SHORT COMMUNICATIONS

SOCIAL ORGANIZATION OF A TRIO OF BEARDED VULTURES (*GYPAETUS BARBATUS*): SEXUAL AND PARENTAL ROLES

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KEY WORDS: *Bearded vulture*, Gypaetus barbatus; *cooperative polyandry*; *parental roles*; *homosexual matings*; *copulation behavior*, *Spain.*

In birds, cooperative polyandry (Oring 1986) is an unusual mating strategy. In raptors it only happens extensively in the Galápagos Hawk (*Buteo galapagoensis*) (Faaborg and Bednarz 1990), but polyandry has been described as occasionally occurring in some other species, that are usually considered monogamous (e.g., Tella 1993, Arroyo 1996).

The Bearded Vulture (*Gypaetus barbatus*) is a large, territorial vulture which nests on rocky cliffs in certain mountain areas of the southern Palearctic and of the Afrotropical regions (Hiraldo et al. 1979), and that feeds mainly on bones. The species is generally considered monogamous, but in the Pyrenees, polyandrous trios are relatively common (Heredia and Donázar 1990). The Pyrenees (Spanish and French sides) hold a small isolated population of Bearded Vultures which constitutes the bulk of the breeding population in the western Palearctic. In this population, the percentage of territories occupied by trios has increased gradually since 1979, when the first case was reported; 11.5% of 56 territories were recorded in 1988 (Heredia and Donázar 1990); and 15.2% of 92 were observed in 2000 (Heredia and Margalida 2001, M. Razin pers. comm.). These trios generally remain stable from one year to the next, but occasionally they may break up (pers. observ.). Trios tend to be observed in traditional breeding areas with the highest food availability, but their productivity is similar to that of monogamous pairs (Heredia and Donázar 1990). The factor explaining the existence of trios remains obscure, although it seems probable that the formation of such groups might be favored by a reduced availability of suitable sites for reproduction (Heredia and Donázar 1990).

Observing the Bearded Vulture is a difficult task, and this, coupled with its low reproductive success (Heredia and Margalida 2001), accounts for the little information

available on the structure in such formations. In addition, trios were not known until recently. The first observations carried out by Heredia and Donázar (1990) indicated that the two male members of a trio copulate with the female and that both males provide food for chicks. However, no detailed data are available to quantify the behavior and parental contribution of each individual in these groups.

In this paper, the copulatory behavior and sexual relationships in a Pyrenean Bearded Vulture trio are described in detail for the first time, and the individual investment of the three birds in parental activities are examined.

STUDY AREA AND METHODS

We conducted the present study in the Catalonian Pre-Pyrenees (northeastern Spain), between 1991 and 1992. This is an area with isolated calcareous massifs (maximum altitude of 2070 masl) and Mediterranean vegetation.

The trio studied was formed in 1986 after an adult bird joined the territory already occupied by a reproductive pair. No successful breeding occurred between 1986–89, after which this group first bred as a trio in 1990. The study site was visited in bouts of two consecutive days at 5-d intervals resulting in a total of 699 hr of observation distributed as follows: pre-laying period (October–December 1991) 212 hr; incubation (December 1991–February 1992) 101 hr; and nestling period (April–July 1991 and February–May 1992) with 253 and 133 hr, respectively. We made observations with spotting scopes from vantage points at a distance of about 300 m from the nests.

Birds were sexed using size criteria and based on differences noted in their parental activities. Females are slightly larger than males (Hiraldo et al. 1979) and tend to be more intensely colored (Negro et al. 1999). In this respect, the male that appeared to be subordinate (male B) was smaller and showed a paler ventral coloring compared to the other individuals (the female and male A). Males are more active than females in supplying material to the nest and in territorial defense behavior (Margalida and Bertran 2000a, Margalida and Bertran 2000b). The identification of the birds was based on comparison of the molt patterns and the individual markings and patterns on pectoral bands and crowns. The long molting

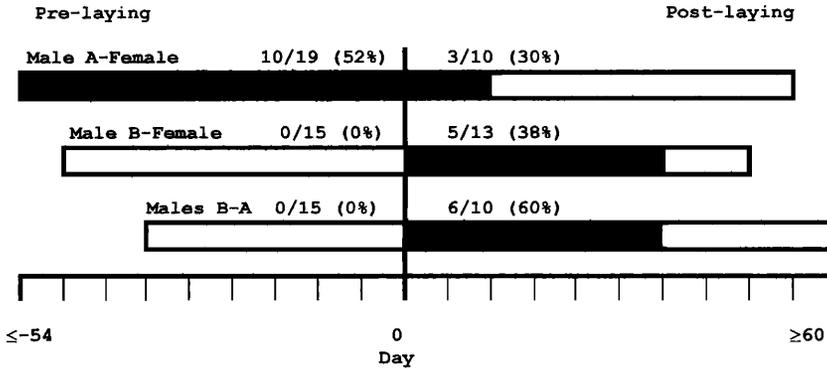[1] Corresponding author's e-mail address: margalida@gauss.entorno.es

