

# Hatching asynchrony, sibling aggression and cannibalism in the Bearded Vulture *Gypaetus barbatus*

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We report data on laying and hatching asynchrony in the Bearded Vulture *Gypaetus barbatus*, and provide the first detailed description of the provisioning of nestlings, sibling aggression and cannibalism. The results suggest that brood reduction was mediated through the age and size differences between siblings, which resulted in the superior competitive ability of the older chick. Thus, brood reduction occurred through starvation facilitated directly by the older chick's aggression. The results support the hypothesis that the second egg probably functions as insurance in case the first egg does not hatch. The insurance-egg hypothesis is supported by the following facts: 1) in three of six breeding attempts, the second egg produced a chick when the first egg failed to hatch or the first chick died young. At least two of these B chicks fledged; 2) in the Bearded Vulture most breeding failures occur during the hatching period and thus the insurance value of last-hatched eggs would be especially important in this species; 3) clutch replacement, an alternative to laying an insurance egg, is relatively uncommon in this species and 4) the laying interval (5–7 days) and the hatching asynchrony (5–8 days) of this species are the longest recorded in any raptor, suggesting that they might represent an adaptive mechanism facilitating the rapid loss of the second chick if the first one hatches.

In the great majority of bird species with obligate brood reduction (those in which more than 90% of last-hatched chicks die, Simmons 1988), the parents produce two eggs, and then fledge only one chick. In most of these cases, sibling aggression is responsible for brood reduction (Mock & Parker 1997). Adaptive brood reduction strategies may be facilitated either by asynchronous hatching or by a decrease in the size of the last-laid eggs. Large species generally have small final eggs, supporting a brood reduction hypothesis (Edwards & Collopy 1983).

Two main hypotheses have gained recent attention in the discussion about the significance of obligate siblicide in species laying two eggs. The 'insurance hypothesis' proposes that the second egg may be an insurance in case the first egg does not hatch (Meyburg 1974, Stinson 1979, Parker & Mock

1987, Anderson 1990, Mock *et al.* 1990). Alternatively, obligate siblicide might be the consequence of an evolutionary trend favouring the raising of high-quality offspring (Simmons 1988, 1997).

The Bearded Vulture *Gypaetus barbatus* is a long-lived species with one of the longest breeding cycles known in raptors (6 months, Margalida *et al.* 2003). Both sexes invest a significant amount of parental effort during this period (Margalida & Bertran 2000). Bearded Vultures regularly lay two-egg clutches, but usually raise a single chick (Brown 1990, Heredia *et al.* 1991b, Margalida *et al.* 2003, but see Barrau *et al.* 1997). The highly specialized diet and feeding habits of this species (bones, which are scarce, dispersed and temporally unpredictable) require both sexes to make a significant contribution to the breeding process, and may impose a clear upper limit to brood size, precluding the raising of two chicks. Obligate siblicide is suspected, but information on behaviour of young chicks is scarce and even contradictory. Sibling aggression has been reported in broods of a captive pair (Thaler &

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Pechlaner 1980), whereas the only observations of brood reduction reported in wild pairs in Africa suggest that there is no aggressive behaviour in siblings (Brown 1990).

The population of the Spanish Pyrenees is characterized by low productivity (0.43 fledglings per breeding pair per year,  $n = 115$ , Margalida *et al.* 2003) and low annual reproductive output (fewer than 40 fledglings per year, pers. obs.). To increase the stock of native captive breeders in reintroduction projects, potential management techniques include boosting productivity by removing the second egg in two-egg clutches (Heredia 1991a) for artificial incubation (Negro & Torres 1999). Thus, knowledge of the breeding biology of this threatened species has important implications for its management and conservation.

Here we report data on laying interval between first and second eggs and hatching interval in European Bearded Vultures, and provide the first detailed description of the provisioning of nestlings, sibling aggression and cannibalism in wild pairs of this species.

## METHODS

Between 1992 and 2000, we intensively monitored the breeding of 20 pairs of Bearded Vulture in Catalonia, north-east Spain. Laying started in the second week of December and continued until the middle of February. Hatching dates ranged from 5 February to 7 April. Fledglings took their first flights as early as 21–28 May and as late as 29 July (Margalida *et al.* 2003). Our study area holds a relatively high population density of Bearded Vultures and an abundant food supply (Margalida & García 2002). The average annual maximum and minimum temperatures within the study area do not rise above 30 °C (July) or fall below –5 °C (January), respectively. The average annual precipitation was more than 800 mm, with 78 days of precipitation falling mainly as snow between December and February. During this period (1992–2000) some data on asynchronous hatching were obtained by using 20–60× telescopes to observe nests A and C, whose nest contents could be viewed directly during 2000 and 1995, respectively. In nests A and C we were able accurately to determine laying dates by means of daily observations.

