requires much less work than, for example, the coordinated surveys used by Antor *et al.* (2005). Increasing the number of survey points across the whole geographical range of bearded vultures in Spain and France would greatly improve the accuracy of population size estimates and would be very helpful for the conservation of the species.

ACKNOWLEDGEMENTS.—Thanks to all the Natural Protection Agents of Aragón for helping us gather data for this study, and a special thanks

to J. A. Sesé for his valuable contributions to this work. Thanks to the Bearded Vulture Conservation Foundation, FCQ, for 20 years of work in marking birds and also for taking sightings data and for the disposal of GPS data. We thank J. L. Tellería and A. Margalida for his helpful complement to this manuscript and to D. Oro for providing the necessary data.

### BIBLIOGRAPHY

- AMSTRUP, S., MACDONALD, L. and MANLY, B. 2006. *Handbook of Capture-Recapture Analysis*. Princeton University Press. Princeton.
- ANTOR, R. J., ALCÁNTARA, M. and GIL, J. A. 2005. Evolución de la fracción preadulto de la población pirenaica de quebrantahuesos (*Gypaetus barbatus*): resultados de 10 años de censos simultáneos (1994-2003) y propuesta para el periodo 2004-2007. *Revista de Anillamiento*, 15: 16-19.
- ANTOR, R. J., MARGALIDA, A., FREY, H., HEREDIA, R., LORENTE, L. and SESÉ, J. A. 2007. Age of first breeding in wild and captive populations of Bearded Vultures (*Gypaetus barbatus*). *Acta Ornithologica*, 42: 114-118.
- ARROYO, B. and RAZIN, M. 2006. Effect of human activities on bearded vulture behaviour and breeding success in French Pyrenees. *Biological Conservation*, 128: 276-284.
- BÁGUENA, G., SÁNCHEZ-CASTILLA, E. and ANTOR, R. J. 2007. *Criterios para la Reintroducción de una Especie Amenazada: El Quebrantahuesos en el Parque Nacional de los Picos de Europa*. Organismo Autónomo Parques Nacionales. Madrid.
- BRETAGNOLLE, V., INCHAUSTI, P., SEGUIN, J. F. and THIBAUT, J. C. 2004. Evaluation of the extinction risk and of the conservation alternatives for a very small insular population: the bearded vulture *Gypaetus barbatus* in Corsica. *Biological Conservation*, 120: 19-30.
- BRETAGNOLLE, V., MOUGEOT, F. and THIBAUT, J. C. 2008. Density dependence in a recovering osprey population: demographic and behavioural processes. *Journal of Animal Ecology*, 77: 998-1007.