Figure 1.   Temporal distribution of individual copulation behavior and success in a trio of Bearded Vultures in relation to the day on which incubation began (day 0). Shading indicates the time period during which behaviors were observed with probable contact of the cloaca; the proportions and percentage (in parentheses) of successful copulations are indicated.

process facilitated identification of the birds during much of the study period.

Bearded Vultures usually copulate on an exposed area of the cliff where they are nesting (Bertran and Margalida 1999). During the sexual activity period, all copulation attempts and related behavior were recorded. We noted the individuals involved in each copulation attempt and whether this was successful or not. A copulation was recorded as being successful behaviorally if cloacal contact was observed. We noted whether the female accepted or refused a copulation attempt. The relative frequency of copulations was estimated daily as the number of attempts hr^{-1}. The temporal distribution of copulations was examined in relation to the day on which incubation began (day 0). Laying was estimated with a maximum error of 5 d. Clutch size in this species is habitually two eggs, which are laid at intervals of 3–7 d, and incubation starts as soon as the first egg is laid (Hiraldo et al. 1979, Brown 1990, pers. observ.). We quantified the individual contribution to the following parental tasks: nest building, territorial defense, incubation, brooding, and feeding of the chick. We recorded prey deliveries, chases against conspecifics or birds from other species (principally Griffon Vultures [*Gyps fulvus*] and Common Ravens [*Corvus corax*], see Margalida and Bertran 2000a), and deliveries of nest material. Data were analyzed with nonparametric tests because data were not normally distributed (Sokal and Rohlf 1981). Values are presented as means ±SD.

RESULTS

The trio showed an extended copulation period (114 d). Similar to monogamous pairs (Bertran and Margalida 1999), the first copulation attempts were noted in November and continued until the early stages of chick rearing in March. We observed a total of 123 copulation attempts (including both successful and aborted ones). Of these, the female copulated with one of the males in 74% of cases, whereas in the remaining 26%, the two males copulated with one another (homosexual copulations).

During the pre-laying period, male A's copulation attempts with the female were more frequent than those of male B (male A: 0.33 ± 0.26, $N = 40$ copulation attempts h^{-1} vs. male B: 0.18 ± 0.21 copulation attempts h^{-1}, $N = 21$; Mann-Whitney U-test, $P = 0.047$). Most copulation attempts by male A (90%, $N = 40$) took place in the presence of male B, while male A witnessed male B's copulation attempts in 48% of the cases ($N = 21$; Fisher exact test, $P = 0.003$). During 25% of 16 cases in which male A tried to copulate with the female while sharing the same perch with male B, the latter interfered aggressively in the copulation attempt; although on only one occasion did he succeed in interfering with the attempt. In contrast, male A did not demonstrate any aggressiveness when he witnessed copulation attempts by male B. The response of the female to the sexual advances of the two males differed substantially. Male A obtained successful copulations from the early attempts (54 d before laying) and these continued until 12 d after egg-laying took place. Successful copulations by this male made up 52.6% and 30% during pre-laying and after egg-laying periods, respectively (Fig. 1). In contrast, the female did not accept most copulations initiated by male B during the pre-laying stage: the male was rejected in 15 of 21 copulation attempts. However, successful copulations by male B were observed around the onset of incubation, and these continued for 24 d longer than those of male A. Copulations between male B and the female were performed when male A was at the nest.

Both males displayed bisexual behavior, although the proportion of homosexual mounts attempted by male B was significantly greater (male B: 45.4% of 66 copulation attempts vs. male A: 3.5% of 57 copulation attempts; $\chi^2 = 25.82$, df $= 1$, $P < 0.001$). None of the observed attempts of homosexual mounts were forced or refused and 97% of these occurred in the presence of the female. On four occasions, male A was mounted immediately af-

Table 1. Frequency and percentage of territorial defense attacks by individual group members observed during pre-laying and post-laying periods.