To record laying dates, nests were observed at least twice daily, at dawn and at dusk. The laying interval was estimated as the number of days elapsed between the laying of the first and second eggs, both

included. The first time that an egg was seen at the nest was taken as the laying date.

During the prelaying periods of November 2000, 2001 and 2002 a transmitting video camera was installed at five Bearded Vulture nests (A & B in 2000, D & E in 2001, and D & F in 2002: see details in Margalida *et al.* 2002). Nest A was occupied by a recently formed pair, whose first breeding attempt occurred in 1997. This nest was monitored by video camera during prelaying (November–December), incubation (January–February) and on the first days of chick rearing until breeding failure occurred, 4 days after hatching, probably as a result of natural causes (pers. obs.). Nest B was occupied by a polyandrous trio that have been studied since 1985 (Bertran & Margalida 2002). This nest was intensively monitored by video camera during the prelaying (September–December), incubation (January–March) and chick-rearing (March–July) periods. Nest D was occupied by a monogamous pair, whose territory has been known since 1980. This nest was monitored during prelaying, incubation and chick-rearing periods. Nest E was occupied by a recently formed pair, whose first breeding attempt occurred in 1998. This pair was only monitored during prelaying and 2 weeks of the incubation period because of a failure in signal transmission. Nest F was occupied by a monogamous pair whose territory had been known since 1991. The monitoring of this pair was carried out only during prelaying and incubation. Nests B and D were observed during hatching and on the first days of the nesting period for a total of 120 h (mean  $\pm$  sd = 9.9  $\pm$  1.3 h per day) and 121.5 h (mean  $\pm$  sd = 12.1  $\pm$  0.9 h per day), respectively. Observations were from dawn to dusk each day.

In nests monitored by video cameras, hatching duration of each egg was defined as the time elapsed in hours between the first observation of a hole in the egg until the time the chick was seen to be completely free of its eggshell. Hatching asynchrony was defined as the time in hours between hatching of the first and the second egg.

After hatching, we video-recorded all feeding bouts and aggression between siblings (older chick, or C1, and younger chick, or C2) in nests B and D. Based on these data, we calculated the following variables: frequency of feeding (number of feeds per hour), number of items swallowed by C1 in each feeding bout, duration of feeds, duration of each fight between the siblings and, whenever possible, the number of pecks.

**Table 1.** Egg-laying, incubation and hatching periods in the Bearded Vulture in the Pyrenees.

Nest-year (nest altitude m asl)	Laying interval (days)	Hatching start of 1st egg (day)	Hatching start of 2nd egg (day)	Hatching process of 1st egg (h)	Hatching process of 2nd egg (h)	Hatching of C1 (day)	Hatching of C2 (day)	Hatching asynchrony (days)	Age at which C2 died (days)
A-2001 (1250)	6	No hatch	53	–	18	–	54	–	–
A-2000 (1000)	–	–	–	–	–	54	54	6	–
B-2001 (1100)	7	53	53	20	46	54	55	8	4
C-1995 (1150)	–	–	–	–	–	–	–	7	–
D-2003 (1600)	6	52	51	< 16	< 17	53	52	5	7
D-2002 (1600)	6	51	52	< 24	< 24	52	53	7	5
E-2002 (1400)	5	–	–	–	–	–	–	–	–
F-2003 (1650)	6	–	–	–	–	–	–	–	–

**Table 2.** Quantitative details of nestling provisioning by Bearded Vultures in the Pyrenees. Data in bold type refer to the period when two chicks were present in a nest.

