

Copulation behaviour in the Egyptian Vulture *Neophron percnopterus*

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This paper presents the first detailed description of copulation behaviour in the Egyptian Vulture. The study was carried out in northern Spain during 1989–91. Pair copulations began around 25 days before laying and were uncommon after the first egg was laid. Some copulations (11.6%) were observed during the nestling period. Two extra-pair copulation attempts were observed. The copulation behaviour of Egyptian Vultures seems to be exceptional when compared with other raptors: mate attendance was intensive, especially during the days prior to laying and copulation frequency was high even considering only those performed in the nesting territory: 55 ± 18 copulations/female between days -15 and 0 , and a maximum of 9 copulations/female/day during the presumed fertile period. Some copulations also occurred during foraging trips.

Vultures are single-brooded and long-lived birds in which pair-bonds may be maintained from one year to the next.¹ They exploit scarce and unpredictable trophic resources² and, as a consequence, they need to spend long periods of time away from the nest foraging. Such wide-ranging foraging movements may influence the copulation behaviour developed by the species. This paper examines the copulation patterns of the Egyptian Vulture *Neophron percnopterus*, a species which maintains exclusive nesting territories. Courtship activity of the Egyptian Vulture takes place at the end of the winter and, as in other vulture species, courtship feeding does not occur; the usual clutch size is 2 and inter-egg interval is between 3 and 8 days.^{1,3,4} We describe the occurrence of copulations in the territory and in foraging areas, extra-pair copulations, and examine how our observations compare with those other raptors in which paternity guarding behaviour is observed.

STUDY AREA AND METHODS

The study was carried out in the region of Bardenas Reales (Ebro Valley; Northern Spain; 42°10'N, 1°30'E). Some observations were also made in the neighbouring region of Los Monegros. The observations were carried out between March and August 1989–91. Three pairs were involved in the main observations during the pre-laying period and nine pairs in the post-laying period; the observations lasted from dawn to dusk. In another 18 pairs we conducted partial daily surveys during pre-laying. Observations were made by telescope from points at 200–400 m from the nests in order to avoid disturbance.

We recorded the attendance times of males and females at the nesting territory (defined as the area defended around the nest; mean = 18 ha, $n = 7$ territories). We assumed, from radio-tracking studies,⁵ that the birds spent all their time foraging when out of the territory. We also recorded the time of arrival and departure from the nesting territory and whether the birds arrived alone or together. Additionally, for

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each copulation observed, we recorded its duration (in sec), and whether the copulation attempt was successful (apparent cloacal contact) or not. Within each pair, sexes were easily identified from the copulation behaviour and from plumage patterns.

To study seasonal variations in copulation frequencies we divided the breeding cycle in 10-day periods. Two variables were considered for each period: (a) the total hourly frequency of copulation: number/hours of observation; (b) hourly copulation frequencies when the 2 adults were together in the territory. Mean and standard deviations were calculated considering 60 min samples within each period and pair. Copulation frequencies followed a Poisson distribution. For these calculations, data from all the pairs were pooled together as was done in other studies concerning raptor copulation behaviour.⁶⁻⁸ In our case, lack of data made it difficult to carry out tests of homogeneity but the copulation frequency during pre-laying (day -20 to 0) did not differ among the 3 most studied pairs (Kruskall-Wallis test, total hourly frequency: $H=0.727$, $df=2$, $P>0.105$; hourly frequency when the 2 adults were present together: $H=0.470$, $df=2$, $P=0.791$).

Copulation frequencies are presented in relation to the start of laying (day 0). Allowing 2-4 days for laying and 42 days for incubation (starting with the first egg), this date was estimated by counting back 42 days from the hatching date.¹ The hatching date was known from direct observations or deduced from the length of the fourth outermost primary of the chick. Since the growth pattern of this measure is not influenced by the nestling's condition, it may be used to predict its age and, therefore, the laying date.⁹

RESULTS

We observed 43 copulation attempts within nesting territories (Fig. 1). None of them occurred at the nest. The first recorded copulation occurred on day -25 before the laying of the first egg and the last egg on day -1. Most copulations (86.0% of the total of attempts) were recorded during the 3 weeks before the beginning of laying, being slightly more frequent between days -20 and -11 (46.5%) than between days -10 to -1 (34.8%). Other copulation attempts (11.6%) occurred during

the early and central nestling periods. Most attempts were successful (90.7%). The mean duration of successful copulations was 13.7 sec ($sd=4.7$, $n=18$).

