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SHORT NOTES

Prolonged incubation of non-viable eggs in the Bearded Vulture *Gypaetus barbatus*

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Abstract. We present the frequency and duration of prolonged incubation in the Bearded Vulture and test different hypotheses on the possible adaptive significance of this behaviour. The mean and median prolonged incubation lasted 29 and 25 days respectively (n = 10), i.e., 54% and 46% respectively longer than the average incubation period. There was a negative correlation between the duration of prolonged incubation and the egg-laying date: prolonged incubation lasted longer in earlier clutches than in later ones, and territories with many breeding attempts showed short incubation prolongations. On the other hand, no correlation was found between the duration of prolonged incubation and productivity or breeding success. The results suggest that more experienced birds, which occupy higher quality territories and lay their eggs earlier, prolonged their incubation to a greater extent. Although prolonged incubation may constitute an example of adaptive behaviour, the extensive periods documented in some cases do not appear to support this assumption.

Key words: Bearded Vulture, *Gypaetus barbatus*, energy constraints, prolonged incubation, unhatchable eggs, birds of prey

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Abnormally long incubation periods have been documented in several bird species (Skutch 1962, Holcomb 1970). This behaviour occurs regularly in the Procellariiformes (e.g. Boersma & Wheelwright 1979, Chaurand & Weimerskirch 1994, Huin 1997) and occasionally in the Podicipediformes (Kloskowski 1999, Nuechterlein & Buitron 2002). It has been linked to intermittent incubation or egg-neglect, as a consequence of long foraging distances (Pefaur 1974, Boersma & Wheelwright 1979) or the avoidance of predation (Nuechterlein & Buitron 2002), respectively.

Prolonged incubation could be an adaptive mechanism, since it provides a margin of safety for eggs that take longer than usual to hatch (Holcomb 1970, Ferguson & Sealy 1983, Huin 1997). Very few cases have been documented in raptors and generally refer to anecdotal observations of eggs that are addled or infertile and the data only reflects the occurrence of this behaviour at the species level (Margalida et al. 2006a).

The Bearded Vulture is a long-lived, cliff-nesting raptor that inhabits mountain regions of the Palearctic and Afrotropical regions (Hiraldo et al. 1979). In monogamous pairs, both sexes play similar roles during the incubation period (Margalida & Bertran 2000). In polyandrous trios, the incubation is shared by the three members (Bertran & Margalida 2002). The death of the embryo due to low temperatures appears to have selected for the near constant presence of one of the adults at the nest (Brown 1990, Margalida & Bertran 2000) and, in addition, the risk of predation is very low, thus probably not important in evolutionary terms. However, human disturbance (see Arroyo & Razin 2006) can cause egg-neglect and lead to low temperatures affecting the development of the embryo. This factor, and the infertility of the eggs, can cause cases of prolonged incubation in this species.

In the case of successfully hatched clutches, there does seem to be a link between the number of days of neglect and the length of the incubation period (Pefaur 1974). However, the factors that determine how long incubation is prolonged in the case of non-viable eggs are not clear. Incubation of dead eggs are notably longer than any period of development for a viable egg (see Margalida et al. 2006a). Since the time and energy demands during incubation can represent an important component of reproductive cost (Reid et al. 2002), and with the absence of embryonic vocalisations (common during late incubation) that would allow the parents to determine the viability of the eggs (Brua et al. 1996), it is expected that the incubation will not be prolonged excessively. It has been suggested that the prolonged incubation behaviour is related to the time interval in which an entire clutch would normally hatch, and the species with large clutches that hatch asynchronously may be more likely to prolong incubation than the species whose eggs hatch in a short time interval (Marks 1983). In accordance with this hypothesis, we can predict that incubation of non-viable eggs should last longer in two-egg clutches. In addition, because time spent incubating may increase with increasing food availability (Drent et al. 1985, Rauter & Reyer 1997), we predict that prolonged incubation should occur more often in high quality territories (with more food supply avalaible) than in low quality territories, given that in the former there is less conflict between incubating and foraging. Since clutches laid earlier during the year usually occur in territories occupied by more experienced pairs, which generally have greater breeding success and productivity, it is likely that prolonged incubation will last longer in those nests.

