

## COPULATIONS THROUGHOUT BREEDING IN A COLONIAL ACCIPITRID VULTURE<sup>1</sup>

ALISTAIR ROBERTSON<sup>2</sup>

Zoology Department, University of Witwatersrand,  
 Johannesburg 2001, South Africa

*Key words:* Apparently monogamous; copulations; prelaying; postlaying; extrapair.

In various falconiforms, evidence of a high frequency of copulations as well as their occurrence after egg-laying suggests that the function of this behavior may not be restricted to fertilization (Newton 1979). Also, in apparently monogamous species, most copulations occur between mated partners; however, copulations between individuals that are not paired to each other (extrapair copulations, EPCs) have been observed in over 20 avian families to date (McKinney et al. 1984). Here I present observations on the associated behavior and frequency of copulations, including EPCs, in a monogamous and colonial accipitrid vulture.

### STUDY AREA AND METHODS

Observations were conducted at a colony of about 55 Cape Vultures (*Gyps coprotheres*) in a ravine of the Potberg, Cape Province, South Africa. Between May 1981 and May 1982, I spent 12 days each month (07:00 to 16:30), regardless of weather conditions, observing birds from the side opposite the nesting and roosting cliffs. The concluding activities of the 1980 breeding season, all stages of the 1981 season and the initiation of the 1982 season were covered. Individuals and sexes of these large birds (8 to 10 kg) are visually indistinguishable in the field; however, some breeding birds were recognizable as they had been ringed as nestlings. Ages were estimated using the characters given in Mundy (1982), and sexes were determined by observation of copulation where at least one participant was ringed. With the exception of nest-building, male and female Cape Vultures share duties related to rearing each season's single offspring, and probably pair-bond for life (Robertson, in press, A. F. Boshoff, pers. comm.). In 1981, 17 breeding pairs produced 16 eggs (1982: 18 pairs and 17 eggs).

### OBSERVATIONS

Copulations were easily noted due to the male's distinctive hoarse call as he grips the female's ruff while balancing on her back (as described for the White-backed Vulture *G. africanus*, Mundy 1982). With lateral motions of his tail, the male knocks the female's tail from side to side before leaning back and pressing his tail down to ejaculate when the cloacae are juxtaposed. While on the nest, both birds spend much time bending over and picking at the nest contents which, in effect, positions the female's back for the male, who then mounts from the side or rear. Of 32 timed bouts, the male was on the female's back for 42 sec (range 22 to 56 sec), although in at least 12 other cases, the male stood on the female's back for longer than 3 min before being jabbed off. Some males gave the impression

of being inexperienced by moving around on the female's back and not attempting to juxtapose cloacas. Thus in 17 of 31 observed attempts at nest 57 in 1981, no cloacal contact occurred. This was observed to lesser extents at other nests, although it is often difficult to judge.

As with White-backed Vultures (Houston 1976), no discernible display occurred at nests before or after copulation, although pairs were occasionally seen to allopreen necks gently, both before and after the event. A form of scapular action display (Berruti 1981) generally occurred just after a bird landed at a nest, where it turned its head and placed its bill at the junction of its wing and body. Less often, both members of a pair engaged in this behavior. In all cases, copulations preceded initiation of nest-building at nest sites.

Between May 1981 and May 1982, 1983 copulations were observed, of which 1906 (96%) involved resident pairs at their nest sites. The diurnal pattern of copulations was approximately bimodal, with most occurring in mid to late afternoon (Fig. 1). On average, 68% of copulations at nest sites occurred during the prelaying period, and fewest during incubation (Table 1). Most nests were active in the following season, so values recorded for the post-fledging dependence period are biased upwards as they include copulations related to the next season's prelaying period (these periods overlapped in time, Robertson 1985).

