

Breeding behaviour of the Bearded Vulture *Gypaetus barbatus*: minimal sexual differences in parental activities

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Monogamous biparental care is expected to occur when opportunities for extra-pair copulations are rare, and both parents are required to raise the chick. Bearded Vultures *Gypaetus barbatus* fulfill these conditions. Contributions by male and female Bearded Vulture to nest building, nest defence, incubation, nest attendance and chick feeding were studied over five years in eight pairs from the Pyrenees (Catalonia, northeast Spain). Overall, the sexes show equal investment, although the degree of parental effort developed differs depending on the specific activities. During pre-laying, males were significantly more active than females in supplying material to the nest and in territorial defence behaviour, which increased (in both sexes) as the season advanced. Incubation was shared equally both by day and by night. During chick-rearing, the nest was attended by both sexes and the presence of both parents at the nest decreased in parallel with the growth of the chick. Activities related to chick feeding were also equally divided. These results are discussed in the context of female selection of mates and the particular ecology of this species.

In general, the degree of investment by each parent differs considerably between social mating systems such as monogamy, polygyny and polyandry (Clutton-Brock 1991). Biparental monogamous care occurs in a large number of bird species (Lack 1968), although the degree of investment in the parental activities may vary between sexes and species (Clutton-Brock 1991). In monogamous birds, the roles of males and females are generally divided between specific activities. For example, while males are more active in territorial defence, females are more directly concerned with care of the offspring (Clutton-Brock 1991). Nevertheless, parental obligations are subject to selective and ecological pressures such as the conflict of interests between sexes and the availability of food (Trivers, 1972, Emlen & Oring 1977, Westneat *et al.* 1990). Monogamy with biparental care is predicted to occur when the opportunities for additional matings are scarce and when extensive care by males and females is necessary for successful rearing (Alexander & Borgia 1979). The vultures (order Falconiformes) are suitable for examining some of these questions, despite being difficult birds to observe. They are monogamous birds which pair for a long period, generally produce a single

chick which takes a long time to grow (Cramp & Simmons 1980) and their feeding habits seem to require the participation of both sexes in the rearing of the offspring (Newton 1979, Mundy *et al.* 1992).

The Bearded Vulture *Gypaetus barbatus* is a large osteophagous vulture which inhabits mountain areas of the southern Palearctic and the Afrotropical region (Hiraldo *et al.* 1979). It is sexually monomorphic, monogamous and territorial, nests on large rocky outcrops, and rears a single chick each year (Hiraldo *et al.* 1979, but see Barrau *et al.* 1997). The Bearded Vulture feeds chiefly on the bones of medium sized ungulates (Hiraldo *et al.* 1979, Brown & Plug 1990, Heredia 1991a, Donazar 1993), which implies extensive searching (Brown 1990) and the complicated manipulation of a food (see Boudoint 1976) that is scarce and unpredictable. Concerning its reproductive biology, no detailed information exists on the relative contribution of the sexes during the breeding season, with the exception of data given by Brown (1990) for the African subspecies *G. b. meridionalis*. Although Brown (1990) gave information on the participation of males and females during the different phases of reproduction, no detailed quantification of the division of parental tasks has been presented. An in-depth study of the reproductive biology of the species is needed to develop actions based on objective criteria

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for the recovery and/or conservation of currently extinct or threatened European populations. A progressive decline in breeding performance has been observed in different European populations (Donazar 1993) and, although clutches of two eggs are generally laid (Frey *et al.* 1995, pers. obs.) with some exceptions (Hiraldo *et al.* 1979, Barrau *et al.* 1997), only one chick was ever seen. Although various factors may be involved in this decline (e.g. human disturbance, inter- and intraspecific interactions, breeding experience and weather conditions), the fact that only one chick is fledged might be related to the great investment this species has to dedicate to breeding.

Although a considerable research effort is currently being made with diverse approaches to improve the viability of reintroduction programmes that are being carried out in the Alps and in the south of Spain (e.g. Bustamante 1996, Mingozzi & Estève 1997, Negro & Torres 1999), no specific study of its breeding biology has been carried out.

The aim of this paper is: (1) to evaluate the contribution in terms of parental investment of Bearded Vulture males and females in the different parental activities developed during courtship and breeding, and (2) to describe aspects of the reproductive biology in relation to chick growth in the nest.