In this paper, we report several cases of abnormally long, unsuccessful incubation periods in the Bearded Vulture in the Pyrenees (NE Spain), and, for the first time in a raptor species, test predictions related to their potential function.

Bearded Vultures nest in rocky cliffs situated at altitudes of 650–2300 m and prefer to locate their nests in caves that provide them with a microclimate that protects from the low winter and high spring and summer temperatures. In the Pyrenees, egg-laying takes place between December and February (average 6 January, n = 69) and clutches are generally (80%) 2 eggs (Margalida et al. 2003). The laying interval is 6 days, the incubation period (i.e. the time between the laying and hatching of the first egg in a clutch) is 53–54 days and hatching asynchrony is 6 days (Margalida et al. 2003, Margalida et al. 2004). Replacement clutches are rare and occur after premature breeding failure if the eggs are laid early (Margalida & Bertran 2002). The constancy of incubation in the Bearded Vulture, as determined from observations during daylight hours, is 95% (Brown 1990, Margalida & Bertran 2000).

Data were obtained during the intensive monitoring of the population in Catalonia (NE Spain) from 1988–2005. During this period, we intensively monitored breeding biology from the pre-laying period to fledging. We studied a total of 140 breeding attempts (this area contained 12 territories in 1988 and 32 in 2005), which were monitored from the pre-laying to fledging time. The breeding success (number of young fledged divided by the number of years that each pair laid eggs) and the productivity (number of young fledged divided by the number of years that each pair was monitored) of each pair was calculated as an index of high and low quality territories. We consider high quality territories as those with a greater breeding success than low quality territories. Data on egg-laying and nest abandonment were obtained by visiting territories 1–3 times per week. In order to document egg-laying and clutch size, we used 20–60 x telescopes and video cameras (see Margalida et al. 2006b). This study only includes data of clutches for which precise laying and fledging data were known, and only first clutches were considered.

Spearman rank correlations were used to test the relationship between egg-laying dates, breeding attempts, productivity and breeding success with the length of the prolonged incubation (as the percentage (arcsin-transformed) of incubation length). Data are presented as means ± SD. Test were considered significant when $p < 0.05$.

On 10 (7.14%) occasions (n = 140 breeding attempts) we documented cases of prolonged incubation. In nine cases the nest was occupied by a monogamous pair and in one case by a polyandrous trio. Prolonged incubation occurred when clutches were laid in December (three cases), January (six cases) and February (one case), thus including the whole range of phenology documented for the Bearded Vulture in the study area. This behaviour was observed in 10 territories, which constitutes 31.3% of the territories existing in 2005. Mean and median prolonged incubation time in the Bearded Vulture were 29.1 ± 19.4 % (± SD) and 25 days more than average, respectively (n = 10, range 10–73 days). This implies a 53.6 ±

36.3% and 46.3%, respectively, lengthening of incubation (range 15.6–135.2%).

Prolonged incubation has been documented in pairs with both one and two eggs. Although the sample size is small, it appears that incubation was more prolonged in nests with two-egg clutches (28.8 ± 17.1 days, n = 4) than in those with one-egg clutches (21.75 ± 8.1 days, n = 4). Prolonged incubation was observed both in territories occupied by pairs with extensive breeding experience and/or high quality habitats, and in territories occupied by less experienced pairs or by birds that occupied lower quality habitats. A negative correlation was found between the number of breeding attempts monitored in the territory and the length of incubation prolongation (r_s = -0.67, p < 0.025, n = 10): territories with many breeding attempts show shorter incubation prolongations. No correlation was found between the length of incubation prolongation and breeding success (r_s = 0.32, n = 10) or productivity (r_s = 0.25, n = 10). There was a weak correlation between the laying date and the prolongation of the incubation: there was a tendency for the nests with clutches laid earlier to be incubated for longer (r_s = -0.59, p = 0.05, n = 10).