Two extra-pair copulation (EPC) attempts were observed. Both involved the dominant (alpha) male of a trio and involved the female of a neighbouring pair 200 m away. The first attempt (day -2 with respect to the laying date of the female) failed because the female did not cooperate and the intruding male was violently attacked by the pair male. The second attempt (day 5) was successful. The pair male was incubating and did not observe this attempt. Only the first attempt was observed during the standardized periods. Therefore, of 38 copulation attempts over the pre-laying period, 1 extra-pair copulation took place (2.6%).

Although the Egyptian Vultures usually copulated within their nesting territories some did so away from them. Part of the home range of a pair (about 4 km²) was visible from our observation point and in 118 min in which members of the pair were foraging in this area we observed 3 successful copulations while they foraged together. Of these, two occurred (days -13 and -4) on a foraging site 1200 m from the nest and the other (day -4) on a small hill 1100 m from the nest. During a period of 36 min, another 3 copulation attempts (1 successful) were observed on day -12 between the members of another pair in a foraging place 3 km from the nest.

As Egyptian Vultures were not followed during their foraging trips it is impossible to estimate the total copulation rates, since some of the attempts occurred away from the observation areas. Although based on limited data, copulation frequency seems to have been greater away from the nesting territory: thus during the 3-week period before egg-laying there was approximately 1 copulation per hour within the territory (Fig. 1) but about 2 or 3 attempts per hour outside the territory (see previous paragraph). If we consider only the number of copulations performed within nesting territories (which is therefore likely to underestimate considerably total copulation rates) we found the mean number of copulations per hour for the 3 most studied pairs during the 15 days prior to laying was 0.81 ± 0.26 (based on observation periods of

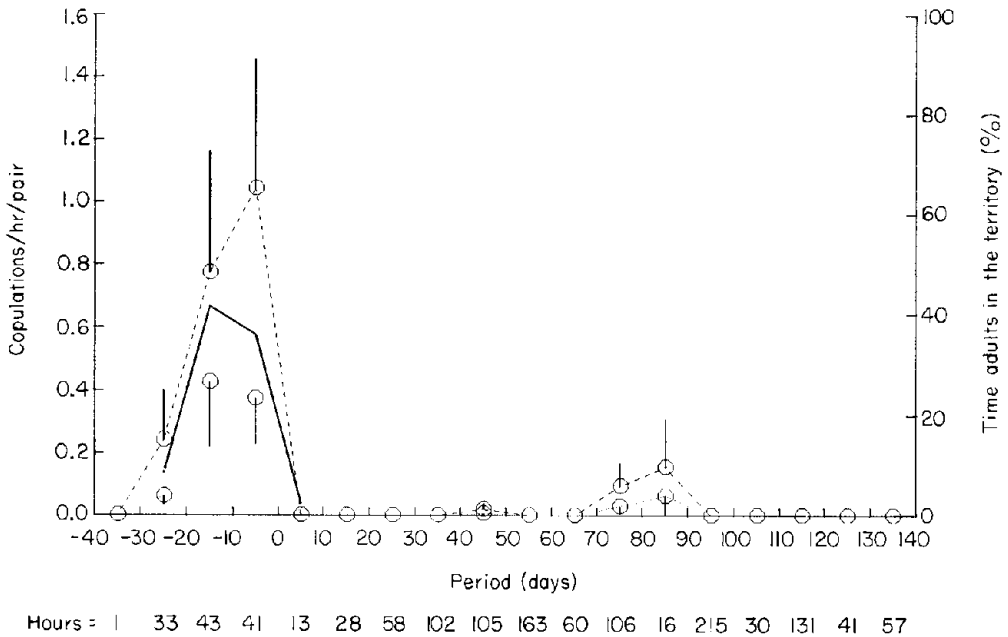


Figure 1. Seasonal variation in the hourly frequency of copulations (based on 60-min intervals) in 10-day periods during the breeding season of the Egyptian Vultures. Each one of the 10-day periods is represented by its central day. Three tendencies are shown; above: copulation frequency when the 2 adults were present in the breeding territory; centre: percentage of time that the 2 adults spent together in the territory during the pre-laying period; below: copulation frequency on the total time of observation. Bars show standard deviations (represented only in one direction). The row below indicates numbers of hours of observation per period.

