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The Condor 101:164–168
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COPULATORY BEHAVIOR OF THE BEARDED VULTURE¹

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Abstract: We describe copulation activity by Bearded Vultures (*Gypaetus barbatus*) at nesting sites in the Pyrenees, northern Spain, between 1993 and 1995. Pairs copulated for an average period of 67 days (range: 50–90) prior to egg laying. Seventy-five percent of attempts ended in successful copulation. Pairs displayed a daily bimodal pattern of copulation, with copulations occurring most frequently in the evening. Low levels of opportunities for extra-pair encounters (0.02 intrusions hr⁻¹) were obtained despite the high density of reproductive individuals present. The high copulation rate observed may be explained by the po-

tential risk of extra-pair copulations occurring while a member of the pair is away foraging, an activity which takes up as much as 65% of time each day. This species also showed a pattern of pair attention similar to that of other species of raptors in which males guard their females during the fertile period.

Key words: *Bearded Vulture, copulations, extra-pair copulations, Gypaetus barbatus, nesting sites, paternity assurance.*

Vultures differ from other raptors in that both sexes have similar parental roles (Newton 1979). Vultures are either socially organized in colonies or solitary (Donazar 1993). Although information on the characteristics of their reproductive behavior is scarce, in

¹ Received 24 February 1998. Accepted 19 August 1998.

both types of social systems extra-pair copulations (EPCs) have been detected in which neighboring birds were involved (Robertson 1986, Donázar et al. 1994).

The Bearded Vulture (*Gypaetus barbatus*) is a socially solitary and territorial vulture which nests on rocky precipices and whose reproductive cycle spans practically the entire year (Hiraldo et al. 1979, Cramp and Simmons 1980). The diet of this species is primarily medium sized ungulates (Hiraldo et al. 1979, Brown 1990, Heredia 1991a) which means that it must explore extensive areas far from the nest, as occurs commonly in carrion feeding species.

This paper describes the copulation activity of Bearded Vultures at nesting sites. The pattern of copulation and the presence of both sexes at nesting sites are examined as are incidents which occur during intrusions by potential competitors. The results are compared with those previously documented in other birds of prey.

METHODS

Field work was undertaken between 1993 and 1995 in the central Pyrenees in northern Catalonia (northeastern Spain). The study area includes part of the central zone of the Pyrenees where an abundant food supply (Margalida et al. 1997b) and a high Bearded Vulture population density coincide (Donázar et al. 1993). The study area is 3,750 km² with 15 potentially reproductive pairs of Bearded Vultures resident. The average altitude at nesting sites is 1,482 m (range 700–2,100 m) and the mean distance between sites is 10.4 km (range 4.7–23.2 km). This density is similar to that observed overall on the southern side of the Pyrenees for 51 territories: mean distance to nearest neighbor of 11 km (Donázar et al. 1993).

Eight pairs were monitored for 137–305 hr ($\bar{x} \pm SD = 221.3 \pm 65.1$ hr) from laying until fledging for a total of 2,268 hr. Six of these pairs were observed during courtship for 44–172 hr ($\bar{x} \pm SD = 82.9 \pm 42.7$ hr). The results correspond to the sexual activity shown at the nesting sites which include the area (territory) defended around the nest by pairs (Hiraldo et al. 1979). Data were obtained in an area within 1 km of the nests. The Bearded Vultures normally perched in the proximity of the nest (< 500 m) on exposed outcrops, which facilitated our observations. Observations were made using 10× binoculars and 20–60× telescopes, from dominant vantage points at a prudent distance from the nests (> 400–600 m). We noted the time, duration, and location of copulations, the length of time adults were present at nesting sites, and other activities and incidents related to copulation behavior. Copulation was considered as behaviorally successful when apparent contact of the cloacas occurred (Hunter et al. 1996). Bearded Vultures show virtually no sexual dimorphism (Hiraldo et al. 1979), and consequently, recognition of the different members of a pair was based on comparison of the molts and other characteristics of the plumage (Margalida et al. 1997a). The long molting process facilitated identification of the birds during extensive periods of time. Individuals were sexed according to the positions which they adopted during mounting.

The relative frequency of copulation was estimated from the number of attempts hr⁻¹. The frequencies ob-

tained were combined in time in periods of 10 days dating backwards from egg laying (day 0). The clutch size in this species is between one and two eggs (Hiraldo et al. 1979), and incubation starts as soon as the first egg is laid (Brown 1990). In four of these pairs, the beginning of incubation was known from direct observations and in the four remaining pairs from the hatch date of the chick, assuming 55 days of incubation (53–58 days, Hiraldo et al. 1979). Values presented are $\bar{x} \pm SD$.