As mentioned, not all copulations occurred at nest sites; 76 (4%) were observed at roosts. The temporal pattern of these extra-nest copulations was similar to the pattern observed at nest sites, in that peak frequency occurred around the time of egg-laying, and copulations continued sporadically thereafter (Fig. 2). Of these copulations at roosts, 11 where a male had jumped onto a female's back and was aggressively jabbed off were classed as FEPCs (forced extrapair copulations, McKinney 1975) or resisted

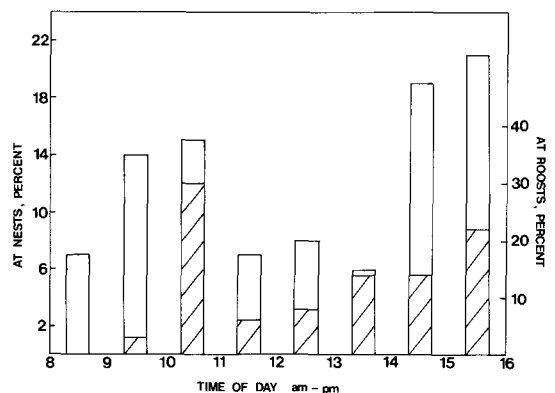


FIGURE 1. Diurnal pattern of copulations at nest sites ( $n = 734$ ) and roost points (hatched bars), May to July 1981. Egg-laying was spread over one month; values are drawn from 32 observation days preceding the last date of laying, and depicted as percentages of respective subtotals.

<sup>1</sup> Received 3 February 1986. Final acceptance 13 May 1986.

<sup>2</sup> Present address: Waterford Kamhlaba UWC, Box 52, Mbabane, Swaziland.

TABLE 1. Frequency of copulations observed per period of breeding. Values for nest 61 are bracketed as the nestling disappeared before fledging. Nests other than 29, 45, and 3 produced eggs in the subsequent season.

Nest	Pre-laying period	% of total	Incubation period	% of total	Nesting period	% of total	Post-fledging	% of total
6	31	76	8	19	0	0	2	5
17	47	62	8	11	20	27	0	0
16	42	39	2	2	15	14	49	45
4	44	73	0	0	13	22	3	5
61	16	(59)	0	(0)	(11)	(42)	—	—
26	47	—	6	—	—	—	—	—
18	37	—	1	—	—	—	—	—
30	38	—	0	—	—	—	—	—
13	27	—	2	—	—	—	—	—
57	30	—	0	—	—	—	—	—
55	46	—	0	—	—	—	—	—
63	49	69	0	0	0	3	20	28
7	112	96	0	0	0	3	1	1
29	38	—	5	—	—	—	—	—
45	21	—	0	—	—	—	—	—
3	45	—	0	—	—	—	—	—
	$\Sigma = 670$	$\bar{x} = 69, 2$	$\Sigma = 32$	$\bar{x} = 5, 3$	$\Sigma = 53$	$\bar{x} = 11, 5$	$\Sigma = 75$	$\bar{x} = 14$

matings (Estep and Bruce 1981). In 6 of the 11 cases, one of the birds was from a known nest site (4 males, 2 females). These contrasted with three unforced extrapair copulations (UEPC, Gladstone 1979) where the female did not resist and it is possible that insemination was achieved. Thus, the nest no. 17 male copulated with an unidentified adult female at a roost point before returning to his partner incubating the egg, and the nest no. 13 female was involved in an EPC at a roost about six days before laying an egg. In pairs which reared young, copulations increased to an approximate average of 6/pair/day until egg-laying and, in most cases, did not occur again in the subsequent few weeks (Fig. 3). Figure 4 depicts the pattern of copulations

over the breeding cycle for the same four pairs as the previous Figure, and Figure 5 the pattern for four nests which, for different reasons, failed to rear offspring in 1981.

DISCUSSION

Various features of Cape Vulture copulations are apparent: (a) copulations occur over a longer period than one might deem necessary for insemination of the Cape Vulture's single egg clutch. However, the onset and duration of spermatogenesis and ovulation in these vultures are unknown; (b) copulations continue, at a reduced frequency, after egg-laying; i.e., at least 20% occurred in a nonfertilization context. Also, in some pairs which had failed in breeding, copulations continued at the nest site; (c) of the few EPCs observed, most attempts were apparently forced on the female, but some females did not offer resistance. However, because not every breeding vulture was recognizable, the number of EPCs documented here is probably less than the "true" value: some of the copulations at roosts (Fig. 1) may have been EPCs.