STUDY AREA AND METHODS

Fieldwork was undertaken between 1992–96 in the central Pyrenees (Catalonia, northeast Spain). The study area is 3750 km² and is characterized as being a zone with a high population density of Bearded Vultures (García *et al.* 1996) and abundant food supply (Margalida *et al.* 1997a). The average maximum and minimum temperatures within the study area do not rise above 30°C (July) or fall below –5°C (January), respectively. The average annual precipitation was more than 800 mm, with 78 days of precipitation annually which falls mainly as snow between December and February (Bertran & Margalida 1996). The weather conditions and the availability of food varied little throughout the entire study period. The average altitude of the nests is 1482 m asl (range 700–2100 m) and the average distance between nests of neighbouring pairs is 10.4 km. The Griffon Vulture *Gyps fulvus*, the Golden Eagle *Aquila chrysaetos* and the Raven *Corvus corax* stand out as the most abundant species with which the Bearded Vulture shares its territory or which nest close to its nesting areas. These species compete with the Bearded Vulture for nest-sites (Fernández & Donazar 1991, Margalida &

García 1999) and occasionally for food (Bertran & Margalida 1997).

The monitoring of pairs began in September of each year, coinciding with the first signs of nest-building activity, and ended when the chick fledged. Fledging occurs between June and August, since in the Pyrenees the timing of laying may vary between pairs by more than two months (Heredia 1991b). Eight pairs were studied during 2180 h distributed in the following ways. (1) Pre-laying was studied in five pairs for 647 h of observation spread over 121 field days. This period spans between three and four months prior to egg-laying (Bertran & Margalida 1999). (2) Incubation lasts from 53–58 days (Hiraldo *et al.* 1979) counted from the laying of the first egg (the clutch may be single or double) until hatching. During this period six pairs were studied for 298 h spread over 42 days. (3) The first flight of the young occurs between 106 and 130 days after hatching (Sunyer 1991). During this phase eight pairs were studied for 1235 h spread over 160 days. The observations include all the daylight hours (05:00–20:00 h, solar time), the shortest period of observation being 6 h and the longest 14 h ($x \pm sd = 8.6 \pm 1.5$ h).

Observations were made using 20–60× telescopes from vantage points which allowed for a good view of the nest (300–600 m). Because the species shows no obvious sexual dimorphism (Hiraldo *et al.* 1979), identification of the partners was based on the individual characteristics of their plumage in flight. Similarly, perched birds could be identified from peculiarities of the shapes of their pectoral bands and crowns (see Hiraldo *et al.* 1979, Margalida *et al.* 1997b). The sex of the birds studied was based on their positions during copulations (Bertran & Margalida 1999).

To examine the relative contributions of the sexes to nesting activities, we examined the following activities: (1) nest building and maintenance of the nest (five pairs), (2) defence of the nesting site (eight pairs), (3) attendance at the nest during incubation (six pairs) and rearing (eight pairs) and (4) provision of food (seven pairs) and feeding the chick (six pairs). For each member of the pair the absolute frequencies and time dedicated to each of the following parental behaviours was noted: (a) attention to the clutch and chick (percentage of time during which each sex remains at the nest) and (b) average time (min) and frequency (number of episodes/h) of feeds. The time of feeds also includes the time for manipulation and preparation of the remains, given that these are worked at intermittently. Likewise, we measured the absolute frequencies of nest defence attacks (chases of, and fights in flight

with, conspecifics and other species to expel them from the vicinity of the nest), and the frequency of visits by adults to the nest and their purpose, including the provision of material, relief during incubation and delivery of prey items. The night-time presence at the nests (six pairs during incubation and eight during rearing) was estimated from watches carried out at dusk and dawn. To examine the differences in the patterns of attention of both sexes in relation to the phase of incubation and age of the chick, the incubation and chick-rearing periods were subdivided into periods of four and eight fortnights, respectively.

Non-parametric tests were used in the statistical treatment of most data, although the *t*-test and analysis of variance (ANOVA) were used when data were normally distributed. Where results from ANOVA were significant, a posteriori testing involved the use of the Scheffe's test ($P < 0.05$) to identify inter-group differences (Sokal & Rohlf 1981). Values are presented as means $\pm$ sd.