RESULTS

We observed a total of 189 copulation attempts during the breeding season. With the exception of one case where copulation occurred on the nest, all others took place on rocky substrate away from the nest (approximately < 500 m), normally at the perching sites most frequented by the pairs.

During the prelaying period, we recorded 184 within-pair copulation attempts, in 125 (67.9%) of which we were able to ascertain whether there was cloaca contact. The proportion of behaviorally successful copulations varied between 56.1% and 100% ($75.1 \pm 18.2\%$). The mean duration of behaviorally successful copulations was 10.2 ± 1.5 sec ($n = 84$). The first copulation attempts were observed between 90 and 50 days (66.7 ± 14.9) prior to egg laying. The pairs progressively increased sexual activity (Fig. 1), the highest frequency of copulation attempts being obtained between 30 and 21 days (0.91 ± 0.40 attempts hr⁻¹) prior to egg laying, declining thereafter (0.39 ± 0.21 attempts hr⁻¹, days -10 to -1). The proportion of all copulations that were behaviorally successful (Fig. 1) followed a markedly different temporal distribution ($\chi^2_6 = 45.2$, $P < 0.001$). We recorded the highest proportion of behaviorally successful copulations between days -40 and -1, with a constant, although nonsignificant increase ($\chi^2_3 = 4.1$, $P > 0.05$) being maintained throughout this period. The maximum number of behaviorally successful copulations observed in a single day was six in one of the pairs (days -17 and -7, six mounts observed on each of these days) and five in another pair (day -17, of eight mounts observed). The minimum time interval observed between two behaviorally successful copulations in one of the pairs was 6 min (day -17 at 10:25 and 10:31, respectively).

Copulation activity normally ceased when laying of the first egg took place. Nevertheless, outside of the fertile period (day +87) we recorded, in one of the eight pairs monitored, five unsuccessful copulation attempts occurring on the same day. As a consequence, the frequency obtained during the post-laying period was 0.003 attempts hr⁻¹ ($n = 1,771$ hr of observation).

The daily pattern of copulation pertaining to the fraction of the reproductive period between the days -40 and -1 suggests a bimodal distribution (Fig. 2). Two maximum peaks are seen early in the morning (06:00–06:59, 1 attempt hr⁻¹) and in the evening (15:00–15:59, 1.08 ± 0.48 attempts hr⁻¹), with a progressive increase from the afternoon onwards. Proportionally, copulation attempts were less successful early in the morning (06:00–09:59, 59.1% of 22 cases) than during the middle of the day (10:00–13:59, 81.1% of 37 cases) and the afternoon (14:00–17:00, 80.3% of

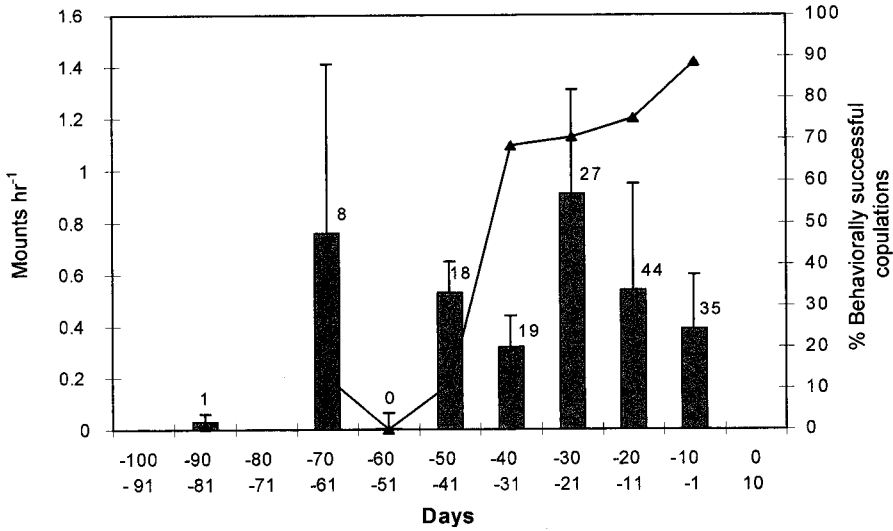


FIGURE 1. Seasonal pattern of mounts (number hr⁻¹ of observation) of six pairs of Bearded Vultures (columns; *n* = 184 mounts). Triangles indicate the percentage of successful copulations. The number of copulation attempts per period of days is listed above each column.

66 cases), the differences approaching statistical significance ($\chi^2_2 = 4.70, P < 0.10$).

