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First breeding age in captive and wild Bearded Vultures *Gypaetus barbatus*

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Abstract. We present data on the age of first breeding in captive and wild Bearded Vultures. The mean age of first breeding (egg-laying) in the captive population was 7.7 years for females and 8.9 for males. The first offspring was raised on average by 8.3-year-old females and 9.7-year-old males. In wild Bearded Vultures, first-time-paired and territorial individuals were recorded when they were 6.5 years old, on average. The mean age of first breeding was 8.1 years, whereas the mean age of first successful breeding was 11.4. Paired females were recorded at the age of 6.5 years and breeding at 6, whereas the youngest recorded paired males were 6.4 years old and breeding at 7. 39.5% of the marked birds alive over 6 years were recorded as not yet territorial, suggesting the existence of a substantial fraction of adult floaters without breeding territories. Pyrenean Bearded Vultures are characterized by delayed reproduction, with the first breeding attempt taking place well after the acquisition of full adult plumage. We discuss whether deferred breeding in this increasing population could be explained by the increase in density and/or mortality rate in the younger age groups, which could affect the age of maturity.

Key words: Bearded Vulture, *Gypaetus barbatus*, age of first breeding, delayed maturity

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The availability of robust estimates of the demographic parameters is critical in modelling the evolution and viability of small populations. Among these parameters, age at maturity has been suggested to be an influential life-history trait with significant consequences for population dynamics (Oli & Dobson 1999, 2003). Due to its very small population size and isolation, the four remaining European populations of the Bearded Vulture (Alps, Corsica, Crete and Pyrenees) are threatened and there is a need to perform population dynamics and viability analyses in order to guide their conservation management (Bretagnolle et al. 2004).

The Bearded Vulture is a cliff-nesting and territorial species that feeds on bone remains of medium-size ungulates. In Europe it lives in mountainous zones of the Pyrenees (France and Spain), the Alps (Austria, Switzerland, Italy and France, where it was reintroduced in 1986), the south of the Balkans and the islands of Corsica and Crete (Heredia 2005). This species is a long-lived bird of prey with a maximum lifespan of at least 45 years in captivity (H. Frey, pers. obs.) and a mean lifespan in wild birds of 21.4 years (Brown 1997), a low fecundity rate (clutch size of two eggs with obligate siblicide, Margalida et al. 2003, 2004) and a long generation time.

The Pyrenean population is characterized by low productivity (0.4 fledglings/territorial pair/year) and low annual reproductive output (about 40 fledglings, Heredia 2005). This low reproductive output precludes rapid recovery from a possible population decline and may be due to the deferred breeding and/or low productivity. There is evidence that birds in this population delay first reproduction substantially beyond the age at which they are physiologically mature and the age at which they acquire adult plumage.

Delayed maturity might be favoured if the costs (e.g. reduced survival, future reproduction) outweigh the benefits (Pyle et al. 1997, Tavecchia et al. 2001), although studies using lifetime reproductive success generally do not agree with this assumption (Newton 1989, Viallefont et al. 1995). In population modelling, the long deferred age of first breeding may have a significant influence on the outcome of the population (Authors unpubl. data). However, information on this parameter was not yet accurately known. Here we present data about the age of first breeding in captive and wild Bearded Vultures.

The field part of the study was carried out in the Pyrenees (NE Spain). The mountain range of the Pyrenees (21 000 km^2) extends in a west-east direction from the Atlantic Ocean to the Mediterranean Sea. Most breeding birds inhabit the central Pyrenees (Aragon and W of Catalonia).

Between 1987 and 2006, 55 nestling birds (4 reared in captivity and later freed by the hacking method) were marked with colour metal leg bands, wing tags and VHF transmitters in the central southern Pyrenees (R. Heredia unpubl. data, FCQ unpubl. data). Between 1994 and 2006, 44 Bearded Vultures were captured at feeding sites in the wintering area in the central southern Pyrenees (50% juveniles, 34% subadults and 16% adults). Birds were caught (including 16 recaptured) using cannon-nets and each one was marked following the same nestling procedure, and aged using plumage characteristics (the extent of white in the head, the moult of covers and the moult of flight feathers, see Heredia & Margalida 2005).

In this species, the correspondence of the age with the characteristics of the plumage presents an important variability, in such a way that from two years of age notable differences may exist between individuals of the same age. In general, the females reach adult plumage before the males (Heredia & Margalida 2005) and in many cases they do it when they have barely reached 5 years of age. However the peculiarities of the plumage seem to correspond objectively with the real age of the individual when the characteristics of the contour plumage is added (e.g. head, neck, covert feathers) and the flight feathers (remiges and rectrices).