RESULTS

Nest building

We observed the provision of material to five nests on 134 occasions, of which 27 (20%) took place after laying. The material selected for the construction of the nest consisted of branches and wool which were transported with the talons and bill. Males provided material on 97 occasions (72%), as against 37 (28%) in the case of females. During the pre-laying period the contribution of the males in each of the pairs studied was significantly greater than that of the females (males: $77 \pm 11.1\%$, females: $23 \pm 11.1\%$; Mann-Whitney $U = 25$, $P < 0.001$, $n = 5$).

Nest defence

A total of 272 interspecific and intraspecific territorial defence attacks was observed, of which $67 \pm 23.4\%$ were carried out by males (range 22–100%) and $33 \pm 23.4\%$ by females (range 0–78%, Mann-Whitney $U = 52$, $P = 0.036$, $n = 8$). In seven of the eight pairs studied the males defended the nest more actively than the females. Over the three nesting periods considered, pre-laying accounted for most of the difference between sexes in the frequency of attacks on intruders ($\chi^2_2 = 7.64$, $P < 0.02$; Table 1). This was the period during which males were significantly more aggressive than females.

The frequency of territorial attacks by both sexes

increased as the nesting cycle progressed and was highest in periods 2 and 3 (males: Kruskal-Wallis $H_2 = 6.46$, $P < 0.05$; females: Kruskal-Wallis $H_2 = 19.38$, $P < 0.001$).

Nest attendance

Incubation

During this period, males and females cover the clutch continuously and the mean interruption time in four pairs was 2.32 ± 0.6 min. The total percentage interruption was $5.6 \pm 0.7\%$ ($n = 4$). The main interruptions were related to changeovers, turning the eggs and preening or arranging the nest, while abandonment of the nest was rare (Margalida *et al.* 1997c). Both sexes contributed to daytime incubation tasks, without any significant difference between the sexes (males: $48 \pm 6.6\%$; range: 35–57%; females: $52 \pm 6.6\%$; range: 43–65%; $t_6 = -0.64$, ns). Although males increased their share of incubation as hatching approached ($47 \pm 11.1\%$ during the first fortnight to $55 \pm 12.1\%$ during the fourth), this trend was not significant (Spearman rank correlation $\rho_6 = 0.22$, ns).

The mean time dedicated to incubating the eggs (excluding the first and last relief each day) was similar in both sexes ($t_6 = -0.47$, ns). Males remained on average 177 ± 64.3 min (range 23–504 min) and females 183 ± 80 min (range 59–550 min). The maximum frequency of nest changeovers took place during the middle of the day (Fig. 1), being highest for males from 11:00–12:59 h and for females from 17:00–18:59 h. On average, a change of relief took place every 3.9 h (64 changes in 249.5 h) which means that (assuming 11 h daily activity) 2.8 changes take place per day.

Brooding

Figure 2 shows the pattern of daily attendance at the nest throughout the chick-rearing period. The nests were attended continuously by either sex during the

Table 1. Variation in the frequency of territorial defence (in brackets the number of attacks/hour) by male and female Bearded Vultures ($n = 8$) throughout the breeding season.

	Male	Female
Pre-laying	41 (0.058)	8 (0.011)
Incubation	24 (0.059)	13 (0.032)
Post-laying	117 (0.080)	69 (0.047)
Total	182	90

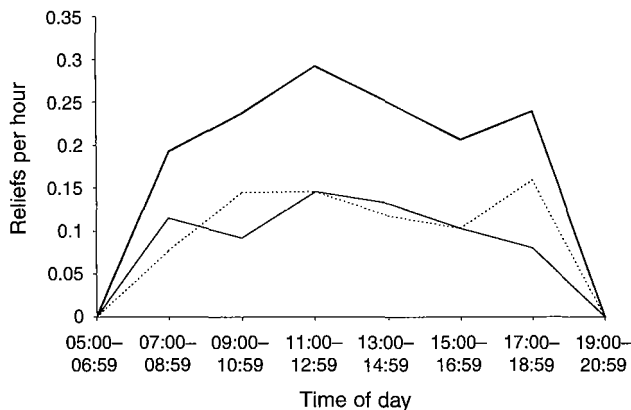


Figure 1. Daytime pattern of reliefs during incubation in the Bearded Vulture ($n = 6$). —, Male; , female; ———, total.

