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PRODUCTIVITY AND FLEDGLING SEX RATIO IN A CINEREOUS VULTURE (*AEGYPIUS MONACHUS*) POPULATION IN SPAIN

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Upon initial review, the mechanism of chromosomal gender determination in birds and mammals seems to be a factor limiting the parents' ability to modify the sex ratio of their progeny (Charnov 1982). However, sex allocation theory (Fisher 1930, Charnov 1982) predicts that the sex ratio can deviate from the expected 1:1, particularly when the costs of rearing the two genders are

different. The optimal sex allocation for individuals can be predicted from three basic non-mutually exclusive hypotheses (reviewed by Frank 1990). (1) Fisher (1930) proposed that parental expenditure in the population should be equal for all sons and daughters, which would result in a population sex ratio biased toward the gender that costs less to produce. (2) Trivers and Willard (1973) hypothesized that if the reproductive return differs between genders depending on parental condition at the time of breeding, natural selection would favor facultative adjustments of offspring sex ratios to obtain the maximum fitness from a breeding attempt. (3) Charnov (1982) generalized Trivers and Willard's hypothesis to cover any socio-environmental variable that might pre-

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dictably affect the fitness of sons and daughters unequally.

Biases in the fledgling sex ratio may reflect an adaptive manipulation by the parents, by mechanisms that are not clearly understood (Krackow 1995). Otherwise, they may arise from nonadaptive mechanisms such as gender differences in chick survival rate between hatching and fledging (Clutton-Brock et al. 1985, Arroyo 2002) due to the parents' inability to rear the more costly sex.

In raptors, as in other groups of birds, some reproductive parameters may reflect the environmental or parental conditions during the breeding season (Dawson and Bortolotti 2000). For instance, a decrease in food intake due to the parents' low foraging efficiency or reduction in food availability may be reflected in such reproductive variables as clutch size (Corbacho et al. 1997) or productivity (Corbacho and Sánchez 2000, Dawson and Bortolotti 2000). Therefore, interannual variations in population productivity may be good indicators of any environmental stresses affecting the birds. This is especially true in Mediterranean environments, where the harsh and highly-variable conditions of summer are a major constraint on reproduction (Corbacho and Sánchez 2000, Costillo et al. 2002a).

Recent empirical studies on raptors have provided evidence for the existence of significant biases in the sex ratio of the progeny depending on the environmental and social conditions experienced by the parents during the breeding season (e.g., Dzus et al. 1996, Appleby et al. 1997, Post et al. 1999, Korpimäki et al. 2000, Byholm et al. 2002, Hipkiss et al. 2002). Most of these studies have focused on species with marked sexual dimorphism in size. In such cases, one can predict that a bias in the sex ratio, whether adaptive or not, will arise as a result of the difference in energy requirements or in vulnerability to adverse conditions between male and female chicks (Torres and Drummond 1997, Arroyo 2002). There have been fewer studies of variations in the nestling sex ratio in species that are monomorphic or have only slight sexual dimorphism (Cooch et al. 1997, Sheldon et al. 1998, South and Wright 2002). The main limitation has been the difficulty of assigning gender to the chicks of these species. However, the advances in molecular techniques in the last decade allow the relatively easy and accurate gender determination of a wide survey of bird species (Ellegren 1996).

The Cinereous Vulture (*Aegypius monachus*) is a large raptor widely distributed throughout the western Palearctic. Except for in the Iberian Peninsula, its populations have been greatly reduced (Cramp and Simmons 1980, del Hoyo et al. 1994). This species is of conservation concern, being classified as near-threatened worldwide (Collar et al. 1994) and as vulnerable in Europe and Spain (Blanco and González 1992, Tucker and Heath 1994). Knowledge of its basic ecology, including aspects related to reproduction, is therefore of great importance for the conservation of the species.

Here, we report the patterns of variation in productivity and fledgling sex ratio in a Cinereous Vulture population in Spain during 3 yr. We analyze whether the inter-year variations in breeding success had any relationship to fledgling sex ratio or on the fledglings' nutritional condition. Also we examined whether there were differences in nutritional condition between the genders that may favor manipulation of the sex ratio in this species under certain conditions.