The copulatory act is considered to serve biological functions other than immediate fertilization (Power 1980), and numerous explanations have been offered to account for the high frequency and prolonged occurrence of this behavior. For example, copulations may serve to induce ovarian activity (Erickson and Zenone 1976) and effect endocrine changes facilitating successive stages of nesting (Hinde 1970). In some waterfowl, copulations are frequent during pair formation when gonads are regressed and sperm are not being produced (Hohn 1947). McKinney et al. (1984) suggested that these mountings were part of a mate assessment process whereby females test male competence in copulating. As mentioned, some males appeared inexperienced; however, even these males eventually juxtaposed cloacas. One must bear in mind that this paper describes the frequencies of copulations only; I could not tell whether insemination occurred during a particular mounting. In other birds, only a proportion of insemination attempts are successful (McKinney et al. 1984). Copulations have also been implicated in pair-bonding (Newton 1979). Noting the strong tactile stimuli in gannet copulations, Nelson (1976) suggested them to be a prolonged source of sexual stimulation; similar stimuli, both tactile and auditory, are apparent in vulture matings. With the exception of allopreening, it is only during these copulations that breeding partners maintain any physical con-

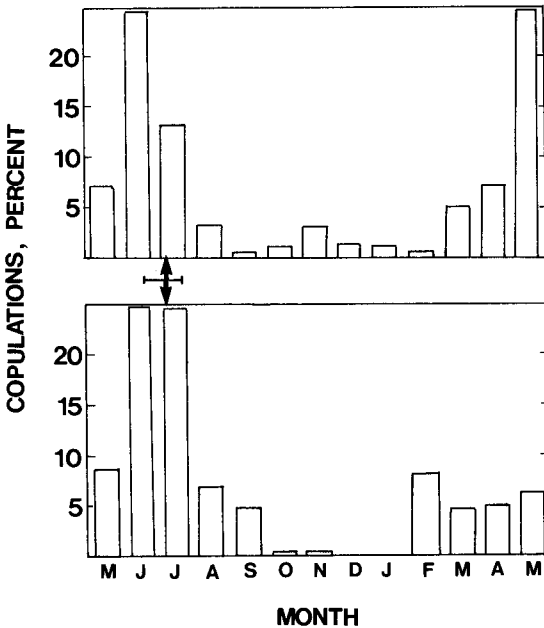


FIGURE 2. Temporal pattern of copulations observed at nest sites (above,  $n = 1906$ ) and roosts (below,  $n = 76$ ), as percentages of respective subtotals. The 1981 average laying date (and range) is indicated.