first (males: $52 \pm 10.8\%$; females: $48 \pm 10.7\%$, $n = 8$) and second fortnights (males: $51 \pm 7.4\%$; females: $47 \pm 9.9\%$) after hatching. The presence of males and females decreased progressively from the third and fifth fortnights, respectively. The marked fall off in attendance to the nest by both parents took place during the sixth fortnight in the case of males ($11 \pm 6.1\%$) and the seventh in females ($14 \pm 6.8\%$) (Fig. 2). The amount of time per fortnight invested by each sex in attending the nest was related to the age of the chick (males: ANOVA, $F_{7,63} = 30.64$, $P < 0.001$; females: ANOVA $F_{7,63} = 10.37$, $P < 0.001$, arcsin-transformed data). In males, significant differences were found between the first four fortnights and the last three, while in females there were differences between the first three and the last two fortnights ($P < 0.05$, Scheffé test). Overall, females spent a higher proportion of time attending chicks than males, although the difference was not significant (males: $29 \pm 2.4\%$, females:

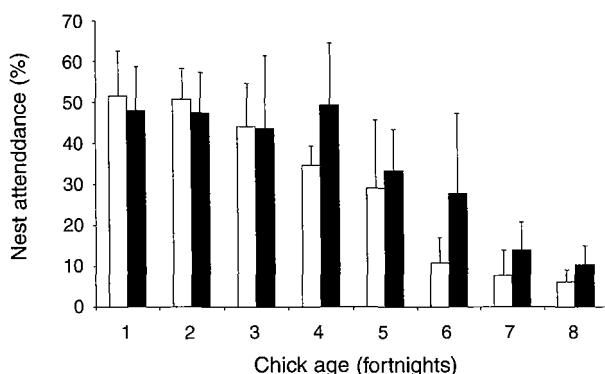


Figure 2. Nest attendance by Bearded Vultures ($n = 8$) throughout the chick-rearing period after hatching of the first egg. □, Male; ■, female. The bars indicate ± 1 sd.

$33 \pm 8.6\%$; $t_8 = -1.35$, ns).

The time the chick remained alone was positively correlated with age ($\rho_8 = 0.88$, $P < 0.01$; Fig. 3), reaching a maximum during the eighth fortnight ($84 \pm 4.8\%$).

Night-time attendance

Both sexes may spend the night at the nest covering the clutch (12 nights for males and 18 for females) and during chick-rearing (12 nights for males and 37 for females), although females spent significantly more time at the nest than males during chick-rearing than would be expected by chance (incubation: $\chi^2_1 = 0.27$, ns, $n = 6$; rearing: $\chi^2_1 = 5.77$, $P < 0.02$, $n = 8$).

Chick feeding

Provision of food

We observed a total of 214 provisions of food to the nest. Prey items were usually transported to the nest using the talons (88%), although some small-sized lightweight remains were transported in the bill (12%). Both sexes carried food (males: $48.8 \pm 16.1\%$, range: 25.7–77.8%; females: $51.2 \pm 16.1\%$, range: 22.2–74.3%, $t_7 = -2.52$, ns). Although both sexes carried food to the chick and no significant difference in the daily rate of provision was observed (males: 0.16 ± 0.04 prey items/h; females: 0.13 ± 0.02 prey items/h, $t_7 = 1.21$, ns), variation was found between pairs ($\chi^2_6 = 23.4$, $P < 0.001$). In males, the maximum frequency in the provision of prey took place during the third fortnight (0.18 ± 0.07 prey items/h) and during the seventh fortnight in females (0.16 ± 0.02 prey items/h), and no temporal variation was observed in this frequency with regard to the age of the chick (males: ANOVA $F_{7,55} = 0.32$, ns; females: ANOVA $F_{7,55} =$