There are two fundamental aspects in which this species differs from other raptors related to studies of sex ratio. Firstly, its sexual dimorphism is only slight, females are larger than males (Donázar 1993). Secondly, clutches are always composed of a single egg (Cramp and Simmons 1980).

STUDY AREA AND METHODS

The study was carried out in 1998–2000, in the Sierra de San Pedro (Extremadura, southwestern Spain). This area and the region of Extremadura in general, support the most numerous populations of Cinereous Vultures in the Palearctic and those that have experienced the greatest growth in Spain in recent decades (González 1990, Tucker and Heath 1994, Sánchez 1998, Costillo et al. 2002b).

At the beginning of each breeding season (February–March), the entire area was surveyed to determine whether pairs were present. Then nesting attempts were monitored periodically during the breeding season to determine which pairs laid a clutch (Breeding Pairs), and how many reared a chick to fledging (Costillo et al. 2002a). As a measure of reproductive success we used the productivity, estimated as the number of fledglings produced per monitored pair. The population's annual productivity was used as an indicator of the breeding conditions that the individuals experienced in the study area.

A variable number of chicks (11–26) were captured in the nests and their blood sampled each year at 45–60 d of age. Assuming that the same pair reused the same nest in successive years (Cramp and Simmons 1980), we selected 12 nests to monitor during the three breeding seasons. In five nests, we were able to sample a chick each year. In the other seven, either the pair did not lay in one of the years, or the chick did not survive long enough to be sampled. In total, blood from 57 chicks was sampled during the study period, 29 of them belonged to one of the selected family groups.

The blood sample was drawn from the brachial vein using 2 ml syringes and disposable needles. A small part (50 μ l) was collected in a capillary tube and transferred to a tube with ethanol. For the remaining sample, plasma was obtained by centrifuging at 8000 g for 10 min, and stored at -20°C . We determined the sex of the chicks using polymerase-chain reaction (PCR) amplifications of the CHD genes (Ellegren 1996). Blood was boiled in NaOH 100 mM for 10 min at 100°C before being added to the PCR reaction. PCR protocols were modified from Fridolfsson and Ellegren (1999). We used the primer set 2552F–2781R, scoring one band in males and two bands in females in a 2% agarose-gel stained with ethidium bromide.

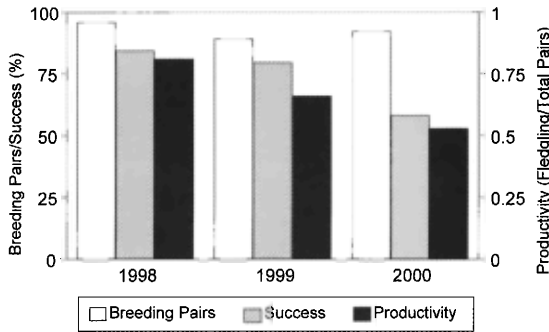


Figure 1. Reproductive performance of the Cinereous Vulture population at Sierra de San Pedro (Extremadura, Spain) in 1998–2000. Breeding pairs = percent of monitored pairs that laid a clutch; Success = percent of reproductive pairs (pairs that laid a clutch) that produced a young; Productivity = Number of fledglings produced per monitored pair.

The alkaline-phosphatase (ALP) concentration was measured in the plasma sample using a multiparametric autoanalyzer (Falcor 300, Menarini Diagnostics, Barcelona, Spain) with the reagents recommended by Menagent (Menarini Diagnostics). This variable was used as an index of chicks' condition at the moment of sampling, because it has been found to be positively associated with physical condition in the chicks of this species (Villegas et al. 2002).

The annual fledgling sex ratio is expressed as the proportion of males. The G -test was used to analyze deviations from the proportion 1:1, inter-yearly differences in this parameter, and in the productivity. Inter-year and gender variations in the chicks' physical condition were analyzed using a two-way analysis of variance in which sex and year were used as the principal factors and the alkaline-phosphatase concentration as the dependent variable (Zar 1999).