Nest B					Nest D				
Day after hatching of first egg	Food items delivered per h	Feeds per h	Average duration (min) of feeds	Average items ingested per feed	Day after hatching of first egg	Food items delivered per h	Feeds per h	Average duration (min) of feeds	Average items ingested per feed
1	0.20	0.40	5.8 ± 1.1	6 ± 3.8	1	0.10	0.40	3.2 ± 1.9	11 ± 7.6
2	0.11	0.22	3 ± 1	7 ± 3.5	2	0.38	0.57	3.7 ± 3.0	7.2 ± 7.2
3	0.85	0.75	6.1 ± 2.3	8.5 ± 6.1	3	0.31	0.82	1.9 ± 1.1	6.5 ± 4.5
4	0.13	0.40	11.3 ± 2.1	40.3 ± 15.3	4	0.33	1.56	3.9 ± 1.9	13.4 ± 8.7
5	0.14	0.14	9	28	5	0.40	0.70	5.3 ± 1.2	19.7 ± 8.8
6	0.22	0.44	7 ± 3.5	16.5 ± 10.7	6	0.37	1.62	3.3 ± 1.6	11.5 ± 6.8
7	0	0.60	7 ± 7	5 ± 2.3	Average	0.32 ± 0.11	0.9 ± 0.5	3.6 ± 1.1	11.6 ± 4.8
8	0.09	0.76	5.8 ± 3	9.5 ± 5.4	7	<b>0.41</b>	<b>0.82</b>	<b>3.6 ± 0.7</b>	<b>17.5 ± 5.9</b>
Average	0.21 ± 0.26	0.37 ± 0.23	6.2 ± 2.4	13.9 ± 12.7	8	<b>0.18</b>	<b>1.64</b>	<b>3.7 ± 2.6</b>	<b>17.6 ± 12.6</b>
9	<b>0.09</b>	<b>0.91</b>	<b>8.4 ± 3.9</b>	<b>17.7 ± 11.6</b>	9	<b>0.45</b>	<b>1.18</b>	<b>4.4 ± 3.6</b>	<b>15.3 ± 10.1</b>
10	<b>0.09</b>	<b>0.82</b>	<b>9.5 ± 6.5</b>	<b>20.1 ± 17.2</b>	10	<b>0.19</b>	<b>1.52</b>	<b>6.1 ± 10.4</b>	<b>14.3 ± 16.4</b>
11	<b>0.33</b>	<b>1.22</b>	<b>4.8 ± 5.5</b>	<b>6.6 ± 5.5</b>	11	<b>0.55</b>	<b>1.45</b>	<b>6.4 ± 6.1</b>	<b>20.1 ± 19.3</b>
12	<b>0</b>	<b>0.63</b>	<b>8 ± 3</b>	<b>15 ± 10.7</b>	12	<b>0.09</b>	<b>0.27</b>	<b>4.5 ± 0.9</b>	<b>17.7 ± 4.8</b>
13	<b>0.01</b>	<b>0.60</b>	<b>7 ± 3.2</b>	<b>11.5 ± 8</b>	13	–	–	–	–
Average	0.10 ± 0.13	0.84 ± 0.25	7.5 ± 1.8	14.2 ± 5.3	Average	0.31 ± 0.18	1.1 ± 0.5	4.8 ± 1.2	17.1 ± 2.04

## RESULTS

### Egg laying, incubation and hatching interval

Mean ( $\pm$  sd) laying interval was estimated to be  $6 \pm 0.63$  days (range 5–7,  $n = 6$ ) and the incubation started with the laying of the first egg. Hatching of first-laid eggs started  $52 \pm 1$  days (range 51–53,  $n = 3$ ) after egg-laying. On average, the first chick to hatch (C1) did so after  $53.25 \pm 0.96$  days of incubation and the hatching process lasted from a little less than 16 h to 20 h ( $n = 3$ ) (Table 1). Hatching of the second egg started after  $52.25 \pm 0.96$  days of incubation

(range 51–53,  $n = 4$ ). On average, the second chick to hatch (C2) did so after  $53.6 \pm 1.14$  days of incubation (range 52–55,  $n = 5$ ) and the process lasted from a little less than 17 h to 46 h ( $n = 4$ ). Therefore, mean hatching asynchrony was estimated as  $6 \pm 1.14$  days (range 5–8,  $n = 5$ , Table 1).

### Nestling feeds

Table 2 gives details of nestling provisioning. In neither nest did the adult birds deliver food or feed C1 until 24 h after it had hatched. The chicks were fed small bits of flesh torn from the food remains delivered to the nest.

**Table 3.** Details of aggressive interactions between siblings during 4 days of monitoring, in nests B and D, of Bearded Vultures in the Pyrenees. Day refers to age of C2 after hatching.