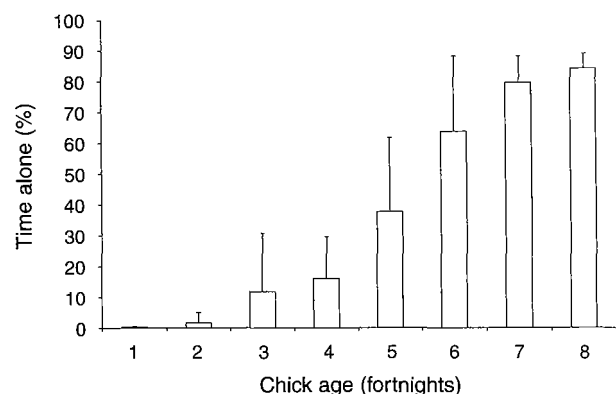


Figure 3. Temporal variation in the percentage of daytime when the chick remained alone ($n = 8$). The bars indicate ± 1 sd.

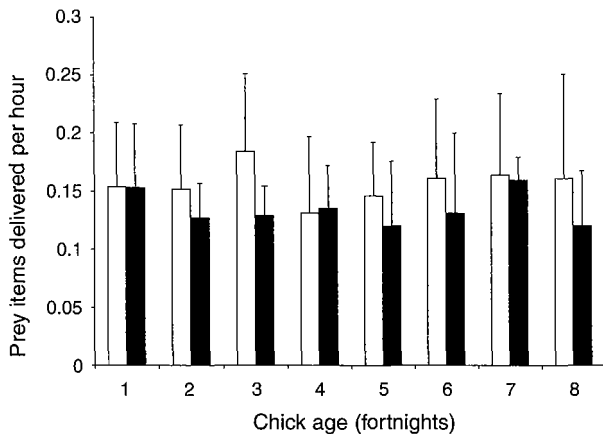


Figure 4. Pattern of delivery rates of prey items by Bearded Vultures ($n = 7$) throughout the chick-rearing period. □, Male; ■, female. The bars indicate ± 1 sd.

0.83, ns; Fig. 4). Figure 5 shows the daily rhythm of delivery of prey items undertaken by each sex, with a maximum peak for both males and females between 09:00–11:00 h. No significant differences between the sexes were found in the daily pattern of provision ($\chi^2_7 = 3.85$, ns).

Feeding duration and frequency

Of 427 feeding events registered, on no occasion was regurgitation observed as a method of feeding the chick. The prey items brought to the nest were prepared and broken to facilitate their ingestion by the chick. The average duration of chick feeding was similar in both sexes (males: 19 ± 2.4 min; females: 19 ± 2.6 min), with no significant difference in the time invested by each of them ($t_6 = -2.13$, ns, Fig. 6).

The duration of feeding by males and females was related to the age of the chick (males: ANOVA $F_{7,47} =$

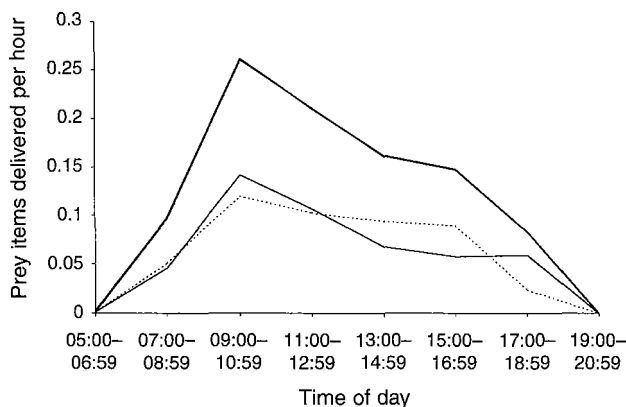


Figure 5. Daily pattern of delivery rates of prey items to the nest by Bearded Vultures ($n = 7$). —, Male; , female; — — —, total.

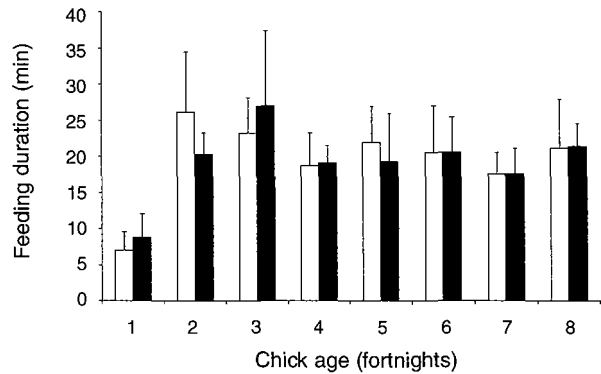


Figure 6. Temporal variation in time spent feeding chicks by Bearded Vultures ($n = 6$) during the chick-rearing period. □, Male; ■, female. The bars indicate ± 1 sd.

