

Copulatory behaviour in the colonial Eurasian Griffon vulture *Gyps fulvus*

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Abstract We examined copulation patterns and associated sexual behaviour in the colonial Eurasian Griffon vulture *Gyps fulvus* during the pre-laying period. Eurasian Griffon vulture pairs conducted an average of 71.7 copulation attempts per clutch, with an average copulation frequency of 1.2 copulation attempts per day. Low copulation frequencies compared to other raptors and absence of mate-guarding suggest that this species does not possess adaptive behaviour aimed at increasing paternity assurance. However, the gradual increase in copulations during the fertile period is consistent with the sperm competition hypothesis.

Keywords Eurasian Griffon vulture · Extra-pair copulation · *Gyps fulvus* · Sperm competition

Introduction

In birds, frequent copulations constitute a paternity-assuring strategy when males are unable to guard their females during the fertile period. The aim is to reduce the risk of extra-pair copulations (EPCs) that may lead to extra-pair paternity (Birkhead et al. 1987; Birkhead 1988; Birkhead and Møller 1992). This strategy is often found in colonial bird species, in which mate-guarding is not practical, and EPCs are more frequent (Møller and Birkhead 1993). Because higher breeding densities also imply more opportunities for EPCs and sperm competition, the risk of

extra-pair fertilizations (EPFs) is supposedly higher in colonial than in solitary bird species.

To reduce the risk of cuckoldry, males may adopt one or both of two strategies: (1) guard their mates closely, as has been described in other vulture species (Donazar et al. 1994; Bertran and Margalida 1999) or (2) copulate frequently during the fertile period (Birkhead and Møller 1992). In accordance with the paternity-assurance hypothesis, colonial raptors should copulate more frequently than solitary species (Birkhead et al. 1987; Møller 1987), and a higher presence of males (mate-guarding) during the fertile period would be expected.

The Eurasian Griffon vulture *Gyps fulvus* is a cliff-nesting, socially monogamous colonial species that may nest in large colonies of over 150 pairs (del Hoyo et al. 1994). Both sexes incubate the eggs and feed the chicks with an equal division of labour during the breeding season (Xirouchakis and Mylonas 2007). However, descriptions of the amount of time females remain unattended during the fertile period, which would test the mate-guarding hypothesis, are non-existent, and even published behavioural studies on sexual activity in vultures are very scarce (Donazar et al. 1994; Bertran and Margalida 1999; Xirouchakis and Mylonas 2007). We report here our study of the copulation frequency and behaviour associated with sexual activity in the Griffon vulture during the pre-laying period.

Methods

Data for this study were collected during a single breeding season (1998–1999) in the Alta Ribagorça (central Prepyrenees, north-east Spain, 42.35°N, 0.74°E). Observations were conducted between November 1998 (when the Pyrenean Griffon vulture population initiates its sexual

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activity) and February 1999 in a colony of nine breeding pairs. We monitored four pairs simultaneously and recorded their behaviour. Three of these pairs laid eggs. The pairs were selected on the basis of the excellent viewing conditions provided by the cliffs in an 800-m radius around the nest-sites. Birds were observed with a 20–60× telescope at a distance of 100–300 m from the rock face where the nests were located. The Griffon vulture shows virtually no sexual dimorphism. Consequently, the identity of the pair members was based on a comparison of the moults and other plumage characteristics, and birds were sexed according to the positions they adopted during mounting.

Observations were performed weekly. On each observation day, birds were monitored during all daylight hours from 0600 to 1800 hours. Observations finished a week after egg-laying. In total, we conducted 144 h of observations (average 9.5 ± 1.5 h/day) during the pre-laying period and 23 h 50 min during the incubation period in order to determine that sexual activity had finished.

The following information was recorded for each observed copulation attempt: (1) the identity of the pair involved; (2) the place where the attempted copulation took place; (3) whether the copulation was successful or not (i.e. whether cloacal contact was achieved during mount); (4) whether there was any vocal activity. The duration of the copulation attempts was measured with a stopwatch (in seconds), and all included mounting movements. For each pair we recorded the time that males and females spent within the breeding territory (nest site and nearby area). The frequency of copulations was estimated as the number of attempts per hour. The frequencies obtained were combined in time periods of 7 days, dating backwards from egg-laying (day 0 was considered as the egg-laying date). We determined the onset of laying by direct observation (i.e. the behaviour of the adults in the nest, incubation and changeovers).