Day	Nest B				Nest D			
	Attacks per h ( <i>n</i> )	Average duration (s)	Pecks ( <i>n</i> )	Total time (s) of aggression (range)	Attacks per h ( <i>n</i> )	Average duration (s)	Pecks ( <i>n</i> )	Total time (s) of aggression (range)
1	0.18 (2)	1	–	2 (1)	1.73 (19)	8.3 ± 8.1	67	158 (1–22)
2	3.18 (35)	11.0 ± 7.5	–	386 (2–29)	3.54 (39)	11.6 ± 8.6	236	462 (1–32)
3	1.2 (11)	29.8 ± 28.6	–	505 (3–90)	2.95 (31)	12.8 ± 12.3	233	411 (1–50)
4	2.5 (20)	17.6 ± 16.3	–	352 (2–59)	4.54 (50)	11.5 ± 8.3	339	587 (1–33)

In both nests the parents fed only C1, which was more active and called for food more insistently than did its sibling. When feeding took place, the parents did not distribute food equally between the chicks nor did they interfere when C1 responded aggressively towards C2. Nevertheless, during several episodes of aggressive behaviour in nest D, the parents appeared agitated and stopped feeding in order to cover the chicks. During feeds, the parents favoured C1, mainly because it stood in a more erect position. C1 also pounced on C2 and did not let it move. The size difference between chicks and the superior competitive ability of C1 prevented C2 from defending itself or having access to the food provided by the parent.

In nest B, C2 was fed on only three occasions (three pieces of food on the second day, one on the third and one on the fourth), when C1 was satiated. This happened always after C1 had been fed or was resting asleep. In nest D, C2 was fed on 10 occasions (three pieces of food on the first day, three on the second, four on the third and four on the fourth), on each of these occasions by getting ahead of C1 and snatching the food from the adult's bill. On seven other occasions, it tried unsuccessfully to seize the food from the adult's bill.

### Sibling aggression

#### *Nest B (2001)*

In total, 68 aggressive interactions were recorded in the 39 h of observation while both chicks were in the nest. Attacks represented  $0.9 \pm 0.5\%$  (range 0.005–1.3%,  $n = 4$ ) of the total daylight hours. Bouts of aggression lasted between 1 and 90 s and the mean length of the attacks was  $17.1 \pm 7.6$  s ( $n = 68$ , Table 3). Although the analysis had low power because of the small sample size, no significant relationship was found between the average fre-

quency of feeds and the frequency of aggression ( $r_{11} = -0.04$ , ns), between the length of feeds and length of the attacks ( $r_{11} = 0.1$ , ns), or between the length of the feeds and the number of attacks ( $r_{11} = 0.46$ , ns).

On only three occasions ( $n = 4$  pecks) did C2 peck in return. In 35 aggressive bouts, totalling 396 s (average  $10.7 \pm 8.2$  s, range 2–33), 204 pecks were counted (average  $5.8 \pm 4.6$  pecks, range 1–19,  $n = 35$ ), representing an average frequency of 32.5 pecks/min of aggression. The number of pecks that C1 directed at C2 increased with the length of the attacks ( $r_{35} = 0.89$ ,  $P < 0.001$ ). Thus, during C2's first day of life, it was attacked on only two isolated occasions. But between its second and fourth day it was attacked far more often (Table 3). On its fourth day after hatching, C2 was already very weak and at the end of the recording period that day (15:00 h) it moved very little. The chick died at the age of 4 days.

#### *Nest D (2002)*

A total of 159 aggressive interactions was recorded in the 43.5 h of observation while both chicks were in the nest. Attacks represented  $1.03 \pm 0.4\%$  (range 0.4–1.5%,  $n = 4$ ) of the total daylight hours. C1 initiated 143 attacks and C2 only 16 (seven on the first day, five on the second, two on the third and two on the fourth). Bouts of aggression by C1 lasted between 1 and 50 s and the mean length of the attacks was  $11.3 \pm 9.5$  s ( $n = 143$ , Table 3). Bouts of aggression by C2 lasted only 1–5 s and the mean length of the attacks was  $1.6 \pm 1.2$  s ( $n = 16$ ). No significant relationship was found between average frequency of feeds and the frequency of aggression ( $r_{11} = 0.52$ , ns) or between the length of feeds and the length of attacks ( $r_{11} = -0.11$ , ns) or even between the length of feeds and the number of attacks ( $r_{11} = 0.26$ , ns).

In nest D, C2 retaliated on 16 occasions ( $n = 21$  pecks). In 143 aggressive bouts an average of  $6.12 \pm 5.16$  pecks occurred (range 1–26,  $n = 875$  pecks). The number of pecks that C1 directed at C2 increased with the length of the attacks ( $r_{143} = 0.81$ ,  $P < 0.001$ ) and with the age of both chicks. So, during C2's first day of life after hatching, it was attacked on 19 occasions, but between its second and its fourth day it was attacked 2–3 times as often (Table 3). On its fifth day, at 06:55 h C2 moved very little and at 12:29 h the adult lifted up C2's carcass and left it at the side of the nest. The chick died at the age of 5 days and observations were discontinued.