RESULTS

The percentage of Cinereous Vulture pairs initiating a clutch was similar in the 3 yr of study ($G = 0.52$, $df = 2$, $P = 0.77$). Productivity, however, declined from 0.81–0.53 during the study period (Fig. 1). There were statistically significant differences among years ($G = 28.9$, $df = 2$, $P < 0.01$), with the lowest value in 2000 (1998 vs. 2000: $G_{adj} = 27.6$, $df = 1$, $P < 0.01$;

1999 vs. 2000: $G_{adj} = 5.77$, $df = 1$, $P < 0.05$).

Of the 57 chicks monitored, 32 were males and 25 females, so that the overall fledgling sex ratio for the 3 yr was 56.1%. This was not significantly different from 50% (Table 1). By years, there was an increase in the proportion of males in 2000 (0.7), although the difference from the 1:1 proportion was not statistically significant in any year (Table 1). Likewise, there were no inter-year differences in the proportion of males ($G = 1.057$; $df = 2$, $P = 0.78$). The results were the same for the analysis of the 29 chicks of the selected family groups (Table 2).

The fledglings' physical condition, as measured by the ALP concentration (Table 3), differed among years ($F_{2,51} = 4.17$, $P = 0.02$), but not between sexes ($F_{1,51} = 1.01$, $P = 0.31$), and the interaction of these factors was not significant ($F_{2,51} = 0.73$, $P = 0.49$). In 2000, the chicks of both genders exhibited condition indices that were lower than in 1998 and 1999 (Table 3).

DISCUSSION

The inter-year differences found in the productivity reflect differences in the breeding conditions experienced by the individuals in the three seasons. At the time of breeding, the environmental, parental quality, or both were poorer in 2000, than in 1998 or 1999. The decline (Fig. 1) was mainly due to egg loss or the death of hatchlings, as the percentage of pairs that initiated a clutch was similar in each of the 3 yr. This decrease in productivity was accompanied by a significant decline in nutritional condition of the chicks at the time of sampling (Table 3). Costillo et al. (2002a) suggested adverse weather conditions as the cause of this decline in the area in the year 2000. Rain and cold at the time of hatching significantly affected the parents' capacity to provide food, thus could have led to a decrease in the hatchlings' physical condition, and even to their death from starvation (Donázar et al. 1988, Corbacho and Sánchez 2000, Dawson and Bortolotti 2000).

Various studies on raptors have found evidence for the parents being able to adjust the sex ratio of their progeny, or for the existence of a gender bias in early nestling mortality, according to each year's parental or ecological conditions (e.g., Olsen and Cockburn 1991, Wiebe and Bortolotti 1992, Dzus et al. 1996, Korpimäki et al. 2000, Arroyo 2002, Van den Burg et al. 2002). These studies

Table 1. Sex ratio variation at the fledging stage in Cinereous Vultures by year in Spain. Sex ratios are expressed as percentage of males.

YEAR	MALES	FEMALES	SEX RATIO	G-TEST	P-VALUE
1998	6	5	54.5	0.00	1.00
1999	13	13	50.0	0.00	1.00
2000	13	7	65.0	1.26	0.26
Pooled	32	25	56.1	0.63	0.43

Table 2. Sex-ratio variation at the fledging stage in Cinereous Vultures by year, within selected groups in Spain. Sex ratios are expressed as percentage of males.

YEAR	MALES	FEMALES	SEX RATIO	G-TEST	P-VALUE
1998	3	4	42.8	0.00	1.00
1999	7	5	58.3	0.08	0.77
2000	7	3	70.0	0.91	0.34
Pooled	17	12	58.6	0.55	0.46

used model species with marked sexual dimorphism and with brood sizes greater than one, in which gender-dependent food demand in combination with hatching asynchrony cause the cost-benefit ratio of rearing male and female chicks to differ (Dijkstra et al. 1998).

