POLYANDROUS TRIOS IN A POPULATION OF EGYPTIAN VULTURES (Neophron percnopterus)

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Polyandry is a breeding strategy adopted by few birds. Among raptors, the only species to show it with some frequency are the Galápagos Hawk (Buteo galapagoensis) and the Harris' Hawk (Parabuteo unicinctus; Oring 1986). The Egyptian Vulture (Neophron percnopterus) is a monogamous bird (Cramp and Simmons 1980) that occasionally forms polyandrous trios (Perennou et al. 1987), though the frequency with which this happens remains unknown. In a recent review of the Spanish breeding population (1324–1373 breeding pairs; Perea et al. 1990), no documented case of polyandry was included and only two trios have been recorded in Bardenas Reales (northern Spain, J.A. Donázar and O. Ceballos pers. comm.).

In the Ebro Valley of Spain, I monitored 58 pairs of Egyptian Vultures between 1980 and 1991 (Tella 1991a). During this study I documented the presence of two reproductive trios made up of two male birds and one female. Sex of the members of the first trio was determined by the observation of consecutive copulations by each male with the same female when all three birds were present. This trio was discovered in 1982 and persisted until 1990 when the first unsuccessful reproductive attempt by the group was recorded. After that, no more than two of the members of the original group were seen together. In 1991 the trio's definite dissolution was established after 32 visits to the breeding territory.

The second trio was found in 1991 in a territory that had previously been occupied by a pair since 1989. In this case it was impossible to observe any copulation, but we assumed from other behavior that they were a polyandrous trio. I observed the participation of all three individuals in reproductive tasks (courtship flights, access to the nest, and standing with the nestlings and fledglings) giving behavioral evidence of cooperative polyandry. No genetic measures of paternity were made.

Taking into account only territories where I could determine the mating system after at least 10 visits of 1-3 hr spaced throughout the breeding cycle (N=37), the two recorded polyandrous trios amounted to 5.4% of breeding females. This incidence is similar to that verified in Bardenas Reales (O. Ceballos and J.A. Donázar pers. comm.), but much lower than that shown by B. galapagoensis (39-68%, Oring 1986), P. unicinctus (46%, Mader 1975; although J.C. Bednarz [pers. comm.] believed the frequency was closer to 20% in Arizona), and the Bearded Vulture (Gypaetus barbatus) in the Pyrenees (14.3%), a species in

which polyandry is also an exceptional phenomenon (Donázar 1991). No difference was detected between the production of young/pair/yr between trios ($\bar{x} = 1, N = 5$) and neighboring pairs ($\bar{x} = 0.97, N = 144$) of Egyptian Vultures in similar territories.

Several reasons for the formation of trios have been proposed (Oring 1986). In this case, the explanation does not seem to be an imbalanced sex ratio caused by a higher death rate of females (Newton 1979). The data available are scarce—only two of the 38 birds found dead in the study area (Tella and Torre 1990, Tella 1991a, Tella and Mañosa in prep.) were identifiable to sex (one male and one female). However, the presence of a large nonbreeding population fluctuating between 30% and 50% of the total population (Tella 1991a, 1991b), seemed enough to replace the low numbers of breeding birds. On three occasions the reconstitution of pairs after one of the birds died was observed.

According to Newton (1979), polyandry may be the result of food shortage which may favor the cooperation of males to permit a higher probability of successful reproduction (Perennou et al. 1987, Bednarz and Ligon 1988). Nests in the study area were placed in two main habitat types: the ribera (riparian areas and irrigated plains of the Ebro river) and the secano (dry areas; Tella 1991c) The availability and diversity of food resources (cattle, fish, birds, and rabbits) were significantly higher in the first habitat than in the latter because of the proximity to rivers (t = -7.88, df = 35, P < 0.0001) and rubbish dumps (t = -3.12, df = 35, P < 0.01). Both trios were located in the area with greatest resources, the ribera. Thus, this evidence does not support the food-shortage hypothesis.

Alternatively, trios may be favored because of available space. This proposal is probably most appropriate for the Bearded Vulture (Donázar 1991), and for the population of the Egyptian Vultures of Badenas Reales, where this species is known to have its greatest density (Ceballos and Donázar 1990). The population of Egyptian Vulture that I monitored in this study appears to be going through a regression. Numbers have decreased 25% in the last decade, leaving several empty territories which were seldom occupied again (3.6–8.5%/yr; Tella 1991a). This could suggest ecological saturation caused by important changes in the environment during the last 40 yr (decrease of European rabbit supply caused by myxomatosis, major

agriculture and cattle range decreases, and increasing human population pressure in the area), after which many territories became unsuitable for the species. In this situation, polyandry could be an advantage for male birds who would otherwise not be successful in reproduction and may assure the occupation of favorable territories after the death of one male cooperator. It may also improve survivorship and long-term reproductive success (Faaborg et al. 1980, Faaborg 1986, Donázar 1991). If this assumption is valid, and if the present population decline and saturation of resource continues, the frequency of polyandrous females may increase much like the pyrenaic population of Bearded Vulture did under similar circumstances (Heredia and Donázar 1990).

RESUMEN.—El seguimiento de una población de alimoches, caracterizada por encontrarse en regresión y por presentar una importante fracción no reproductora, ha permitido constatar la existencia de dos tríos poliándricos. La proporción de tríos (5.4%) es inferior a la hallada en otras rapaces poliándricas. La aparición de los mismos no parece responder a la escasez de alimento ni se ve traducida en un aumento del éxito reproductor. Tampoco se cree debida a un desequilibrio en la razón de sexos ni a la saturación del espacio. Se propone como explicación más probable una disminución de la capacidad de carga del medio, situación ante la cual la formación de tríos puede resultar una estrategia ventajosa a largo plazo.

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