Most territorial birds and breeding pairs have been monitored annually through the whole Pyrenean range and data on the breeding status of marked birds were collected. Territories were visited regularly (minimum 1 visit/week) between November-August, increasing field effort during egg-laying (December–February) and chick-rearing (February–August) periods in which territories were visited more frequently. Resighting data were obtained through a network of observers who generated more than 11000 observations of the 99 marked birds. This data provided basic information about bird movements and settlements. Data on pairing and rearing were obtained via radio-tracking, ringing data and nest monitoring. 34.5% of the previously mentioned records would correspond to the individuals considered in this study, even if only 15.2% belonged to the breeding period. The breeding period would cover, in the case of a successful breeding attempt, from the last months of a "calendar year" October–November, until the months of July–August of the following year. Consequently, for breeding purposes, the corresponding age on 1 March of the year was assigned to each individual, coinciding with the birth date according to phenology dates obtained in the Pyrenees (Margalida et al. 2003).

Of the 99 marked individuals, 21 were found dead and 26 were considered as not being monitored after not having been traced for various years (these individuals being considered as those who could have died, lost their wing-tagging, or might left the Pyrenees). Of the 52 remaining, 10 would be young individuals, 6 had subadults and the rest adults (individuals older than 6 years). In this study 30 marked individuals were included; based on the fact that they showed signs of breeding at least once (see above). For the calculations, only 23 individuals were taken into account (including 5 who have died and of those that reliable breeding data were available), as the rest were excluded as the exact age was unknown because there were insufficient information available. We considered pairing with territorial activity (first-pairing) when the paired Bearded Vulture was seen indicating an active breeding territory,

or with a new partner presenting territorial behaviour, or defending a territory against conspecifics and heterospecifics during the breeding period. We considered breeding (egg-laying) when the first breeding attempt was recorded or a chick was present in the nest. Successful breeding was recorded when the young fledged successfully.

In captivity the age of first breeding was also studied within the European breeding network for the Bearded Vulture. This international cooperation includes 30 zoos, three smaller breeding centres in the Netherlands, France and Switzerland and two main breeding centres, the Vienna Breeding Unit in Austria and the Centro de Cria Guadalentin in Spain. 125 Bearded Vultures were kept in breeding facilities in 2003. As from 1978 (the beginning of the Alpine Bearded Vulture reintroduction project), 65 different pairs have been established. This captive breeding population derives from 37 founder birds (20 males and 17 females) of *Gypaetus barbatus*, mainly birds from Asia and the former Soviet Union. Only very few birds were received from Greece (one male and one female) and Spain (two males). Their offspring (up to now about 250 birds) have been used for the reintroduction of the species into the Alps, where it was extirpated at the beginning of the 20th century, and the increase of the zoo population. A total of 107 birds (52 males and 55 females) with an age of at least four years (F1, F2 and F3 generation) have been analysed for this study. Because in several cases man participates in rearing, in order to calculate the age of first breeding attempt (egg-laying) and the age at which the first chick was reared successfully by captive birds, we only considered naturally reared birds that have been raised only by their parents or foster parents and not by man (with the exception of the first few days after hatching).

Values presented are mean ± SD.

In the wild, Bearded Vultures were first recorded paired and territorial at a mean age of 6.5 ± 1.62 years (n = 23). The youngest birds paired were recorded when 5 years old and 81.6% (n = 38) of the marked birds alive of 5–6 years old (potential age of first breeding) were recorded as not yet territorial. Considering only the individuals that were alive and monitored (n = 38), 39.5% of the individuals older than 6 years were recorded as not yet territorial, suggesting the existence of a substantial fraction of adult floaters without breeding territories.

Ten birds were recorded as breeders (having laid eggs). The youngest known age of breeding was 6 years and the latest was 12 years. The mean age of first breeding was 8.1 ± 1.79 years (n = 10). It was 8.3 ± 2.06 years for the females (n = 8) and 8 ± 1.41 for males (n = 2). Mean age of first successful breeding in the wild population was 11.4 ± 3.91 (n = 5). It was 10 ± 2.71 years for the females (n = 4) and 17 for males (n = 1). No data was available on birds older than 19 years.

In the wild, females also seem to breed earlier than males. While females were recorded as paired when 6.5 ± 1.91 years old (n = 14) and breeding at 6 (n = 1), the earliest males were recorded as paired at the age of 6.4 ± 1.91 years (n = 9) and breeding at 7 (n = 1).

In captivity neither copulations nor egg laying or brooding (e.g. when offered egg dummies) was ever observed in Bearded Vultures younger than five years.

Out of 107 birds (52 males and 55 females) 59 (55%) did not reproduce (31 males and 28 females; 59% males and 51% females). Among them, only 15 were 4 years old. Eighteen birds (16.8%) older than 10 years — 14 males (27%) and 4 females (7.2%) — never had a clutch.

The mean age of first breeding was 7.7 ± 1.63 for females (n = 21) and 8.9 ± 2.13 for males (n = 15). The first offspring was raised by females of the age of 8.3 ± 2.00 on average (n = 16) and 9.7 ± 2.36 for males (n = 13), respectively. The youngest known age of breeding was 5 years in males (n = 1), just as in females (n = 1). The oldest age of first breeding was 17 years in females (n = 1) and 20 in males (n = 1).

