Male-male mountings in polyandrous bearded vultures *Gypaetus barbatus*: an unusual behaviour in raptors

Joan Bertran and Antoni Margalida


Male-male mountings appear to be very common in polyandrous bearded vulture *Gypaetus barbatus* trios. We observed sexual activity in two trios that occupied the same territory in different years. We recorded a total of 167 copulation attempts. The percentage of male-male mountings recorded was 26.1 and 11.4%, in the period of 1991–1992 and 2000–2001, respectively, with respect to total, homo- and heterosexual matings. We conclude that homosexual interactions do not appear to be directly associated with intrasexual competition (i.e. hierarchical dominance, sperm competition). Rather, our results are more consistent with the idea that this behaviour can regulate the aggression of the males in these groups.

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Same-sex mounting has been described in a large number of bird species (Bagemihl 1999), but information on this type of behaviour among birds of prey in the wild is virtually non-existent. Studies on some bird species suggest that homosexual interactions express diverse forms of intrasexual competition. For example, in cattle egrets *Bubulcus ibis* and tree swallows *Tachycineta bicolor*, male-male mountings seem to be directed towards establishing hierarchical dominance (Fujiooka and Yamagishi 1981, Lombardo et al. 1994). Alternatively, in the pukeko *Porphyrio porphyrio* mounts between males (Jamieson and Craig 1987) have been interpreted as subtle forms of sperm competition. Birkhead and Møller (1992) suggested that during some homosexual interactions, dominant males solicited copulation from subordinate males in order to cause them to waste their ejaculates. Finally, homosexual mounts between polygynous females of oystercatcher *Haematopus ostralegus* are also viewed as a behaviour aimed at reconciling two opponents after intrasexual conflicts (Heg and van Treuren 1998).

Here we describe homosexual interactions between polyandrous males of bearded vulture *Gypaetus barbatus*. This is a large bone-eating vulture, which breeds in mountainous areas of the southern Palearctic and Afro-tropical region (Hiraldo et al. 1979). In nearly all of their breeding range they are socially monogamous, but in the Pyrenees polyandrous trios are relatively common (Heredia and Donázar 1990). In the Pyrenees, bearded vultures defend a small breeding site (an area of 300 m around the nest site, Hiraldo et al. 1979) and engage in copulations over a long period (Bertran and Margalida 1999), usually from early November until the laying of the first egg (December—February). The clutch generally consists of two eggs, but only one chick survives (Margalida et al. 2003). Both sexes participate in breeding activities in a similar way, although males play a more active part in nest-building and territorial defence, whilst tending the nest is more pronounced in females (Margalida and Bertran 2000a, b).

Male-male mountings or copulation attempts (some of which resulted in cloacal contact in the same way as male-female copulation) were recorded as a regular phenomenon in those polyandrous groups that were monitored systematically (Margalida et al. 1997, Bertran and Margalida 2002). The social organisation of bearded vulture trios has not been well documented. Earlier observations suggest that males involved in the trios contributed to caring for the young, but the idea that one of them was dominant over the other in the...
matings was not discarded (Donázar 1991). In this respect, the first detailed behavioural data obtained in the territory studied here seem to indicate a defined social rank consisting of an alpha male which is distinguished because he provides most of the parental care, and a second male that is operationally subordinate (Bertran and Margalida 2002). Preliminary observations revealed that some of the mountings between the males were not forced or rejected, although in some cases they happened after conflicts related to heterosexual matings (Bertran and Margalida 2002).

In this paper we describe homosexual interactions between males, which occurred in two polyandrous trios, in order to evaluate this behaviour in a context of male-male competition, dominance assertion, sperm competition and avoidance of aggression.

Methods
The study population
The Pyrenees contain 101 breeding bearded vulture territories 16 of which are occupied by polyandrous trios (R. Heredia and M. Razin pers. comm.). The bearded vulture population is distributed throughout the Pyrenees but is denser in the central Pyrenees (Donázar et al. 1993). 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). We carried out fieldwork in a territory located in the central pre-Pyrenees in Catalonia, north-eastern Spain. In this territory, a trio was formed for the first time in 1986 after an adult bird joined the territory already occupied by a reproductive pair. No successful breeding occurred between 1986–89, and this group first bred as a trio in 1990 (Bertran and Margalida 2002).