5.31, $P < 0.001$; females: ANOVA $F_{7,47} = 4.61$, $P < 0.001$). The mean feeding time in the first fortnight (males: 7 ± 2.6 min; females: 9 ± 3.3 min) was significantly shorter ($P < 0.05$, Scheffé test) than during the remaining fortnights.

The mean number of feedings/h was 0.23 ± 0.02 in males and 0.27 ± 0.05 in females and there was no significant difference in the mean frequency of feeding carried out by each sex ($t_6 = -1.33$, ns; Fig. 7). The temporal pattern showed how the maximum frequency of feeding by males and females took place during the fourth fortnight (males: 0.35 ± 0.2 feedings/h; females: 0.34 ± 0.12 feedings/h). The frequency of feeding increased progressively in both sexes up until the fourth fortnight and decreased from the fifth fortnight onwards, the drop being significant in the case of males (ANOVA $F_{7,47} = 2.59$, $P < 0.04$) but not for females (ANOVA $F_{7,47} = 1.94$, $P > 0.05$). There was no correlation between the duration and frequency of feeding invested by males ($\rho_8 = 0.09$, ns)

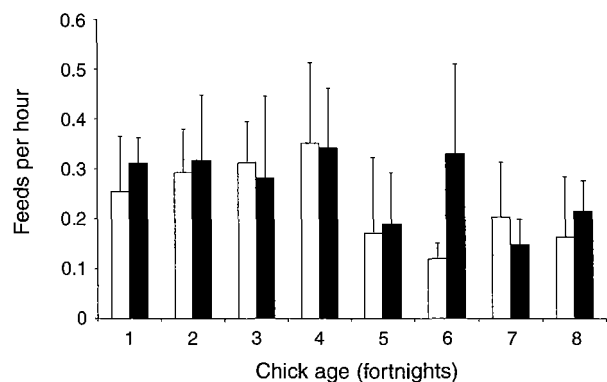


Figure 7. Frequency of chick-feeding by Bearded Vultures ($n = 6$) in relation to the age of the chick. □, Male; ■, female. The bars indicate ± 1 sd.

and females ($p_8 = 0.05$, ns) during the growth of the chick.

DISCUSSION

Pre-laying

During this phase, the principal activities undertaken by Bearded Vultures within their territory are those related to nest building, territorial defence and sexual activity, and as occurs generally in raptors, they took place mainly during the morning (Newton 1979). It is during the pre-laying period that the sexes differ most in their contribution, the male contribution being significantly greater. Nest-building activity took place throughout three to four months prior to laying, a much longer interval than has been described in other vultures, which generally begin this activity two to three weeks prior to laying (Mendelssohn & Leshem 1983, Mundy *et al.* 1992). In parallel with nest-building, the pairs defended the immediate area around the chosen nesting site. In both activities, males were significantly more active, which might reflect a demonstration of their reproductive ability (mate selection by females; Wiklund 1990, Andersson 1994) given the considerable energetic cost which these activities represent. For example, the supply of material to the nest has been associated in some species with sexual activity (copulation success; Tortosa & Redondo 1992), which in the Bearded Vulture lasts for a long time prior to laying (68 days; Bertran & Margalida 1999).

As has been suggested for other species, the lower contribution of the females to these activities might be related to avoiding an excessive drain on energy reserves, which would reduce their physical condition below that necessary for egg formation (Pierotti 1981), and may influence the decision to reproduce (Chastel *et al.* 1995). This greater activity by males could also be related to the relative costs and benefits of parental investment. In this regard, the costs to the male of not helping with the construction of the nest would outweigh the benefits, since the female is compromised by the energy demands of egg production. The absence of courtship feeding in the Bearded Vulture (Bertran & Margalida 1999) means that this source of additional energy, which can be important for the nutritional improvement of the female during egg formation is absent (Nisbet 1973, Lundberg 1980). Thus male effort in nest building and defence may be of great importance to the female. For example, the most evident function of mate-feeding in the Lesser Kestrel