- CARRETE, M., DONÁZAR, J. A. and MARGALIDA, A. 2006a. Density-dependent productivity depression in Pyrenean Bearded Vultures: implications for conservation. *Ecological Applications*, 16: 1674-1682.
- CARRETE, M., DONÁZAR, J. A., MARGALIDA, A. and BERTRAN, J. 2006b. Linking ecology, behaviour and conservation: does habitat saturation change the mating system of bearded vultures? *Biology Letters*, 2: 624-627.
- DONÁZAR, J. A., MARGALIDA, A., BUSTAMANTE, J., HERNÁNDEZ, F., ROMERO-PUJANTE, M., ANTOR, R. J., GARCÍA, D., CAMPION, D. and HEREDIA, R. 2005. Aplicación de modelos predictivos en la selección del cortado de nidificación por el quebrantahuesos en los Pirineos: cambios a largo plazo (1991-2002). In, A. Margalida and R. Heredia, (Eds.): *Biología de la Conservación del Quebrantahuesos Gypaetus barbatus en España*, pp. 139-154. Organismo Autónomo Parques Nacionales. Madrid.
- GIL, J. A., DÍEZ, O., BÁGUENA, G., LORENTE, L., PÉREZ, C., LOSADA, J. A. and ALCÁNTARA, M. 2010. *Juvenile Dispersal of the Bearded Vulture (Gypaetus barbatus) in the Pyrenees (Spain-France)*. Fundación para la Conservación del Quebrantahuesos. Zaragoza.
- HEREDIA, R. 1991. Alimentación suplementaria. In, R. Heredia and Heredia, B. (Eds.): *El Quebrantahuesos (Gypaetus barbatus) en los Pirineos*, pp. 101-108. Colección Técnica, ICONA. Madrid.
- HEREDIA, R. 2005. Status y distribución del quebrantahuesos en España y diagnóstico de la situación de la población en la UE. In, A. Margalida and Heredia, R. (Eds.): *Biología de la Conservación del Quebrantahuesos Gypaetus barbatus en España*, pp. 21-37. Organismo Autónomo Parques Nacionales. Madrid.
- HEREDIA, R. and SUNYER, C. 1989. *Seguimiento de la Reproducción y Dispersión juvenil del Quebrantahuesos en los Pirineos*. ICONA. Unpublished report.
- HUNT, W. G. 1998. Raptor floaters at Moffat's equilibrium. *Oikos*, 82: 191-197.
- MARGALIDA, A. and BERTRÁN, J. 2000. Breeding behaviour of the bearded vultures *Gypaetus barbatus*: minimal sexual differences in the parental activities. *Ibis*, 142: 225-234.
- MARGALIDA, A. and BERTRÁN, J. 2005. Territorial defence and agonistic behaviour of breeding bearded vultures *Gypaetus barbatus* toward conspecifics and heterospecifics. *Ethology Ecology & Evolution*, 17: 51-63.
- MARGALIDA, A. and GARCÍA, D. 2011. Intraspecific nest usurpation in the bearded vulture *Gypaetus barbatus* in Catalonia (NE Spain). *Ardeola*, 58: 303-308.
- MARGALIDA, A., CARRETE, M. and DONÁZAR, J. A. 2007. Cae la productividad del quebrantahuesos. *Quercus*, 253: 14-20.
- MARGALIDA, A., HEREDIA, R., RAZIN, M. and HERNÁNDEZ, M. 2008a. Sources of variation in mortality of the bearded vulture *Gypaetus barbatus* in Europe. *Bird Conservation International*, 18: 1-10.
- MARGALIDA, A., DONÁZAR, J. A., BUSTAMANTE, J., HERNÁNDEZ, F. J. and ROMERO-PUJANTE, M. 2008b. Application of a predictive model to detect long-term changes in nest-site selection in the bearded vulture *Gypaetus barbatus*: conservation in relation to territory shrinkage. *Ibis*, 150: 242-249.
- MARGALIDA, A., ORO, D., CORTÉS-AVIZANDA, A., HEREDIA, R. and DONÁZAR, J. A. 2011. Misleading population estimates: biases and consistency of visual surveys and matrix modelling in the endangered bearded vulture. *PLoS One*, 6: e26784.
- MCCCLINTOCK, B. T. and WHITE, G. C. 2011. From NOREMARK to MARK: software for estimating demographic parameters using mark-resight methodology. *Journal of Ornithology*, 152 (Supplement 2): 541-650.
- MINTA, S. and MANGEL, M. 1989. A simple population estimate based on simulation for capture-recapture and capture-resight data. *Ecology*, 70: 1738-1751.
- NEAL, A. K., WHITE, G. C., GILL, R. B., REED, D. F. and OLTERMAN, J. H. 1993. Evaluation of mark-resight model assumptions for estimating mountain sheep numbers. *Journal of Wildlife Management*, 57: 436-450.
- ORO, D., MARGALIDA, A., CARRETE, M., HEREDIA, R. and DONÁZAR, J. A. 2008. Testing the goodness of supplementary feeding to enhance population viability in an endangered vulture. *PLoS One*, 3: e4084.