In both nests, all aggressive interactions took place in the presence of at least one of the adult birds. The first attack took place 25 h after C2 hatched. C1 behaved aggressively while C2 was feeding, moving or calling. C2 was only rarely attacked when it remained inactive. Most of the pecks (nest B: 79%) were directed at C2's head and neck, although C1 also occasionally pecked the wool of the nest. C2's head movements or bill movements when calling probably attracted most of the attacks. In both cases, the C2 chick died from starvation facilitated directly by the older chick's aggression, as no serious injuries were seen. Thus, sibling aggression is a factor contributing to the death of C2, at least by intimidating the smaller chick, so reducing its begging frequency.

### Cannibalism

#### *Nest B (2001)*

When observations began on day five at 08:00 h, C2 was no longer next to C1. At 10:51 h, during a feeding bout, we watched the female handling an item, which she fed to C1. The food item was the partly eaten remains of C2. The remains of C2 were fed to its sibling between its fourth day of age and the first hours of the fifth day.

### DISCUSSION

One hypothesis about the adaptive significance of hatching asynchrony suggests that it facilitates the selective death of the youngest chick (Amundsen & Slagsvold 1996, Viñuela 2000). In raptors, the brood reduction hypothesis is often assumed to explain hatching asynchrony (Stinson 1979, Wiebe & Bortolotti 1995). Hatching asynchrony promotes the establishment of intrabrood size hierarchies (Stokland & Amundsen 1988, Viñuela 1996), and sibling aggression facilitates brood reduction. Our

results show that the hatching asynchrony of 5–8 days observed in Bearded Vultures (much longer than the 3–4 days in other obligately siblicidal raptors; Edwards & Collopy 1983) facilitates the death of the last-hatched chick with a relatively low intensity of sibling aggression (as compared, for example, with the Black Eagle *Aquila verreauxii*, Gargett 1990). Thus, brood reduction in the Bearded Vulture, rather than being by food availability, was apparently mediated through the age and the size difference between siblings, which resulted in the superior competitive ability of C1. During the first weeks after hatching, items delivered to the nest generally contain fresh meat (Margalida & Bertran 2000, 2001, Margalida *et al.* 2001). However, despite such food being abundant in the nest, there was no evidence of food distribution but rather a clear favouritism for the first-hatched chick. In the three cases of brood reduction in Bearded Vultures documented by Brown (1990), neither sibling aggression nor infanticide were responsible for the death of C2. A possible explanation for this could be that second eggs in southern Africa are 10% smaller than in the Pyrenees ( $170 \text{ cm}^3$ ,  $n = 2$  vs.  $189 \text{ cm}^3$ ,  $n = 6$ ; Brown 1990, and M. Hernández and our unpubl. data, respectively) meaning that the chicks hatching from them had a very low chance of survival because they came packaged with little surplus energy. Nevertheless, Brown's (1990) study indicated that, relative to adult mass, the African Bearded Vulture lays proportionally larger eggs. The similarity in size between first eggs in southern Africa ( $194 \text{ cm}^3$ ,  $n = 2$ , Brown 1990) and Pyrenees ( $193 \text{ cm}^3$ ,  $n = 7$ , M. Hernández and our unpubl. data) supports this hypothesis.

Our results and the observations of Thaler and Pechlaner (1980) suggest that sibling aggression is a factor contributing to the death of C2, at least by intimidating the smaller chicks, and so reducing their begging frequency. No serious injuries were observed in chicks, in contrast with many other siblicidal species, and thus damage from physical attacks was not the direct cause of death. In our study, from the second day onwards sibling aggression became frequent. The start of aggression coincided with the age at which C1 was fed for the first time. This suggests that (a) it is the movement and noise from C2 that elicits this aggression, (b) C1 was protecting its food supply and/or (c) C1 had to feed before spending energy on sibling aggression. The behaviour of C1 seemed to be mainly intimidatory to prevent C2 from feeding. The attacks only represented 1% of the total daylight hours, in contrast to the 9.2% in the Black Eagle,

another obligately siblicidal species with a two-egg clutch (Gargett 1978). It may be that in the Bearded Vulture, in which size differences between siblings are large, C1 can quickly intimidate C2 with relatively few attacks (see Edwards & Collopy 1983). In captivity, sibling aggression occurred from the first to the sixth day, when C2 was removed and fed by hand. These results suggest that brood reduction in the Bearded Vulture is primarily the result of starvation mediated through C1's aggression. In Brown's (1990) study, C2 quickly disappeared from the nest (24, 26 and 48 h after hatching), probably reducing the chance of observing sibling aggression and suggesting natural death.