To our knowledge, these results constitute the first quantitative estimates of the occurrence and duration of prolonged incubation in a raptorial species. Our observations suggest that this behaviour occurs regularly in the Bearded Vulture, both in monogamous pairs and polyandrous trios. Two circumstances could lead to prolonged incubation: the infertility of the eggs, and the death of embryos. In the case of the Bearded Vulture, egg infertility has been documented in several clutches (pers. obs.). It can cause the parents to stay longer on the nest, waiting for hatching. On the other hand, in contrast with many species of Procellariiformes that abandon the eggs for several days (Boersma & Wheelwright 1979), temporary egg-neglect is rarely observed in the Bearded Vulture. However, human disturbance can lead to temporary desertions of the nest (Arroyo & Razin 2006, pers. obs.), and can be one of the factors that causes the death of the embryo and subsequent breeding failure (Margalida et al. 2003). In the study area, temperatures during the incubation period averaged 8°C during daylight hours (Authors' unpubl. data).

Time spent incubating may increase with increasing food availability (Drent et al. 1985, Rauter & Reyer 1997), and when males provision incubating females on the nest (Nilsson & Smith 1988, Hatchwell et al. 1999). This is not the case of Bearded Vultures, where both sexes share the incubation and males not provide food to females. Also, the absence of a correlation between the length of prolonged incubation and productivity or breeding success appears not to support the relationship between food availability and incubation behaviour. However, the relationship between egg-laying dates and the length of prolonged incubation suggests that birds that lay earlier, and are perhaps in better physical condition (generally older individuals nest earlier, produce larger clutches and have greater breeding success, see Forslund & Pärt 1995), incubate for longer. Thus, there may be a link between body condition and the extent of prolonged incubation.

The strongest relationship found was between the "age" of the territory and the extent of prolonged incubation. Pairs with more years of breeding experience may be better able to identify nest failure, or may be more concerned about future than about current reproduction. Nevertheless, another possibility related with the link between body condition and the extent of prolonged incubation could be explained by the high mortality among older breeding adults in the study area (Margalida et al. 2003). In this sense, mate loss would favour the incorporation of younger and less experienced individuals in these territories in which later clutches would be abandoned earlier.

In the case of the Bearded Vulture, as a species with little option for renesting during the same breeding season (Margalida & Bertran 2002), and a low risk of predation, it may be beneficial for the birds to invest extra time and energy in prolonging incubation. However, the adaptive value is questionable. Consequently, some proximate yet unknown factors probably determine the time devoted to nest attendance; hormones are likely to play an important role in regulating the incubation behaviour, as they do in other birds (Collias & Collias 1984, Buntin 1996).

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STRESZCZENIE

[Inkubowanie martwych jaj u orłosępów brodatych]

Wysiadywania martwych bądź niezapłodnionych jaj stwierdzono u szeregu gatunków ptaków — głównie rurkonosych, także u perkozów. Niniejsza praca prezentuje szczegółowe dane dotyczące tego zjawiska u ptaków drapieżnych.

Badania prowadzono w Katalonii (płn.-wsch. Hiszpania) w okresie od 1998 do 2005. W tym czasie monitorowano (od okresu przed składaniem jaj do wylotu młodych) 140 przypadków gniazdowania orłosępów brodatych. W 10 z nich (7.14%) stwierdzono przedłużenie inkubacji jaj — śr. o 29.1 dnia (10–73). Nie stwierdzono korelacji między długością okresu inkubacji martwych jaj a produktywnością par lub ich sukcesem lęgowym. Znaleziono natomiast związek z datą składania jaj — pary wcześniej przystępujące do lęgów wykazywały dłuższy okres przedłużonej inkubacji martwych jaj. Może to świadczyć, że zjawisko to jest charakterystyczne raczej dla bardziej doświadczonych osobników (zajmujące lepsze siedliska, wcześniej przystępujące do lęgów).