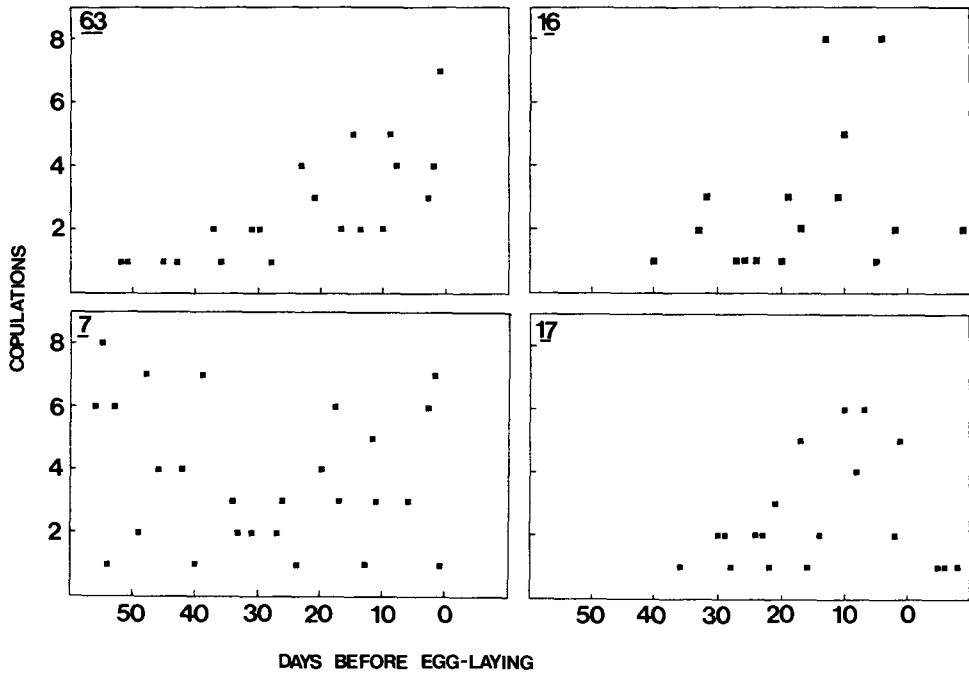


FIGURE 3. Temporal pattern of copulations, relative to the date of egg-laying, at four nests where offspring were reared in 1981.

tact. By comparing postlaying copulations at nests with offspring, with those where offspring had died, one might suppose that they also serve to indicate nest site occupancy. Unfortunately, functions and effects of the copulatory act cannot be distinguished from these observations alone.

Repeated copulations may result in sperm depletion and thus reduce egg fertility (Dewsbury 1982). Although there was a considerable range in the number of prelaying copulations per pair (Table 1), these data do not suggest evidence of this effect, as the few pairs with relatively high

copulation frequencies still produced eggs. The degree to which vultures are fecund during the course of the year is unknown; in American Kestrels (*Falco sparverius*), sperm production peaks early in the breeding season and diminishes by the time repeat clutches are laid (Bird and Lague 1977). Cape Vultures are certainly able to produce second clutches if the first is lost early in the season (Mundy 1982).

Erickson and Zenone (1976) consider that many copulations spread over a long time reflect an attempt by the male to increase his confidence of genetic paternity. This

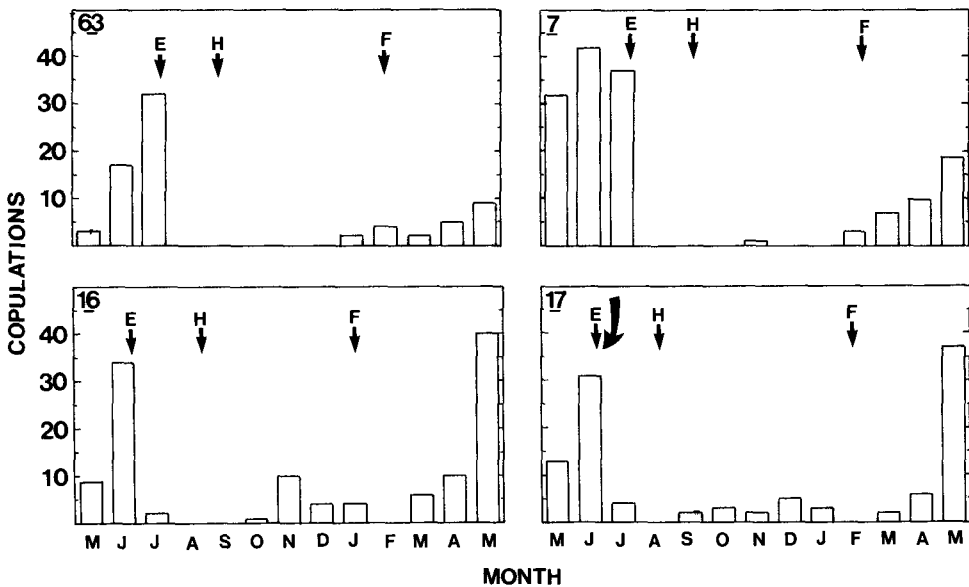


FIGURE 4. Monthly pattern of copulations at four nests where offspring were reared in 1981 and where eggs were laid again in 1982; E—egg laid, H—hatching, F—nestling's first flight. The timing of an EPC involving nest no. 17 male is indicated.