The ice-box hypothesis (Alexander 1974) proposes that C2 chicks act as a larder for C1 that can guarantee survival as food becomes scarce. The abundant food available at the nest, together with the relatively small size of dead chicks, discounts this hypothesis. The absence of a correlation between feeds and sibling aggression rate in our nests also suggests no relationship between food abundance and sibling aggression (Simmons 1988, Gargett 1990, Mock *et al.* 1990). Moreover, in many siblicidal species, the victim's body is not eaten and the benefit from the death of a nest-mate probably derives mainly from decreased competition (Simmons 1988, Bortolotti *et al.* 1991) and increased food resources (Simmons 2002).

Newton (1979) mentions that sibling aggression in raptors occurs especially when the female is absent from the nest. In the Bearded Vulture, one of the parents was always present at the nest during the chick's first month of life (Brown 1990, Margalida & Bertran 2000), when all aggressive interactions took place. In no case did parents intervene or exhibit any behaviour regulating the brood reduction process (see Newton 1979, Forbes 1991), as in other raptor species (Bald Eagle *Haliaeetus leucocephalus*, Gerrard & Bortolotti 1988; Black Kite *Milvus migrans*, Viñuela 1999). Failure of parents to intervene in sibling aggression is consistent with the insurance egg hypothesis, but it is also consistent with other explanations for the production of a second egg (Wiebe & Bortolotti 2000). The presence of a second chick in the nest may increase the first chick's competitive ability (Simmons 1988). In addition, if the second egg is a resource-tracking mechanism related to the expectation of possible food overabundance in the future (see Temme & Charnov 1987), parents should not intervene either, and raising two poorer-quality chicks under conditions of low population density may be adaptive. However, contrary to these predic-

tions, the only documented case of two chicks fledging came from Ethiopia (Barrau *et al.* 1997), and occurred in an area with a high population density (Brown 1977, Mundy *et al.* 1992). This suggests that other factors such as an abundant food supply and a lesser hatching asynchrony may facilitate the successful breeding of both chicks.

We believe that in the Bearded Vulture the second egg probably acts as insurance (see Forbes *et al.* 1997) against the demise of the first laid, as has been suggested in some other raptors (Meyburg 1974, Stinson 1979, Edwards & Collopy 1983). The insurance-egg hypothesis is supported by the following observations. (1) In three of six breeding attempts, the second egg produced a chick when the first egg failed to hatch or the first chick died young. At least two of these B chicks fledged, whereas in the Pyrenees two chicks are never raised (but see Barrau *et al.* 1997 for Ethiopia). In many obligate siblicidal eagles the egg difference is about 12% and smaller eggs may have a poor chance of hatching (Edwards & Collopy 1983, Slagsvold *et al.* 1984). In the Bearded Vulture the difference in size is 2% for wild pairs ( $n = 6$ ) and 9% for captive pairs ( $n = 19$ , H. Frey and A. Llopis unpubl. data), so the second egg is also large enough to act as insurance. (2) In the Bearded Vulture most breeding failures occur during the hatching period (51%,  $n = 39$ , Margalida *et al.* 2003), and thus the insurance value of last-hatched eggs (Wiebe 1996) would be especially important in this species. (3) Clutch replacement, an alternative to laying an insurance egg, is relatively uncommon in this species (Margalida *et al.* 2001, Margalida & Bertran 2002). The costs of re-nesting probably exceed its benefits, as pairs do not have enough time to breed successfully and the effort involved may affect their future survival and breeding success (Lindén & Møller 1989, Simmons 1997). (4) Finally, the laying interval and the hatching asynchrony in this species are the longest recorded among raptors, suggesting that it might be an adaptive mechanism facilitating the rapid loss of the second chick if the first one hatches. However, the insurance value of the second egg does not negate other hypotheses and the observation of second chicks being reared in Ethiopia suggests that in certain areas, and under certain conditions, such as when food is abundant (Barrau *et al.* 1997) these might be important. Finally, in several raptor species various attempts have been made to increase productivity by assuring the production of both young (Hustler & Howells 1986, Gargett 1990, Mock & Parker 1997). The Bearded Vulture is a threatened species and the

rescue of the second chick might provide an important mechanism to improve productivity for conservation and population expansion. Our results suggest that such intervention is possible, although the risk involved in applying this management strategy should be assessed.

