Sex Difference in Breeding Age of Griffon Vultures (Gyps fulvus)

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The age at which young birds first pair and breed is a demographic trait relevant to population dynamics and life-history strategies (Horn 1978). Many species of large raptors occasionally have been recorded breeding as subadults (Newton 1979). This seems to be linked to a shortage of breeding adults when mortality rates are high or, alternatively, to a surplus of subadults in prime breeding condition when environmental factors are especially favorable (Newton 1979). Among subadults and yearling breeders, sex ratios become female-biased in most species (Lack 1968, Newton 1979, Ferrer and Hiraldo 1991). There is, however, evidence for male-biased sex ratios of nonbreeding juveniles and adults in a wide range of avian taxa (Breitwisch 1989).

Among vultures, members of the genus *Gyps* have breeding-age distributions such that subadults are an appreciable proportion of the breeding population (Mundy et al. 1992). However, in spite of implications for predicting breeding dynamics and demography, information on the sex ratios of breeding subadults is lacking for most vulture species. Several instances of known-age female Cape Vultures (*Gyps coprotheres*) breeding in subadult plumage have been recorded (Robertson 1983, 1984), but the possible relationship of sex to breeding age of Griffon Vultures (*Gyps fulvus*) has not been studied. We present data collected in Spain on the sex of Griffon Vultures breeding in subadult plumage.

Methods.—The study was conducted in the gorges of the Riaza River (41°31'N, 3°36'W), north of Segovia Province, Spain. This area includes a complex of cliffs and canyons where an increasing population of Griffon Vultures (Martinez and Cobo, 1993) breeds in high densities (almost 300 pairs over 12 km of cliff in 1994; pers. obs.). Our observations were carried out between December 1994 and February 1995, primarily at selected large eyries (up to 40 breeding pairs) where several pairs could be observed simultaneously, but also opportunistically at other sites (i.e. smaller eyries and vulture gatherings outside the nesting habitat). Some observations were made in 1993–1994, and some in 1995 at other central and western Spanish localities (provinces of Madrid, Guadalajara and Cáceres).

We focused our attention on vulture pairs formed by birds in subadult plumage mated with adults (hereafter, mixed pairs). Griffon Vultures were aged as subadults (four to five years old) or adults (older) according to their general body color, bill color, and especially the color, length, and shape of the ruff feathers (Elosegi 1989). Briefly, vultures with brown, large and lanceolated ruff feathers were subadults and vultures with white and short ruff feathers were adults. Griffon Vulture pairs, where both partners were subadults as well, also have been observed; they constitute a small segment of the breeding population inhabiting the gorges of the Riaza river and other Spanish localities (unpubl. data), but they have not been considered in the present study. The aging criteria have been verified repeatedly by individually banding 145 nestlings, 96 of which were observed subsequently on 383 occasions from 1990 to 1995 (G. Doval and F. Martínez unpubl. data).

We identified the sex of the birds within mixed pairs by recording their position and behavior in copulation attempts. All observations were made by telescope at distances that avoided disturbance to the colonies.

Results.—We observed 38 copulation attempts involving as many as 27 mixed pairs. Copulations or copulation attempts mostly occurred at the nest (86.8%), but it was impossible to determine the actual number of mated pairs because of the low number of marked birds involved (only two subadults banded as nestlings).

Some extrapair copulations could have occurred (Elosegi 1989). Thus, to be conservative, we only considered copulation attempts by pairs that maintained typical pair-bonding behavior (i.e. close contact, allopreening, nest building, etc.) and were able to determine the sex of members of 26 mixed pairs. In all such cases, vultures with subadult plumage were females: Riaza River, Segovia, 1994–1995, n = 20; Riaza River, Segovia, 1993-1994, n = 2; Las Cabreras, Madrid, 1995, n = 1; Aragosa, Guadalajara, 1995, n = 1; Monfragüe, Cáceres, 1995, n = 2. If only successful copulations at nesting sites are considered in order to avoid counting possible extrapair copulations, the sample was reduced to a minimum of 22 breeding pairs. In all cases the subadult partners were females. Two of these females, banded as nestlings, were five years old. Thus, the null hypothesis of equal numbers of males and females being subadults breeders is rejected ($X^2 = 20.04$, with Yates' correction, df = 1, P < 0.001). Similar results were obtained when only mated pairs belonging to the Riaza River population in 1994–1995 were analyzed ($X^2 = 10.08$, with Yates' correction, df = 1, P < 0.001); in this colony a greater number of breeding subadults were sexed. Therefore, in all copulations or copulation attempts observed for mixed pairs actually mated or not (including possible extrapair copulations), we found no subadult partners to be male.

Discussion .- These results demonstrate significant

differences in the sex of subadult Griffon vultures breeding in Spain. There are at least two nonmutually exclusive hypotheses regarding the origin of femalebiased sex ratios of breeding subadults. First, a skewed sex ratio could be responsible for this phenomenon because of a general shortage of adult females via unbalanced sex ratio of fledglings, because of differential mortality before reaching breeding status, or as a consequence of different levels of parental investment in the breeding stage (Breitwisch 1989). Second, the existence of sex differences in the age necessary to reach breeding condition may explain this pattern (Newton 1979).

Information on survival rates of vultures is scanty (Robertson 1984, Houston 1974, Piper et al. 1981), and nothing is known on sex-related mortality patterns of the Griffon Vulture. Further research is needed to determine whether the unbalanced, female-biased, sex ratio of subadult breeders is related to differential mortality before reaching breeding status, and whether it is influenced by the adult sex ratio.

The second hypothesis predicts that the sex ratio in the breeding population is determined by the age at which each sex reaches sexual maturity and/or breeding condition. Both Cape and Griffon vultures have been recorded breeding successfully as subadults, but in all cases they were females paired with adult males (Robertson 1983; pers. obs.). Hence, at least some females reached sexual maturity or breeding capability early in their lives. Another plausible explanation for the skewed sex ratios of adult and subadult Griffon Vultures could be that females may reach breeding condition or maturity earlier than males. Alternatively, the observed pattern could be caused by sex-related differences in the acquisition of adult plumage that would ocur earlier for males than for females. The evidence presented here, however, together with other data for Cape Vultures (Robertson 1983, 1984), suggests that, at least for birds recently incorporated into the breeding population independent of the stage of plumage maturity, breeding females usually are younger than their mates.

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