All of the statistical analyses were carried out to a significance level of 0.05. We tested for differences between weeks using analyses of variances (ANOVAs). Where the results from the ANOVAs were significant, a posteriori testing involving the use of the Scheffé test ($P < 0.05$) to identify inter-group differences was applied. The difference in the amount of time spent by males and females at the nest was tested using the Wilcoxon test for matched pairs. The difference in the copulation success between pairs was tested using Chi-square tests. Values presented are the mean \pm standard deviation (SD).

Results

We recorded a total of 54 copulation attempts during the pre-laying period, of which 49 (90.7%) were successful

(average $90.1 \pm 1.92\%$, $n = 4$ pairs). No differences were found in the copulation success between pairs ($\chi^2 = 0.09$, $df = 3$, $P = 0.99$). All copulation attempts took place at the nest site, and no EPC attempts were observed. All copulation attempts were accompanied by acoustic signals, whose intensity rose as the copulation progressed. On the other hand, very little conspicuous wing movement was observed during copulation. Because no differences were found between pairs (Friedman test $P > 0.05$ for all of the variables considered), the data were pooled.

The first copulation attempts were observed between 61 and 39 days (53.67 ± 12.70 , $n = 3$ pairs) before egg-laying. The mean copulation pattern relative to the onset of laying showed that the highest frequency of copulation attempts occurred between 21 and 14 days before egg-laying (0.42 ± 0.28) and between 14 and 7 days before egg-laying (0.43 ± 0.32 , Fig. 1). Thus, a temporal analysis of sexual activity revealed a significant increase in the frequency of copulation attempts between the second and third weeks (days -21 to -7) before egg-laying (ANOVA $F_{9, 29} = 2.57$, $P = 0.038$, Scheffé test a posteriori $P < 0.05$). Assuming 11 h of daylight during this period of activity in November–February, we estimated a mean of 1.22 ± 0.62 (range 0.69–1.91) copulation attempts per pair/day, which gives an average estimate of 71.70 ± 44.80 copulation attempts per pair/nest (range 26.91–116.51). The maximum number of successful copulations per day was seven (day 12 before egg-laying), while the shortest interval between two successful copulations was 10 min. The duration of copulation attempts averaged 64.57 ± 77.95 s (range 4–394, $n = 49$). The daily copulation pattern showed one peak early in the morning (0600–0700 h, 0.50 ± 0.87 attempts h^{-1}) and another in the evening (15.00–16.00 h, 0.37 ± 0.06 attempts h^{-1}).

The percentage time spent by males and females at the nest was similar (males: $31.86 \pm 26.39\%$; females:

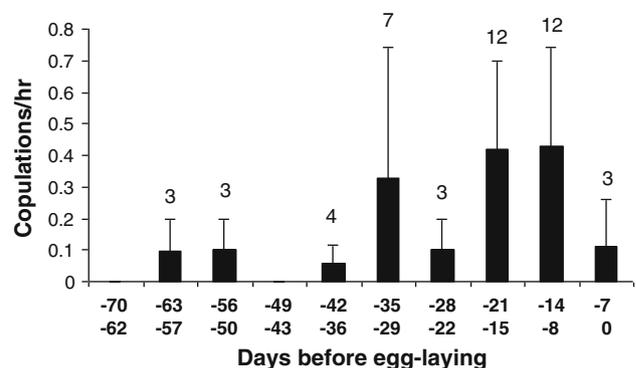


Fig. 1 Temporal pattern of copulation attempts in Eurasian Griffon vultures calculated weekly from 10 weeks before egg-laying until the week of the onset of laying. 0 Egg-laying

$35.17 \pm 32.18\%$, Wilcoxon test, $T = 0.71$, $P = 0.475$). The percentage of time the two sexes spent together at the nest site did not differ over the 10-week monitoring period ($F_{9, 29} = 0.80$, $P = 0.62$). Similarly, the percentage time spent by males at the nest site was similar for all time periods (weeks) relative to the onset of egg-laying ($F_{9, 29} = 0.45$, $P = 0.89$). The females' presence at the nest site, however, did increase as the onset of egg-laying approached ($F_{9, 29} = 4.19$, $P = 0.0036$) and, as a result, the time that the females spent alone was significantly higher during the 2 weeks before egg-laying ($F_{9, 29} = 3.63$, $P = 0.0078$, Scheffé test $P < 0.05$).