Data collection
We collected data during the periods of copulatory activity in two breeding seasons: November 1991–April 1992 and November 2000–January 2001. In the breeding season 1991–1992, the birds that made up the first trio all displayed adult plumage (bearded vultures acquire their adult plumage at the age of 7 years, Hiraldo et al. 1979). During the period 2000–2001, we observed that at least two birds seemed to have been replaced, thus forming a new group. So, the study is based on two trios whose memberships differed although they occupied the same site in widely separated periods. The new birds were a female and a beta male, both adults. The female was considered new because she showed a conspicuous pectoral band that was absent in the female studied in 1991–1992, and also because her laying phenology was significantly delayed (2–3 weeks) compared to the previous female. Laying data vary little from year to year in this species (average ±4 days, Margalida et al. 2003), which suggest that such a big difference is due to a change of female. The beta male of 2000–2001 could be identified conclusively as new because it was marked with a yellow PVC ring which was absent in the former beta male. The PVC ring was detected using a video camera installed in the nest. This male was marked at a nest in the neighbouring region of Aragón (> 75 km from the study area) between 1989 and 1990 (R. Heredia pers. comm.). The birds were sexed on the basis of size and by observing copulations. Females of this species are slightly larger than males (Hiraldo et al. 1979) and in our case the females involved in both trios showed clear differences in body size. The positions adopted during mounting indicated the sex of the birds involved and reverse mountings (female-male) have not been recorded in this species (see Brown 1990, Bertran and Margalida 1999). The birds were identified by specific plumage patterns. Social rank of the males was established with regard to sexual and parental roles, the alpha male having more sexual interactions with the female and providing most of the parental care. In addition, beta males displayed a paler ventral colouring in comparison to the other individuals and in this context a probable relationship between social rank and colouring intensity has been suggested by Negro et al. (1999). The roles of the alpha and beta males involved in each of the trios remained stable in both breeding seasons. In each case, the alpha male that achieved the highest number of copulations with the female contributed more in all the parental activities, whilst the beta male was barely involved at all in the direct care of the offspring, although he did bring an equal number of prey items to the nests (for more details, see Bertran and Margalida 2002).

We collected 399 h of observations during the two periods of copulatory activity (273 h in 1991–1992 and 126 h in 2000–2001). Observations were made with binoculars and 20–60 × telescopes, from a high point 300 m from the nest site. Bearded vultures usually copulate on conspicuous perching sites on the cliff where they are nesting (Bertran and Margalida 1999). We recorded all the homosexual and heterosexual copulation attempts that occurred. Whenever possible, we recorded whether the copulatory attempts observed were successful or not. We considered them behaviourally successful if they ended in cloacal contact (Birkhead and Møller 1992). We also noted the participating individuals, the soliciting individual (we assumed that the bird interested in copulating was the one that approached the other bird 5 min before their sexual interaction), the duration of successful copulations and rejected copulation attempts (we only recorded the rejections that were obvious, when the bird mounting was expelled aggressively by the bird being mounted).
We quantified allopreening behaviour (Cramp and Simmons 1980) during a time of 10 min as the sum of the 5 min before and 5 min after copulation attempts, in order to assess possible appeasement behaviour. Values are presented as means ± SD.

**Results**

We observed a total of 167 copulation attempts at the nesting site. The average percentage of male-male mountings in the two copulatory periods was 18.75% ± 7.35%. The proportion of homosexual mountings did not differ significantly between the period 1991–1992 (32 out of 123, 26.1%) and the period 2000–2001 (5 out of 44, 11.4%; \( \chi^2 = 3.23, df = 1, P = 0.072 \)). We observed apparent cloacal contact during some homosexual mountings. No significant difference was observed in the proportion between successful homosexual and heterosexual copulations (homosexual: 10 out of 32 observations, 31.3% vs. heterosexual: 39 out of 89 observations, 43.8%; \( \chi^2 = 3.65, df = 1, P = 0.054 \)). We did not observe high aggression levels in the males involved in any of the trios. However, the beta males occasionally attempted to interrupt the alpha male’s copulations. In the 1991–1992 period, the alpha male was mounted immediately after the beta male started allopreening the mounting male (16 of 20 cases, 80%; Fisher exact test, \( P = 0.001 \)).

In the case of heterosexual matings, in which allopreening was started by the male in 16 of 20 cases (80%; Fisher exact test, \( P < 0.001 \)).