INDIVIDUALS	PRE-LAYING ($N = 49$)	POST-LAYING ($N = 131$)
Male A	32 (63.3%)	43 (32.8%)*
Male B	3 (6.1%)	61 (46.6%)*
Female	14 (28.6%)	27 (20%)

* Significantly different ($P < 0.05$) in relation to preceding period based on Chi-square test.

ter male B tried to interrupt the former's mating attempt with the female. We observed only apparent cloacal contact (60% of cases, $N = 10$) when male B took the initiative for mating. Male B's behaviorally successful copulations obtained from male A and from the female occurred over the same chronological period (Fig. 1).

Significant differences were found in the material supplied to the nest in relation to the number of individual visits: male A and the female were mostly responsible for this task, delivering material during 67.6% and 58.5% of their 71 and 51 visits, respectively, as Male B only delivered nesting material during 21.4% of 17 visits ($\chi^2 = 14.09$, df = 2, $P < 0.001$).

We registered a total of 180 instances of territorial defense that took place between October 1991 and April 1992. The majority of the attacks (66.1%) were directed at Griffon Vultures (*Gyps fulvus*) and at Common Ravens (*Corvus corax*) (24.4%). The remainder (9.5%) were directed to other raptors and corvids. By periods, we detected significant differences related to contrasting territorial behavior shown by both males. In male A a higher than expected frequency of attacks was observed during the pre-laying period, contrary to that seen during post-laying. In contrast, male B increased his territorial behavior after laying took place ($P < 0.05$, for both cases; Table 1).

The daily investment of the three adults in relation to incubation of the clutch did not differ significantly (male A. 38.5 ± 22.7%; male B: 34.4 ± 22.3%; female: 27.1 ± 20.6%, Kruskal-Wallis $H = 1.85$, df = 2, $P = 0.397$). However, the amount of time invested by male B at the nest

during brooding was significantly less, both in 1991 (male A: 37.08 ± 18.14%; male B: 13.23 ± 14.36%; female 49.69 ± 20.68%; Kruskal-Wallis $H = 35.919$, df = 2, $P < 0.001$) and in 1992 (male A: 46.55 ± 14.25%; male B 19.73 ± 12.38%; female: 33.72 ± 14.96%; Kruskal-Wallis $H = 25.238$, df = 2, $P < 0.001$). The distribution of prey deliveries to the nest by the three individuals did not differ significantly from a theoretical distribution in which all individuals delivered the same number of items ($\chi^2 = 1.30$, df = 2, $P > 0.05$; Table 2). However, significant differences were obtained when comparing the frequency of feedings with that expected from the individual contributions ($\chi^2 = 14.97$, df = 2, $P < 0.001$; Table 2) with male B feeding the chick less than the other two individuals ($\chi^2 = 14.12$, df = 2, $P < 0.001$).

DISCUSSION

This first detailed record of behavior of a reproductive trio of Bearded Vultures suggests a social structure consisting of an alpha pair and a subordinate male. Levels of aggressiveness were not high between the two males in the trio. However, some conflicts associated with sexual activity were observed, and these were always initiated by the presumed subordinate male. Conflicts between the male birds were only recorded during heterosexual copulation attempts, and these were always initiated by the subordinate male. A remarkable aspect of our results is the tolerance shown by the alpha male, and the fact that he accepted a number of mountings by the subordinate male. A similar behavior has been noted in two other Pyrenean groups (Margalida et al. 1997, unpubl. data) In other cooperative breeders, homosexual behavior is seen as a means of appeasement that would increase cohesion within the group (Heg and van Treuren 1998).

Cooperative polyandry in the Bearded Vulture may not provide reproductive compensations in the short term, but may in the long term when overall survival is considered (Heredia and Donázar 1990). In a long-living species such as the Bearded Vulture, being in good condition would permit a greater number of breeding attempts. This species has a long breeding cycle, during which the adult birds are committed to providing food and to chick-rearing, while they also have to obtain food for themselves (Margalida and Bertran 2000a). Therefore, some direct benefit for breeding pairs should be

Table 2. Frequency and percentage of contributions of prey items delivered to the nest and feedings to the chick by individual group members.