Discussion

In our study of this small and not very dense colony, we estimated that the Griffon vultures conducted an average of 71.7 copulation attempts per pair clutch, with an average frequency of 1.22 copulation attempts/day. These results are similar to those obtained in southern Spain (0.91 copulation attempts day⁻¹, Fernández 1975) and in Crete (1.19 copulation attempts day⁻¹, Xirouchakis and Mylonas 2007). Birkhead and Møller (1992) propose that the copulation frequency should be considered as high whenever copulation occurs over 20 times per breeding season or whenever more than two attempts occur per day. Assuming that the copulation frequency would tend to be proportional to the risk of paternity loss, the copulation rate of colonial Griffon vultures (which have an extensive period of sexual activity) would seem to be low in comparison with that of other raptors, which usually exceed 200 copulation attempts per breeding season (see Negro and Grande 2001). More specifically, the average frequency is estimated to be 332 copulation attempts per breeding season for the solitary bearded vulture *Gypaetus barbatus* (Bertran and Margalida 2005) and 55 copulation attempts for the migratory Egyptian vulture *Neophron percnopterus* (Donazar et al. 1994). However, in the colonial Cape Griffon *Gyps coprotheres*, the average number of copulation attempts during the pre-laying period does not appear to exceed 100 (Robertson 1986).

The daily pattern of copulation frequency, with one peak early in the morning and the other at the end of the day, may be explained by Eurasian Griffon vulture's foraging ecology and the risk of EPCs. The hours around midday are those used by the birds to look for food, the availability of which is spatially and temporally unpredictable.

As far as breeding is concerned, the cost of living in a colony includes the risk of losing paternity, given that extra-pair copulations (mainly in large colonies) appear to be common (Møller 1985). We did not observe any EPCs, although Xirouchakis and Mylonas (2007) detected an

incidence rate of 3.3%. It has been suggested that raptors adopt effective behavioural and physiological strategies, such as mate-guarding, and have larger testes that facilitate frequent copulations (Mougeot 2004). Unlike the cases of solitary and territorial vultures (Donazar et al. 1994; Bertran and Margalida 1999), there are no records of male Griffon vultures increasing their presence close to females during their presumed fertile period. As a result, copulation frequency in the Griffon vulture and the absence of mate-guarding would seem to suggest very little behavioural adaptation for protecting paternity. This may also be due to the costs involved in mate-guarding—an increase in energetic demands and reduced foraging efficiency (Møller 1987; Westneat 1994). Nevertheless, a strategy for assuring paternity in this species may be based on increasing the number of copulation attempts when females are presumably fertile. On the other hand, copulations are not as frequent in the Griffon vulture as in solitary species, although their duration is much longer: 64.6 s for the Griffon vulture in this study, 10.2 s for the bearded vulture (Bertran and Margalida 1999) or 13.7 s for the Egyptian vulture (Donazar et al. 1994). In raptors, copulations in colonial species last relatively longer than those in solitary species, which may also constitute a means by which males increase sperm transfer and the probability of fertilization (Mougeot 2004).

Other types of behaviour may also act as a paternity guard in the Griffon vulture. Territoriality, song, aggression and the deceptive use of alarm calls have also been proposed as paternity guards (Birkhead and Møller 1992). In addition, copulation may act as a territorial signal in raptor species (Negro and Grande 2001). In the case of colonial Griffon vultures, the relatively low copulation frequency found could be compensated by (1) copulation length and high acoustic intensity (the calls can be heard at distances of hundreds of metres), which may act as a warning to other males of nest occupancy and the males' overall quality, and (2) a high copulation success rate (90%), which may reduce the number of extra-pair copulation attempts.

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