24, 36 and 12 hr for the three nests). The 2 birds were present together in the territory for 38% of the time. If we assume a daily activity period of 12 hr, the total number of copulations performed within the nesting territory in the 15-day period prior to laying the first egg would have been 55 ± 18 ($0.81 \times 12 \times 0.38 \times 15$). The maximum number of copulations observed per day for the 3 pairs was 9 on day -2, 4 on day -4, and 4 on day -11. Another pair was seen making 3 copulations within 5 hr on day -14.

Territory attendance and mate attendance varied during the pre-laying period (Fig. 1 and Table 1). During days -30 to -21 the females spent more time in the territories than the males, being alone for 75% of this time. In both sexes, the maximum territory attendance occurred between days -20 and -11; the females were alone for 11.3% of the time that they remained in the territory. On the days immediately before laying (-10 to -1), the time that the 2 adults remained together in the territory decreased, but

the females were rarely left alone by the males (1.4% of the time in the territory). Copulation frequency (on the total hours of observations) seems related to the time that the 2 adults spend together in the territory (Fig. 1).

DISCUSSION

Egyptian Vultures began copulating 25 days before laying. The fertile period in this species is unknown. The length of this period depends on the viability of the sperm. In other raptors this has been estimated to be around twelve days.¹⁰ In consequence, some of the copulations may have been out of the female's fertile period. Some 10% of all copulations occurred during the nestling and post-fledging periods. Pair copulations may have multiple functions: fertilization, devaluation of the sperm of other males (see below) and maintenance of pair bonds.^{11,12}

Considering the number of copulations per female between days -15 and 0 the Egyptian

Table 1. Male and female attendance in the territories. The percentage of time spent by the 2 sexes in the territories for each 10-day period, the percentage of time in which each sex was alone, and the percentage of time when the 2 members of the pair were together (mean \pm standard deviation) are shown. min = minutes of observation in each period

Days	Males		Females		Together	min
	Present	Alone	Present	Alone		
-30 to -21	10.9 \pm 9.7	2.4 \pm 2.3	34.0 \pm 32.6	25.5 \pm 24.3	8.5 \pm 7.5	1370
-20 to -11	45.8 \pm 23.8	4.3 \pm 3.8	46.8 \pm 24.4	5.3 \pm 5.7	41.4 \pm 24.5	1901
-10 to -1	36.3 \pm 23.0	0.4 \pm 0.4	36.5 \pm 22.9	0.5 \pm 0.4	35.9 \pm 23.3	2205

Vulture is clearly a species with a high copulation rate (more than 20 copulations/female/clutch).^{11,13} Moreover, the daily number of copulations during the female's fertile period is also well above 2, a number which has been considered appropriate to separate species with low and high copulation frequencies.¹¹ It should be noted that these figures are minima and refer to copulations occurring in the nesting territory only. We cannot estimate the rate of copulations that take place during foraging trips but clearly, if included, the daily copulation rate must be higher than is suggested by the above figures.

These results suggest that the Egyptian Vulture may differ from other raptors¹³ because while it performs a paternity-guarding strategy based on frequent copulations, mate-feeding does not take place and adults remain together for a high proportion of the pre-laying time. Mate attendance patterns seem similar to those performed by other raptors.¹³ We observed that mate attendance increased towards laying, during which the female was never alone in the nesting territory. Whenever it was possible to detect pairs during foraging trips, the 2 birds were also observed together. It is logical to suppose that mate attendance reduces the likelihood of an extra-pair copulation.¹³ In fact, we observed a violent response by a male when his mate was the object of a copulation attempt by a neighbouring male.

Finally, the occurrence of copulations during foraging trips is unusual, probably because studies on raptor copulations very rarely include following the birds during foraging trips.¹² Copulation seems to be energetically expensive and time is required to restore sperm reserves.¹⁴ Thus, it may be difficult to concentrate them in the short period of time spent in

the nesting territory, and the birds may also have to copulate during the time devoted to foraging. Moreover, the existence of copulations outside the nesting areas questions the validity of the seasonal variations in copulation frequencies observed. The copulation frequency in the nesting territories seems closely related to the time that the 2 adults spent in those places, so caution seems necessary when estimating copulation frequency and its seasonal variation in species which spend a large period of time away from the nest, especially if the two members of the pair forage together.

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