INDIVIDUALS	PREY DELIVERIES ($N = 60$)	EXPECTED	FEEDINGS ($N = 108$)	EXPECTED
Male A	24 (40.0%)	20	49 (45.4%)	36
Male B	17 (28.3%)	20	13 (12.0%)	36
Female	19 (31.7%)	20	46 (42.6%)	36

expected from the collaboration of helpers, because searching for food, which is spatially and temporarily unpredictable, remains a difficult task. By remaining in a territory, subordinate males might have a possibility of acquiring an alpha breeding position within the group. By using a helper strategy, B males would be in a position to inherit the territory and the female. This would be particularly important for birds in pre-adult plumage at breeding age, if suitable breeding territories are not available (Heredia and Donázar 1990). Young birds might be capable of evaluating the individual quality of the different territories in the course of their dispersive movements (Bertran and Margalida 1996). Short-term direct benefits of the sexual relationship with the male birds seem more obvious for the females. This hypothesis is based on the fact that during the pre-laying stage, the female only permitted successful copulations by male A, whose total contribution to the breeding effort was larger. Yet, at the time of egg-laying, the female apparently accepted the secondary male furtively, and this coincided chronologically with the latter's increased help contribution (principally territorial defense and provisioning of prey to the nest). In the Bearded Vulture, both sexes share parental duties, but females tend to participate more actively in the direct care of the offspring (Margalida and Bertran 2000a). Thus, polyandrous females may benefit from the males' investment: both males provide parental care and, consequently, the female has more time to fly around (see Birkhead 1998).

Female Bearded Vultures may, because of their larger size, actively refuse males in unwanted copulation attempts (pers. observ.). There may be a relationship between size, coloration, and dominance in this species. For instance, it has been suggested that coloring of the ventral area might act as a status signal (Negro et al. 1999). The coloring is acquired deliberately (Negro and Margalida 2000) and its intensity is directly related to the birds' age and probably to their status as well. Females, which are slightly larger than males and may be behaviorally dominant, show more intense coloring (Negro et al. 1999). In this trio, coloring intensity increased progressively from the secondary male (markedly paler) to the female. A probable relationship between social rank and coloring intensity was also observed among other vulture groups as well (Negro et al. 1999).

Our results suggest a defined hierarchical social rank within groups. In that context, females, due to their larger size and behavioral characteristics, would be able to exert social control within such groups. This would open new and interesting perspectives in the study of these social groups, which should be examined in larger samples.

RESUMEN.—El Quebrantahuesos (*Gypaetus barbatus*) ocasionalmente forma grupos cooperativos (tríos). Durante 1991 y 1992 examinamos la conducta reproductora de un trío Pirenaico (NE España). Nuestras observaciones indican que el grupo estuvo formado por una pareja alfa y un macho secundario. El trio exhibió un periodo inusualmente extenso de cópulas donde la hembra copuló preferentemente con el macho alfa, pero también aceptó aparentemente de forma furtiva al macho secundario, en concreto tras la puesta. Fueron observadas algunas cópulas macho-macho comportamentalmente exitosas, si bien el significado de éstas es desconocido. Nuestros resultados sugieren que la hembra pudo beneficiarse a través de las cópulas de la inversión parental suministrada por ambos machos. En este contexto, les hembras, debido a sus características físicas y comportamentales podrían ejercer un control social dentro de estos grupos.

[Traducción de los autores]

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GENETIC EVIDENCE OF ALLOPARENTAL CARE OF A FEMALE LESSER KESTREL IN AN ALIEN NEST

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Care of nondescendant young (alloparental care) is
relatively common in many bird species (Reidman 1982,
Skutch 1987). In most cases, alloparental behavior occurs
either when nonbreeding birds care for offspring that are
not their own or when reproductive adults adopt or feed
young that are not their own. Provisioning of food by
birds other than the parents is expected more frequently
in communal species because of the increased chance of
exposure of nonbreeding individuals to hungry nestlings
(Jamieson 1989) and also because of the chance of amal-
gamation of nestlings among contiguous nests (Cooper

and Miller 1992). In any case, alloparental care poses a
nonresolved question on its possible adaptive significance
(Jamieson 1989, 1991, White et al. 1991, Ligon and Sta-
cey 1991, Emlen et al. 1991).

The Lesser Kestrel (*Falco naumanni*) is a colonial fal-
coniform in which adoption has been reported (Donázar
et al. 1991). This behavior may occur at high frequencies
in certain populations when nest-site densities are manip-
ulated, and when nestlings are able to move to alien
nests, where they may benefit from alloparental feeding
(but see Tella et al. 1997). Adoptions like this could be
actively sought by nestlings in species in which adults
show no apparent ability to discriminate between their
own and alien young (Tella et al. 1997). In this colonial
species there has also been one case reported in which
two females mated polygynously with the same male and
laid eggs in one nest, though only one female attended
the mixed brood and provided alloparental care to the
unrelated young (Tella et al. 1996). In this paper, how-

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