Falco naumanni seems to be to increase the female's body mass, possibly to allow the laying of earlier and larger clutches (Donazar *et al.* 1991). Similarly, the greater contribution of males in territorial defence might be related to sexual competition (Burger 1981). This is suggested by the seasonal pattern of conspecific occurrence near nests, which during this phase coincides with a greater frequency of visits of individuals of reproductive age (Bertran & Margalida 1996). As such, males may increase their confidence of paternity by mate guarding, although attempts at extra-pair copulation seem to be scarce in this species (Bertran & Margalida 1999).

Post-laying

Nest defence

After laying, there was a progressive increase in the levels of territorial defence behaviour in both sexes, although this was much more pronounced in females. Although this behaviour could be related to a greater presence of the females at the nest or in the territory, it suggests that females increase their investment to protect their offspring once laying has been completed. The increased effort in territorial defence after laying is therefore consistent with the hypothesis that the larger the parental investment accumulated, the larger will be the defensive effort shown (Trivers 1972, Andersson *et al.* 1980). On the other hand, the increase in interference resulting from the increase in this species' population might have resulted in the decrease in breeding success (García *et al.* 1996).

Incubation

Males and females cover the clutch continuously during the day to protect it (Brown 1990, Margalida *et al.* 1997c). During daytime incubation, both sexes attended the clutch in equal proportion. At night, the participation of the males was also confirmed, a result which differs from that obtained by Brown (1990) but which coincides with observations made on captive pairs (Frey *et al.* 1995). Biparental incubation may be necessary in the Bearded Vulture because the difficulty which the search for a spatially and temporally unpredictable food represents. This fact makes it impossible for a single adult to look after the task of incubation given that continuous incubation by one parent may be costly (Brunton 1988) and temporary abandonment to search for food would increase the risk of failure. Observations made of a pair of Griffon Vultures in which the male had died

(Fernández 1975) and of a pair of Bearded Vultures in which the female suffered a temporary illness (Margalida *et al.* 1997c) demonstrate this to be so. In these studies, the adults prolonged their stay at the nest for as long as their energy reserves allowed. In the case of a single sex taking on the task of incubation, a strategy which might reduce the costs involved would be the provision of food to the nest by the other sex (Beissinger 1987). Nevertheless, like courtship feeding, this behaviour does not occur in the Bearded Vulture, probably due to the difficulty and limitations of foraging and the success rate in obtaining food. In this regard, changeover reliefs took place daily, during which the adult bird entering the nest brought no food to its mate, and no greeting or allo-preening occurred. These observations are consistent with those of Brown (1990) in South Africa and imply that each sex must find its own food, and thus the frequency of reliefs would depend on the success in obtaining food (Houston 1976). This situation would appear to be confirmed by the absence of a defined time pattern with regard to the presence of the sexes at the nest. Taking into account the fact that in the Pyrenees this period corresponds in time with the months with the highest snowfall and the lowest temperatures, the frequency of reliefs would be largely determined by weather conditions. Under these circumstances of extreme temperatures, which require the eggs to be incubated continuously, and of predation pressure principally by Ravens, the continuous presence of one of the adults at the nest is necessary to protect the clutch and to allow the relieved adult to obtain food.

Chick-rearing

All activities related to this period were attended to by both sexes. Nest attention was greater in females (but not significantly so) and, in both sexes, decreased in parallel with the growth of the chick. The frequency of feeds and the provision of prey items were divided equally, both frequencies being kept regular throughout chick-rearing.

During the first month of life, the chick was accompanied continuously by one or other parent. The low temperatures and the possibility of predation (principally by Ravens; pers. obs., Layna & Rico 1991) would seem to condition the permanent presence of one or other of the adults at the nest.

The prey remains brought to the nest are prepared at ossuaries, depending on their size, and later at the nest where they are once again processed for the chick. The use of ossuaries throughout rearing varies according to the temporal variation in the diet and the capacity of

the chick to ingest bone remains. Food was carried in the talons or bill and, unlike the results obtained by other authors (Brown 1990 and references therein), regurgitation was observed only during the ejection of pellets, which were later recycled for consumption by the adults themselves (Margalida & Bertran 1996). The significantly shorter time dedicated to feeding the chick during the first fortnight after hatching corresponds to the lower food requirements of the small chick and to the type of prey items selected during this phase which have a high meat content (pers. obs.). This facilitates their manipulation during feeding and as such they do not require laborious preparation (Margalida & Bertran 1997).