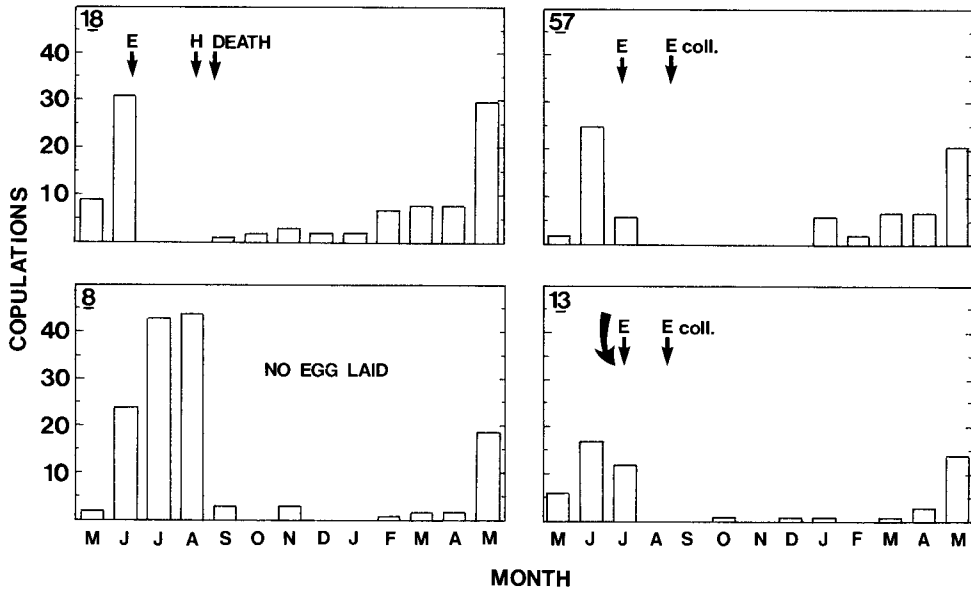


FIGURE 5. Monthly pattern of copulations at four nests where breeding failed in 1981 (E.coll. signifies egg collected by AR). At nest no. 8, no egg was laid in either year; eggs were laid at the other sites in June 1982. The timing of an EPC involving the nest no. 13 female is indicated.

is based on Trivers' (1972) suggestion that in species where the male contributes extensively to parental care it is important, in evolutionary terms, to the male that the egg is fertilized by his own sperm. Limiting copulations to the female's time of ovulation opens the possibility of her being inseminated prior to his efforts. For example, the UEPC of a mated female before egg-laying (nest 13, Fig. 5) probably occurred after insemination by her partner. Nonetheless, even in such cases an intruder may stand a good chance of siring progeny via a successful EPC; when competing inseminations in domestic hens were 4 hr apart, 80% of the progeny resulted from the second insemination (Compton et al. 1978). Studies of captive vultures could yield useful evidence on this aspect of sperm competition, by attempting to falsify this explanation. Across a range of species then, where the male's parental investment is substantial, one would expect increased behavior on the male's behalf to ensure his genetic paternity. Also, more copulations should occur, over a longer period, in colonial as opposed to solitary nesters, because coloniality effectively raises the female's chances of contact with other males (e.g., at communal roosts where EPCs were seen, Gladstone 1979). However, McKinney et al. (1984) caution that, due to the inherent difficulties in documenting EPCs in solitary nesters, it is probably too early to generalize about their distribution in birds of differing nesting dispersion.

Davies and Boersma (1984) consider the different benefits which males and females might derive from mating with more than one individual. Does the occurrence of EPCs influence the pair-bond in any way? For example, a female may be disadvantaged by an EPC if such behavior: (a) has the effect of diminishing some function of the pair-bond (e.g., male parental care) or (b) involves a poor quality cuckold. That most Cape Vulture EPCs appeared to be forced probably reflects the greater chances of benefit of EPCs to males; males certainly appear to initiate these FEPCs.

In conclusion, copulations in mated pairs of Cape Vultures occur in both fertilization and nonfertilization contexts, and this distinction should be borne in mind when considering explanations to account for the behavior. Further studies with captive birds may distinguish between

these proposals. For example, it would be of value to determine the ratio of successful inseminations per copulation, as well as the onset and duration of spermatogenesis and ovulation. Nonetheless, in the colonial breeding situation of Cape Vultures, it is likely that at least some prelaying copulations reflect the male's attempts to ensure his genetic paternity of the single egg clutch, given that other males in the colony will attempt EPCs where possible.