We recorded the time spent by males and females at nesting sites during the 60 days prior to laying (Fig. 3). Time spent at nesting sites was similar in both sexes (males: $35.5 \pm 12.3\%$, females: $44.3 \pm 13.2\%$), and the pattern of presence, up until the moment of egg laying, showed a constant increase which was significant for females (males: Kruskal-Wallis $H_5 = 12.7, P < 0.09$, females: Kruskal-Wallis $H_5 = 11.8, P < 0.04$). The time that females remained at the nest without the presence of the male decreased from $52.4 \pm 19.7\%$ of the time between days -60 and -51 to $14.7 \pm 11.5\%$

in the days immediately prior to egg laying (days -10 to -1).

Other Bearded Vultures visited the nesting sites during the prelaying period. Of the 11 intruding Bearded Vultures recorded on nine occasions, 8 birds were adults and 3 were subadults, with a frequency of 0.02 intrusions hr⁻¹ (*n* = 497 hr). On six occasions it was possible to follow the intruders. On one of these occasions (day -56) the male partner was absent, an adult intruding bird perched next to the female and made a movement with the intention of mounting her. However, the female frustrated the possible attempt by taking flight. On the other five occasions, the resident

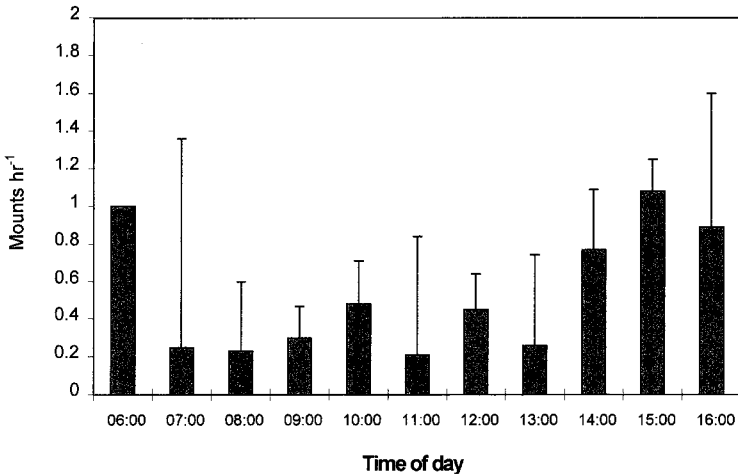


FIGURE 2. Daily pattern of mounts (number hr⁻¹ of observation) of six pairs of Bearded Vulture during the 40 days prior to egg laying (days -1 to -40, *n* = 177 mounts).

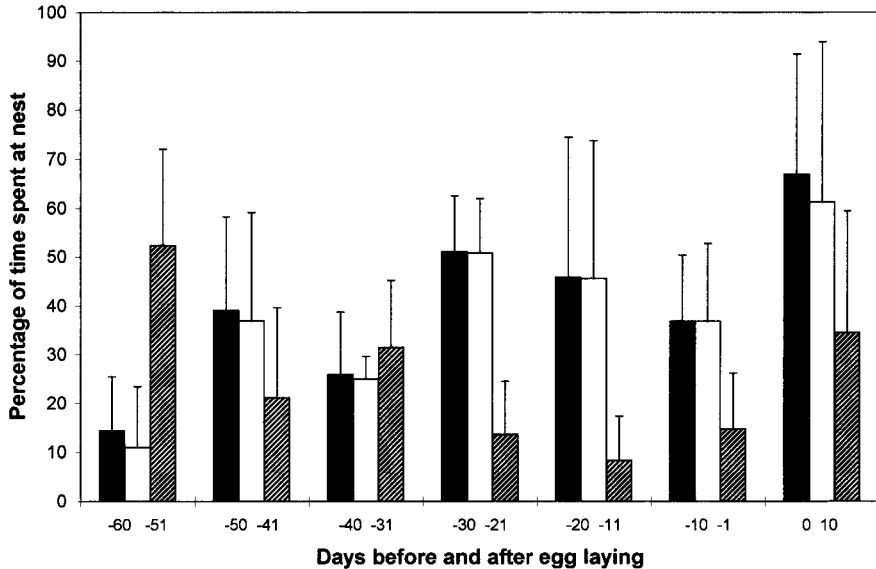


FIGURE 3. The mean (\pm SD) presence (%) of females (solid bar) and males (open bar) and percentage of time females remained unattended (hatched) (of their own time) at nesting sites for the six pairs corresponding to the period between the days -60 and $+10$.

pair copulated shortly after the intruder had been expelled (5.1 ± 4.1 min).