The reduction in time spent attending the chick was most pronounced from 90 days onwards, coinciding with the phase when an increase in the energy requirements of the chick takes place (Newton 1978, Collopy 1984, Komen 1991, Botelho *et al.* 1993). This pattern is related to the increase in time dedicated to searching for food and as such with an increase in the amount of prey brought to the nest. This takes place in parallel with the increase in the number of daylight hours for searching and a greater availability of food, coinciding with the transfer of domestic livestock to pastures at higher altitude. Nevertheless, as Bearded Vultures are opportunistic (Hiraldo *et al.* 1979, Thibault *et al.* 1993), a higher prey provision to the nest may be a response to a greater success in locating food rather than a response to the greater food needs of the chick (Snyder & Snyder 1973, Newton 1978).

The scarce presence of the adults during the final stage (106 days prior to fledging) of nest attendance (16% of daylight hours) is due to the increased time dedicated to searching for food, but also to the increased aggression which the chick shows towards its parents and the increase in its activity, which incites a reluctance of the adults to enter the nest (Alonso *et al.* 1987, Bustamante & Hiraldo 1990, Hubert *et al.* 1995, pers. obs.). The longer absence of the parents at the nest might also be due to the lowered risk of both chick predation and adverse weather. Nevertheless, the time dedicated to the preparation of food was maintained constant during the last two months, which might be explained by a qualitative change in the diet. Although the chick can ingest food remains with greater ease during this phase (pers. obs.), an increase in the provision of bone remains might require a more laborious preparation. This is corroborated by the slight decrease in the frequency of feeds observed from 75 days onwards, which suggests that with the greater ability and capacity of the chick to manipulate and

ingest bone remains, it does not require direct help from the parents. During the final days of nest attendance, the frequency of food provision increased slightly and flights by the adults with food to motivate the young to fledge were not observed (Brown 1990, Sunyer 1991). The wide range of ages of the young at fledging (Sunyer 1991), and the fact that the development of the primary feathers has still not been completed (pers. obs.), suggests that fledging is probably some what accidental in nature as has been described in the Griffon Vulture (Leconte & Som 1996).

Our results suggest that male and female Bearded Vultures invest equally overall in the activities undertaken during the breeding season, although with different degrees of intensity. Females participate more actively (but not significantly so) in the direct care of the offspring (attention and feeding) while males make a significantly greater effort in the activities of nest building and territorial defence. In certain monogamous birds which exploit scarce resources, the investment by the males in the defence of the territory and in the supply of material and food to the nest may result in a reproductive effort almost equivalent to that of the females (Creelman & Storey 1991). In dimorphic raptors, the parental activities show marked differences. This may be an adaptive consequence of the different parental roles of the sexes (Andersson 1994) due to their different costs and benefits in reproduction (Clutton-Brock 1991). Nevertheless, vultures differ from these in their similarity of body size between the sexes, their food habits and their means of obtaining food (Newton 1979).

Specialization in resources which are dispersed and which are temporally unpredictable, together with the fact that their discovery is subject to weather conditions, means that a considerable amount of time is needed to obtain them (Houston 1983, Hiraldo & Donazar 1990) and also makes it necessary to explore large areas which may be located far from the nest (Pennycuik 1972, Houston 1979, Brown 1990). These factors would mean that a single sex could not be responsible continuously for attending to the supply of food to the offspring and its mate. Furthermore, the extensive reproductive cycle of the species (the chick stays in the territory for 2–5 months after fledging and is still dependent on its parents; Brown 1990, Sunyer 1991, pers. obs.), means that the end of one reproductive cycle overlaps with the beginning of the next. This has important consequences for the frequency of breeding. In addition, the few possibilities for initiating a new breeding attempt, the high level of attention

which the clutch and chick require, and the high level of parental investment which both parents must make, necessitate the collaboration of both sexes to breed successfully (Trivers 1972).

ENDNOTE

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