I thank A. F. Boshoff, P. J. Mundy and H.E.H. Paterson for criticizing the dissertation from which this article is drawn, and T. R. Birkhead, and especially, R. E. Simmons for comments on a draft. I greatly appreciate Andre Boshoff's help and encouragement throughout the study. Logistical and material support were provided by the Cape Department of Nature and Environmental Conservation, the Council for Scientific and Industrial Research, the University of the Witwatersrand, and my mother Mrs. M. B. Robertson.

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*The Condor* 88:539-542  
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## LONG-DISTANCE HOMING BY NONMIGRATORY DARK-EYED JUNCOS<sup>1</sup>

VAL NOLAN, JR., ELLEN D. KETTERSON, AND LICIA WOLF  
*Department of Biology, Indiana University, Bloomington, IN 47405*

*Key words: Homing; orientation; navigation; junco; nonmigratory birds.*

In wild birds, as opposed to homing pigeons (*Columba livia*), convincing evidence of navigation, i.e., goal-oriented flight over unfamiliar territory, is rare (Able 1980). We here report instances of homing by Carolina Dark-eyed Juncos (*Junco hyemalis*) that seem likely to have involved navigation. Displaced males traversed distances that were great relative to the small size of the birds' lifetime home range. Furthermore, they did so at speeds inconsistent with the view that they simply searched until they came upon familiar cues and then homed over terrain known from previous experience.

### MATERIALS AND METHODS

Studies were conducted from mid-May to mid-August in 1983 and 1984 at the University of Virginia's Mountain Lake Biological Station (near Pembroke, Virginia, 37°22'N, 80°32'W and approximately 1,158 m above sea level on Salt Pond Mountain). In 1983 we captured, displaced, and released five male juncos in the course of conducting an experiment unrelated to this report. Because some of these returned, we carried out a more structured displacement of males in 1984.

All subjects were mated and were captured at their nests on the day the eggs began to hatch or on the following day. All were banded with individually distinct combinations of color bands and with United States Fish and Wildlife Service numbered bands. The interval between capture and displacement (which was always immediately followed by release) varied, as shown in Table 1. Weights at the time of release were normal, as were other visible

indicators of physical condition. One junco (Bird F, Table 1) was equipped with a radio transmitter (Wildlife Materials, Carbondale, Illinois, weight 1.7 g) glued to its back (Raim 1978). Another (described both as Bird C and Bird H in Table 1) was displaced in both 1983 and 1984. No other individual was used twice. All distances referred to were calculated as rhumb lines, using air pilots' charts.

The birds were transported by automobile on days of fair weather. In 1983, some were placed in large, open, wire cages and others in individual, opaque, paper bags; in 1984, all were in individual, open, wire cages. During transport none could see other juncos, but, except for those in bags, no effort was made to deprive them of information en route.

Because returns were not anticipated in 1983, circumstances attending the releases, except those shown in Table 1, were not recorded. In 1984, three birds were driven for almost 4 hr on 7 June and let go one at a time (several min apart) at about 12:00 at the edge of a highway near Winchester, Kentucky. Each (including the one carrying the radio transmitter) flew into low, shrubby vegetation and disappeared. The remaining three were then driven for about another 4 hr on the same date to Bloomington, Indiana, and let go one at a time at 16:25 on the grounds of the aviary of Indiana University. There was no indication in either Kentucky or Indiana that the birds assembled after having been released.

### RESULTS

Two of three males released in Virginia in 1983 returned to their territories 9 and 16 days later, respectively. Other males had claimed these territories during their absences but quickly withdrew. The third (Male D, Table 1), which had been displaced a shorter distance than the others, was not seen again. All these birds had been transported in paper bags. Two additional males were displaced in a cage to Bloomington, Indiana, in 1983. One returned—in 1984 he occupied a territory adjacent to his former territory—

<sup>1</sup> Received 19 February 1986. Final acceptance 23 May 1986.