The roles of male birds in homosexual copulation attempts were substantially opposed. In the 1991–1992 period, the alpha male was mounted by the beta male in 93.8% of the cases. In contrast, during the 2000–2001 period, the alpha male carried out 80% of the mountings (Fisher exact test, \( P < 0.001 \), Table 1). The males that carried out the highest number of homosexual mountings in each period tended to obtain a larger number of attempts with apparent cloacal contact, although sample size for this behaviour was more limited (n = 32, Table 1). In contrast, the sexual roles of the males in the heterosexual mating remained constant throughout the periods. The alpha male made more copulation attempts than the beta male in both breeding seasons (60.4%, 1991–1992 and 84.6%, 2000–2001), although the proportion of successful copulatory attempts by the alpha male was significantly higher in 2000–2001 (44.8%, 1991–1992 vs. 74.1%, 2000–2001; Fisher exact test, \( P = 0.025 \), Table 1). Altogether, 91.9% of male-male copulatory attempts took place while the female was present at the nesting site (the females spent 45.6% of their time in the nesting areas; range: 31.6–53.5%, n = 2). We did not observe high aggression levels in the males involved in any of the trios. However, the beta males occasionally attempted to interrupt the alpha couple’s copulations (four observed cases in each period). On four occasions (1991–1992 period), the alpha male was mounted immediately after the beta male had tried to interrupt the former’s mating attempt with the female. In the remaining cases, their mounts occurred sporadically, with no apparent associated cause.

**Discussion**

In spite of that the work was based only in two trios, some conclusions can be derived from the observations.

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**Table 1. Number of homosexual and heterosexual mountings and proportion of successful copulations observed, and the number and identity of birds involved during the two study periods.**

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<td>Copulation attempts (n)</td>
<td>Proportion successful copulations</td>
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<td>Homosexual matings</td>
<td></td>
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<tr>
<td>MA-MB(^1)</td>
<td>2</td>
<td>0/2</td>
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<tr>
<td>MB-MA(^1)</td>
<td>30</td>
<td>6/25</td>
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<tr>
<td>Heterosexual matings</td>
<td></td>
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<tr>
<td>MA-F(^1)</td>
<td>55</td>
<td>13/29</td>
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<tr>
<td>MB-F(^1)</td>
<td>36</td>
<td>5/28</td>
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\(^1\): MA: male alpha; MB: male beta; F: female
made. For example, we can eliminate a priori that the homosexual interactions between bearded vulture males reflect aggressive or subtle forms of male-male competition (dominance and sperm competition). Same-sex mountings are seen in many social mammals and also in certain birds (Wagner 1996) as an aggressive dominance display and the usual interpretation of this behaviour is that the dominant individuals mount the subordinate ones and thus establish the social order (see Holhmann and Fruth 2000). In contrast, our results show that the directionality of homosexual mountings varies from one dyad of males to another. Moreover, this supposition is not backed up by the fact that 83.8% of the total homosexual mounts observed were carried out by operationally subordinate males.

Homosexual interactions can be seen as an adaptive behaviour directed towards making the opponent male pay a high cost for ejaculations (Dewsbury 1982, Birkhead and Møller 1992). However, if this was the case, we would expect there to be a high frequency of copulation requests (by the receiving male). However, the frequency of copulation requests by the males that mounted in homosexual matings (54%) was similar to that of the males who were mounted (46%). In addition, the significantly shorter duration of the homosexual mountings with apparent cloacal contact in comparison to heterosexual ones, leads one to question whether sperm is transferred in homosexual interactions.

Instead, our data can more probably be interpreted in a context of specific aggression regulation. An examination of this behaviour suggests that it contains elements of aggression and appeasement. For example, our results show that allopreening behaviour was significantly more frequent in homosexual than in heterosexual matings. Besides, contrary to the case of heterosexual matings in which allopreening is normally initiated by the male (Brown 1990), allopreening in homosexual matings was started more often by the bird that was mounted. Allopreening in birds often serves the function of inhibiting aggressive behaviour (Wilson 1975). Our results suggest similarities to the data collected on polygynous oystercatcher females that stop some aggressive interactions by allopreening and by mounting each other (Heg and van Treuren 1998). However, aggressive encounters are apparently not frequent in polyandrous bearded vulture males (Heredia and Donáz 1990, Bertran and Margalida 2002). Although the conflicts between males are obvious (in contrast with other cooperative breeders, e.g. Eason and Sherman 1995, the beta males attempt to interfere with some alpha couples’ copulations), our results reveal that only 10.8% of the homosexual interactions were preceded by agonistic encounters. One possible explanation for this is that both the directionality of the male-male mountings and the frequency with which they occur are associated with peculiar aggressive characteristcs in each male. Similarly, in the ostrich Struthio camelus australis it was suggested that homosexual displays by male birds constituted a form of suppressing or blocking aggression among them (Sauer 1972). Studies on primates provide examples of homosexual interactions that substitute or inhibit the aggression not associated with previous agonistic encounters (Holhmann and Fruth 2000).

Acknowledgements – B. Arroyo, X. Bellés, H. Källander, J.J. Negro, R. Wagner and an anonymous reviewer improved the manuscript. Sheila Hardie translated the text into English. This study was supported by the Departament de Medi Ambient of the Generalitat de Catalunya and Ministerio de Medio Ambiente.

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(Received 4 March 2002, revised 14 January 2003, accepted 3 February 2003.)