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## REFERENCES

- Alexander, R.D.** 1974. The evolution of social behaviour. *Ann. Rev. Ecol. Syst.* **5**: 325–383.
- Amundsen, T. & Slagsvold, T.** 1996. Lack's brood reduction hypothesis and avian hatching asynchrony: what's next? *Oikos* **76**: 613–620.
- Anderson, D.J.** 1990. Evolution of obligate siblicide in boobies. 1. A test of the insurance-egg hypothesis. *Am. Nat.* **135**: 334–350.
- Barrau, C., Clouet, M. & Goar, J.L.** 1997. Deux jeunes gypaètes barbus (*Gypaetus barbatus meridionalis*) à l'envol dans une aire des monts du Balé (Éthiopie). *Alauda* **65**: 200–201.
- Bertran, J. & Margalida, A.** 2002. Social organization of a trio of Bearded Vulture (*Gypaetus barbatus*): social and parental roles. *J. Raptor Res.* **36**: 65–69.
- Bortolotti, G.R., Wiebe, K.L. & Iko, W.M.** 1991. Cannibalism of nestling American Kestrels by their parents and siblings. *Can. J. Zool.* **69**: 1447–1453.
- Brown, L.H.** 1977. The status, population structure, and breeding dates of the African Lammergeier. *Raptor Res.* **11**: 49–80.
- Brown, C.J.** 1990. Breeding biology of the Bearded Vulture in southern Africa. Parts I–III. *Ostrich* **61**: 24–49.
- Edwards, T.C. & Collopy, M.W.** 1983. Obligate and facultative brood reduction in eagles: an examination of factors that influence fratricide. *Auk* **100**: 630–635.
- Forbes, L.S.** 1991. Hunger and food allocation among nestlings of facultatively siblicidal ospreys. *Behav. Ecol. Sociobiol.* **29**: 189–195.
- Forbes, L.S., Thornton, S., Glassey, B., Forbes, M. & Buckley, N.J.** 1997. Why parent birds play favourites. *Nature* **390**: 351–352.
- Gargett, V.** 1978. Sibling aggression in the Black Eagle in the Matopos, Rhodesia. *Ostrich* **49**: 57–63.
- Gargett, V.** 1990. *The Black Eagle*. Johannesburg: Acorn Books.
- Gerrard, J.M. & Bortolotti, G.R.** 1988. *The Bald Eagle*. Washington, DC: Smithsonian Institution Press.
- Heredia, B.** 1991a. El Plan Coordinado de Actuaciones Para la Protección Del Quebrantahuesos. In Heredia, R. & Heredia, B. (eds) *El Quebrantahuesos (Gypaetus barbatus) en los Pirineos*: 117–126. Madrid: ICONA, Colección Técnica.
- Heredia, R.** 1991b. Biología de la Reproducción. In Heredia, R. & Heredia, B. (eds) *El Quebrantahuesos (Gypaetus barbatus) en los Pirineos*: 27–38. Madrid: ICONA, Colección Técnica.
- Hustler, C.W. & Howells, W.W.** 1986. A population study of Tawny Eagles in the Hwange National Park. *Ostrich* **57**: 101–106.
- Lindén, M. & Møller, A.P.** 1989. Cost of reproduction and covariation of life-history traits in birds. *Trends Ecol. Evol.* **4**: 367–371.
- Margalida, A., Bartoli, M. & Boudet, J.** 2001. Laying date delayed and clutch replacement in the Bearded Vulture (*Gypaetus barbatus*) in the Pyrenees. *Vulture News* **44**: 27–30.
- Margalida, A. & Bertran, J.** 2000. Breeding biology of the Bearded Vulture *Gypaetus barbatus*: minimal sexual differences in parental activities. *Ibis* **142**: 225–234.
- Margalida, A. & Bertran, J.** 2001. Function and temporal variation in use of ossuaries by Bearded Vultures (*Gypaetus barbatus*) during the nestling period. *Auk* **118**: 785–789.
- Margalida, A. & Bertran, J.** 2002. First replacement clutch by a polyandrous trio of Bearded Vultures (*Gypaetus barbatus*) in the Spanish Pyrenees. *J. Raptor Res.* **36**: 154–155.
- Margalida, A., Bertran, J., Heredia, R., Boudet, J. & Pelayo, R.** 2001. Preliminary results of the diet of Bearded Vultures (*Gypaetus barbatus*) during the nestling period, applications in conservation & management measures. In Sakoulis, A., Probonas, M. & Xirouchakis, S. (eds) *Proceedings of the 4th Workshop of Bearded Vulture*: 59–62. Irakleio: Natural History Museum of Crete and University of Crete.
- Margalida, A., Boudet, J., Heredia, R. & Bertran, J.** 2002. Videocámaras para la monitorización de la nidificación del Quebrantahuesos (*Gypaetus barbatus*). *Ecología* **16**: 325–333.
- Margalida, A. & García, D.** 2002. *Pla de Recuperació Del Trenalòs a Catalunya. Biologia I Conservació*. Documents dels Quaderns de medi ambient, 7. Barcelona: Generalitat de Catalunya. Departament de Medi Ambient.
- Margalida, A., García, D., Bertran, J. & Heredia, R.** 2003. Breeding biology and success of the Bearded Vulture *Gypaetus barbatus* in the eastern Pyrenees. *Ibis* **145**: 244–252.
- Meyburg, B.-U.** 1974. Sibling aggression and mortality among nestling eagles. *Ibis* **116**: 224–228.
- Mock, D.W., Drummond, H. & Stinson, H.** 1990. Avian siblicide. *Am. Sci.* **78**: 438–449.
- Mock, D.W. & Parker, G.A.** 1997. *The Evolution of Sibling Rivalry*. Oxford: Oxford University Press.
- Mundy, P., Butchart, D., Ledger, J. & Piper, S.** 1992. *The Vultures of Africa*. London: Academic Press.
- Negro, J.J. & Torres, M.J.** 1999. Genetic variability and differentiation of two bearded vulture *Gypaetus barbatus* populations and implications for reintroduction projects. *Biol. Conserv.* **87**: 249–254.
- Newton, I.** 1979. *Population Ecology of Raptors*. Berkhamsted: T. & A. D. Poyser.
- Parker, G.A. & Mock, D.W.** 1987. Parent–offspring conflict over clutch-size. *Evol. Ecol.* **1**: 161–174.
- Simmons, R.E.** 1988. Offspring quality and the evolution of cainism. *Ibis* **130**: 339–357.