Most raptors exhibit reversed sexual size dimorphism, with the females being larger (Newton 1979). Growth demands, and hence the nutritional requirements, of female chicks are therefore greater, so that females are more costly for the parents to rear and they are more vulnerable to adverse environmental conditions (Richner 1991). Differences between species in the magnitude of their sexual dimorphism are often related to the agility of the prey, with greater dimorphism corresponding to greater agility (Newton 1979). In vultures, which feed on carrion, although the females are larger, the difference is slight, and there is a high degree of overlap in the sizes of the two sexes (Cramp and Simmons 1980, Donazar 1993). Studies of bird species that show little dimorphism have not shown any gender-environment interaction in chick performance (e.g., Sheldon et al. 1998, South and Wright 2002).

Differences in nutritional condition between males and females should most likely be observed when the environmental conditions were seriously limiting—a situation that did not arise in this area during the study period, as deduced from the high percentage of pairs that initiated a clutch and successfully reared a fledgling (Costillo et al. 2002a). Nonetheless, this does not imply that the costs associated with rearing the two genders are equal. In the case that the growth rate or the energy requirements of one sex are greater than those of the other, rearing a chick of the more costly gender in years

with suboptimal conditions, as year 2000 was, would involve greater effort for the parents. The result could be a greater decline in their physical condition over the course of the breeding season, which could compromise chick's survival and even the parents' capacity to breed in the following year (Donazar 1993, Korpimäki et al. 2000, Genovart 2002). In such case, female Cinereous Vultures might obtain fitness benefits by producing a chick of the cheaper sex when the breeding conditions are not optimal (Meyers 1978), with the advantage that, by laying only a single egg, they can allow themselves to reabsorb a zygote of the unsuitable gender without incurring the costs of hatching asynchrony or of a significant lengthening of time on the clutch (Emlen 1997).

In summary, our results suggest a shift toward males of this Cinereous Vulture population's fledgling sex ratio in years with suboptimal breeding conditions (Table 1), although probably because of the small sample size, this bias was not statistically significant. This bias could reflect a greater production of males at hatching or a greater early mortality incidence of females.

RESUMEN.—Estudios empíricos recientes en rapaces han proporcionado evidencias de la existencia de sesgos significativos en la proporción de sexos de volantones en función de las condiciones ambientales experimentadas por los padres durante la estación reproductiva. La mayoría de estos estudios se han centrado en especies con un marcado dimorfismo sexual y con tamaños de nidada mayores que uno. En este trabajo estudiamos los patrones de variación en la proporción de sexos de volantones en una población de la Península Ibérica de *Aegypius monachus*, un ave rapaz con un dimorfismo sexual poco acu-

Table 3. Alkaline phosphatase concentration (UI/L) in male and female Cinereous Vultures during 3 yr in Spain.

YEAR	MALES		FEMALES		POOLED ^a		P ^b
	MEAN ± SD	(N)	MEAN ± SD	(N)	MEAN ± SD	(N)	
1998	1574.5 ± 232.9	(6)	1376.4 ± 186.4	(5)	1484.5 ± 227.4	(11) A	ns
1999	1437.1 ± 262.5	(13)	1343.0 ± 341.0	(13)	1390.0 ± 302.0	(26) A	ns
2000	1168.9 ± 284.9	(13)	1219.6 ± 249.9	(7)	1186.6 ± 267.6	(20) B	ns

^a The different letters in this column indicate that the differences between the year 2000 and the years 1998 and 1999 were significant

^b Probability that concentrations were different between males and females.

sado y con un tamaño de nidada igual a uno, durante el periodo 1998–2000. Analizamos si las variaciones anuales en el éxito reproductivo tienen alguna influencia en la proporción de sexos y en la condición nutricional de los pollos, medida por la concentración de fosfatasa alcalina en plasma, y si ésta muestra diferencias entre pollos de distinto sexo. Tanto la productividad de la población como la condición física de los pollos fue menor en el año 2000 que en los dos años previos. La proporción de sexos no se apartó de forma significativa de 1:1 ni mostró diferencias interanuales significativas, aunque la proporción de machos incrementó a 0.70 en el año de menor productividad. La condición nutricional no mostró diferencias significativas entre pollos de distinto sexo. Estudios más detallados son necesarios para determinar los mecanismos que actúan en la desviación de la proporción de sexos en esta especie.

[Traducción de los autores]

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