DISCUSSION

The Bearded Vulture displays a copulation pattern common in raptors, which is characterized by frequent copulations throughout an extended time period (Negro et al. 1992). The differences found between pairs in the duration of the copulation period are due fundamentally to the fact that the Bearded Vulture is invariably sexually active from November onwards (occasionally towards the end of October, pers. observ.), whilst the phenology of clutches in the Pyrenees may fluctuate by up to 60 days (Heredia 1991b). The average proportion of successful mounts (75%) is greater than that found in the Osprey *Pandion haliaetus* (39%, Birkhead and Lessells 1988), but substantially less than that of a similar species, the Egyptian Vulture *Neophron percnopterus* (91%, Donazar et al. 1994), Goshawk *Accipiter gentilis* (99%, Møller 1987), and Lesser Kestrel *Falco naumanni* (89%, Negro et al. 1992).

In Bearded Vultures, the maximum frequency of behaviorally successful copulations is concentrated during the 40 days prior to egg laying. As a consequence, a considerable number of copulations probably take place outside of the fertile period of the females (Robertson 1986, Donazar et al. 1994). The duration of the fertile period is unknown in vultures (Robertson 1986). Nevertheless, although the Bearded Vulture probably has a longer fertile period than that found in Ring Doves (*Streptopelia risoria*) (which has the shortest known fertile period, Birkhead and Møller 1992), it would still have a copulation frequency higher than that necessary for fertilization of a clutch which nor-

mally contains two eggs (Lake 1975). Frequent copulation has been suggested as an effective method of paternity assurance (Hunter et al. 1992). This would be an optimal strategy for seabirds and raptors which, due to their foraging far from the nest, cannot continuously guard their mates (Birkhead et al. 1987, Birkhead and Møller 1992), although it has been shown that some species attempt to maximize their presence close to their mates during the fertile period (Møller 1987, Birkhead and Lessells 1988).

Our results indicate that the time females remain unattended at the nesting sites decreases as the time for laying nears. However, frequent copulations and mate guarding do not seem to correspond, as has been shown in other raptors, to any real risk of loss of paternity at nesting sites (Korpimäki et al. 1996). The levels of intrusions by Bearded Vulture conspecifics and the proportional risk of EPCs occurring (one probable attempt which was not consummated) may be considered low relative to the population density in the Pyrenees. It should be pointed out nevertheless, that the sexual activity of this species does not seem to be limited to the nesting sites (Donazar et al. 1994, pers. observ.), and as such, the risk of EPCs away from nesting sites (which has not been possible to calculate) could explain the high rate of copulations observed. The Bearded Vulture dedicates a large amount of time each day to ranging over its feeding areas (65% based on the prelaying period), and the large home range allows for overlap between pairs (Hiraldo et al. 1979, Brown 1990). Observations of Bearded Vultures in South Africa revealed that females range alone during the period preceding egg laying (Brown 1990), and as such they may be exposed to EPCs (Simmons 1990). In species where the risks of EPCs are high because

of their foraging strategies, males adapt their copulation frequency to both their own movements and those of their mate (Møller 1987). The fact that the Bearded Vulture copulates more in the evening after rejoining following foraging bouts is consistent with the idea that it is advantageous for males to acquire the last copulations with their mates (Birkhead et al. 1988).

In summary, our results suggest that the Bearded Vulture adopts a preventive strategy based on a high copulation frequency and mate guarding (Korpimäki et al. 1996). The use of both strategies in birds where males do not provide females with food during courtship (Brown 1990, pers. observ.), would be, as highlighted in a previous study, a fact rarely documented in raptors (Donazar et al. 1994). Nevertheless, the fact that these preventive strategies do not seem to show any apparent relationship with the potential risk of the loss of paternity at the nesting sites, leads us to consider other hypotheses alternative to those of sperm competition. Tortosa and Redondo (1992) suggested that a high proportion of copulations during the pre-fertile period would act as an indicator of the optimum physical condition of the male and its relation to reproductive capacity. Petrie and Hunter (1993) proposed a theoretical model whereby copulation acts as a means for reducing the potential risk of losing the partner.

We thank J. Boudet, J. Feixa, D. García, R. Heredia, P. Pelayo, R. Pelayo, and P. Romero for their assistance during field work, and S. Mañosa, J. Real, O. J. Arribas, X. Bellés, D. García, X. Parellada, and two anonymous referees for reading and discussing this paper. S. Cahill translated the text into English. This study was supported by the Departament d'Agricultura Ramaderia i Pesca de la Generalitat de Catalunya, Minuartia Estudis Ambientals, and a LIFE Program of the European Union (94/E/A221/E/01126/ASJ).

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