Delayed acquisition of adult plumage is associated with deferred breeding (Newton 1979). An increase in resource availability (nest sites or food supply) can boost the number of subadult breeders (Wyllie & Newton 1991, Broomer et al. 1998). In the Pyrenees, the absence of records of Bearded Vultures breeding in subadult plumage is in accordance with the youngest recorded age of breeding (6 years). The youngest age at which raptors can breed appears to depend on the age at which they mature physiologically. In this sense, food supply, mates and nesting places are constraining factors, which may exert an important influence and variations have been detected in the age of first breeding, depending on whether they are in decline or in an expansive phase (see Evans et al. 1998,

Newton et al. 1989, Bowman et al. 1995). On the other hand, delayed maturity has been interpreted as an evolutionary strategy to gain useful experience and, in the long run, to increase individual fitness (Newton 1979).

In the case of Pyrenean Bearded Vultures, it seems that in response to habitat saturation a significant proportion of unpaired birds become potential breeders by entering high quality territories, or by forming polyandrous trios as a strategy to increase their individual performance, having clear negative consequences to population demography (Carrete et al. 2006b). In this increasing population, a possible explanation of deferred breeding may be related to the increase in density (Donázar et al. 2005, Carrete et al. 2006a), that could affect age at maturity (Krüger 2004).

In the endangered Cretan population (5 breeding pairs), subadults have been observed paired and even breeding (Xirouchakis & Grivas 2002). This isolated population has suffered high adult mortality due to human activities that may have caused a substantial shortage of adults and allowed the subadults to fill the territorial vacancies and breed (see Balbontín et al. 2003). A similar case is known from Corsica (10 remaining breeding pairs), where recently subadults birds have joined the breeding population (J. F. Seguin, pers. comm.). Therefore, the cases of wild Bearded Vultures breeding before acquiring full-adult plumage are very rare and probably related to a chronic shortage of adults. On the contrary, subadult birds are often found paired in other large raptors (Steenhof et al. 1983, González et al. 2006), and especially in vultures of the genus *Gyps* (Mundy et al. 1992, Blanco et al. 1997).

Our results suggest that Bearded Vultures are among the birds with long deferred reproduction, as are many large raptors. Thus, in captivity, Bald Eagles *Haliaeetus leucocephalus* first produced eggs at the age of six years, White-tailed Eagles *H. albicilla* at eight, Lappet-faced Vultures *Torgos tracheliotus* at nine, and California Condors *Gypnogyps californianus* at six (Newton 1979, Meretsky et al. 2000). Only some seabirds may breed later in the wild (9–12 years in some albatrosses and petrels; Russell 1999). All these species have extreme K-selected life-history strategies, which means they generally exhibit a delayed maturity, low annual reproductive outputs and very long life expectancy. Long deferred maturity together with low reproductive rates may have significant consequences for the species reproductive output and demands high adult survival rates to reach population stability. The Pyrenean Bearded Vulture population suffers considerable man-induced adult mortality (Margalida et al. in press) that shortens life expectancy and produces a substantial drop in the lifetime reproductive output when increasing the age at first breeding. This substantial effect of age at first breeding on the population growth rate has also been predicted for other long lived species which also have relatively low values of adult survival rate (Noon & Biles 1990). In this sense, age-specific mortality of immatures favours an increase in reproductive effort and hence, as a consequence, an increase in the age of maturity (Reznick et al. 1990). Conversely, a mortality rate that increases in the older age groups could favour a decrease in the age of maturity (Roff 2001).

In the former modelling efforts of the Pyrenean Bearded Vultures, the population growth rate was predicted to be sensitive to deferred first breeding (R. J. Antor unpubl. data). These results are of primary interest for the viability modelling of this threatened population under the current man-induced adult mortality (Margalida et al. in press).

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STRESZCZENIE

[Wiek orłosępów przystępujących po raz pierwszy do lęgów]

Orłosępy brodate tworzą w Europie cztery małe izolowane populacje (Alpy, Korsyka, Kreta i Pireneje). Ze względu na ciągłe zagrożeniem gatunku wymarciem, istnieje potrzeba poznania jego dynamiki populacyjnej w celu prowadzenia skutecznych działań ochroniarskich. Kluczowym zagadnieniem może być w tym przypadku zwłaszcza wiek, którym orłosępy przystępują do rozrodu.

Badaniami objęto 23 osobniki z populacji pirenejskiej oraz 107 osobników przetrzymywanych w ponad 30 europejskich ogrodach zoologicznych i ośrodkach hodowlanych. Dziko żyjące orłosępy tworzą pary i zajmują terytoria średnio w wieku 6.5 roku. Średni wiek przystępowania do lęgów w tej populacji wyniósł 8.1 lat (ptaki w wieku 6–12 lat), natomiast pierwsze lęgi zakończone sukcesem wyprowadzały osobniki średnio 11-letnie (10 lat w przypadku samic, 17 — w przypadku samców).

W niewoli nie obserwowano kopulacji ani znoszenia jaj u ptaków młodszych niż 5 lat. Do pierwszych lęgów samice orłosępów przystępowały w wieku 7.7 lat, natomiast samce — w wieku 8.9 lat. Udane lęgi wyprowadzały samice ponad 8-letnie i prawie 10-letnie samce.