- Simmons, R.E.** 1997. Why don't all siblicidal eagles lay insurance eggs? The egg quality hypothesis. *Behav. Ecol.* **8**: 544–550.
- Simmons, R.E.** 2002. Siblicide provides food benefits for raptor chicks: re-evaluating brood manipulation studies. *Anim. Behav.* **63**: F19–F24.
- Slagsvold, T., Sandvik, J., Rofstad, G., Lorentsen, R. & Husby, M.** 1984. On the adaptive value of intra-clutch egg-size variation in birds. *Auk* **101**: 685–697.
- Stinson, C.H.** 1979. On the selective advantage of fratricide in raptors. *Evolution* **33**: 1219–1225.
- Stokland, J.N. & Amundsen, T.** 1988. Initial size hierarchy in broods of the shag: relative significance of egg size and hatching asynchrony. *Auk* **105**: 308–315.
- Temme, D.H. & Charnov, E.L.** 1987. Brood size adjustment in birds: economical tracking in a temporally varying environment. *J. Theor. Biol.* **126**: 137–147.
- Thaler, E. & Pechlaner, H.** 1980. Cainism in the Lammergeier or Bearded Vulture at Innsbruck Alpezenoo. *Int. Zool. Yearb.* **20**: 278–280.
- Viñuela, J.** 1996. Establishment of mass hierarchies in broods of the Black Kite *Milvus migrans*. *Condor* **98**: 93–99.
- Viñuela, J.** 1999. Sibling aggression, hatching asynchrony, and nestling mortality in the black kite (*Milvus migrans*). *Behav. Ecol. Sociobiol.* **45**: 33–45.
- Viñuela, J.** 2000. Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. *Behav. Ecol. Sociobiol.* **48**: 333–343.
- Wiebe, K.L.** 1996. The insurance-egg hypothesis and extra reproductive value of last-laid eggs in clutches of American Kestrels. *Auk* **113**: 258–261.
- Wiebe, K.L. & Bortolotti, G.R.** 1995. Food-dependent benefits of hatching asynchrony in American Kestrels *Falco sparverius*. *Behav. Ecol. Sociobiol.* **36**: 49–57.
- Wiebe, K.L. & Bortolotti, G.R.** 2000. Parental interference in sibling aggression in birds: what should we look for? *Ecoscience* **7**: 1–9.

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