- RAZIN, M., LIOTOUT, B., ORABI, P. and TERRASSE, M. 2009. Distribution, population, breeding and conservation of the vulture populations in France. *Munibe*, 29 (Supplement): 144-153.
- SCHAUB, M., ZINK, R., BEISSMANN, H., SARRAZIN, F. and ARLETTAZ, R. 2009. When to end releases in reintroduction programmes: demographic rates and population viability analysis of bearded vultures in the Alps. *Journal of Applied Ecology*, 46: 92-100.
- SESÉ, J. A., ANTOR, R. J., ALCÁNTARA, M., ASCASO, J. C. and GIL, J. A. 2005. La alimentación suplementaria en el quebrantahuesos: estudio de un comedero del Pirineo occidental aragonés. In, A. Margalida and R. Heredia, (Eds.) *Biología de la conservación del quebrantahuesos Gypaetus barbatus en España*, pp. 279-304. Organismo Autónomo Parques Nacionales. Madrid.
- SIMÓN, M. A., LLOPIS, A., CARRASCO, A. L., GODINO, A., BAUTISTA, F., ROMERO-PUJANTE, M., HERNÁNDEZ, F. J., DEL BARCO, M., MACÍAS, E. and HORTELANO, M. A. 2005. El proyecto de reintroducción del quebrantahuesos en Andalucía: resultados del Centro de Cría de Guadalentín. In, A. Margalida and R. Heredia, (Eds.) *Biología de la Conservación del Quebrantahuesos Gypaetus barbatus en España*, pp. 255-268. Organismo Autónomo Parques Nacionales. Madrid.
- TUCKER, G. M. and HEATH, M. F. 1994. *Birds in Europe: Their Conservation Status*. Birdlife International. Birdlife Conservation Series No. 3. Cambridge.
- WHITE, G. C. 1996. NOREMARK: population estimation from mark-resighting surveys. *Wildlife Society Bulletin*, 24: 50-52.
- WOUTERSEN, K., GARCÍA, D., MORENO, F. and GRASA, M. 2009. Estatus, distribución y parámetros reproductores de las poblaciones de aves carroñeras en Aragón. *Munibe*, 29 (Supplement): 89-104.
- XIROUCHAKIS, S. M. and TSIKIRIS, R. 2009. Status and population trends of vultures in Greece. *Munibe*, 29 (Supplement): 154-171.

Received: 9 June 2011

Accepted: 1 March 2012

Editor: Beatriz Arroyo

## APPENDIX 1

Number of bearded vultures (immatures and adults) observed during the different surveys in March 2010.

$m_i$  = number of individually marked animals;  $u_i$  = number of unmarked animals.

[Número de quebrantahuesos inmaduros y adultos observados durante diferentes censos en marzo de 2010.  $m_i$  = número de animales marcados individualmente;  $u_i$  = número de animales no marcados.]

	IMMATURES		ADULTS	
	$m_i$	$u_i$	$m_i$	$u_i$
survey 1	4	11	2	11
survey 2	4	30	2	15
survey 3	3	27	2	11
survey 4	4	17	1	8
survey 5	2	11	5	24
survey 6	3	14	0	15
survey 7	3	11	2	14
survey 8	1	7	1	14
survey 9	3	16	1	12
survey 10	2	33	0	13
survey 11	2	15	1	11
survey 12	4	10	0	8
survey 13	3	34	3	16
survey 14	1	23	3	21
survey 15	0	8	0	18
survey 16	3	14	2	14
survey 17	3	11	1	15
survey 18	1	5	0	8
survey 19	3	29	2	23
survey 20	2	17	1	14
survey 21	2	14	3	7
survey 22	0	8	0	12
survey 23	6	28	2	18
survey 24	2	16	3	16
survey 25	5	10	0	10
<b>Total</b>	<b>66</b>	<b>419</b>	<b>37</b>	<b>348</b>