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Brief report

Rate, timing and success of clutch replacement by colonial Griffon Vultures *Gyps fulvus*

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1. Introduction

After losing a clutch, most single-brooded bird species may raise young from replacement clutches when certain parental and environmental conditions concur (Lack 1968). These factors include the timing of laying, the availability of food, the duration of parental care and the age of parents (Milonoff 1991, Martin 1995). Clutch replacement may be an adaptive breeding strategy to cope with high nest predation rates in short-living birds because of the slim prospects of future breeding attempts (Martin 1995). Vultures are large single-brooded and long-lived birds with low breeding rates and long breeding periods (Mundy et al. 1992, Donázar 1993). They usually maintain pair-bonds and occupy the same territories and nest sites from year to year. Based on general avian life history (Martin 1995), one can expect low renesting rates in vultures because of a combination of the traits mentioned above. Replacement clutches have been ocassionally recorded in most vulture species (Mundy et al. 1992), but almost nothing is known on the frequency and timing of renesting, nor on the success and age of renesting breeders. In this paper we present data on these aspects for a colony of Griffon Vultures *Gyps fulvus* in Spain. To our knowledge, these are the first data on renesting at the population level of a vulture species.

2. Methods

During 1992 we monitored the breeding performance of 32 Griffon Vulture pairs occupying a single canyon in the gorges of the Riaza River (41°31'N, 3°36'W), north of Segovia Province, central Spain. During 1994–1997 we counted Griffon Vulture pairs on the area and monitored their breeding performance (Blanco et al. 1997a). The censuses and the monitoring of breeding performance were carried out by regular and intensive observations of the nests throughout the breeding season to determine laying dates and fledging success of each pair (Martínez et al. 1997). We observed at a distance the presence of eggs in the nests, recorded the start of incubation, or calculated the date of hatching based on nestling age (Elosegi 1989). All these criteria and an incubation period of 55 days (own data) were assessed to determine laying dates within 10-day periods from 10 December onwards.

We divided the birds into two age classes. Griffon Vultures were aged as subadults, when they had not yet acquired full adult appearance (at 5–6 years old), on the basis of overall body color, bill color and, in particular, the color, length, and shape of the ruff feathers (Elosegi 1989, Blanco & Martínez 1996). The age structure of breeding pairs was categorized into three classes: adult-adult (adult pairs hereafter), adult-subadult (mixed pairs) and subadult-subadult (subadult pair). The age distribution was recorded for more than 64% of the pairs and more than 82% of the individuals each year (n = 307–379 pairs).

When vultures were absent from the nest or showed no incubation activity after laying, nests were regularly checked to verify breeding failure. Subsequent monitoring allowed us to detect each new breeding attempt. All vulture pairs presumably involved in a renesting attempt belonged to the same age class as the initial breeders, except in the only case where we detected the death of one of the partners (see Results). Therefore, it is likely that all pairs involved in a second attempt were detected and were the same that built the nest and laid the initial clutch.

The time intervals between the dates of laying and failure and between failure and replacement were calculated as the minimum and maximum possible period according to the range in days derived from the inclusion of such dates in 10-day periods starting from 10 December. All observations were made by telescope at distances that avoided disturbing of the birds in the colony.

3. Results

Overall, 20 of the 533 pairs (3.8%) with breeding failure were involved in renesting (Table 1). There was no difference in the proportion of renesting pairs among years ($X^2_4 = 1.60, P = 0.81$). The exact causes of breeding failure were unknown except for one case in 1995 in which one adult died at the nest. Afterwards, the non-banded but presumably widow, also adult, partner remated rapidily with a subadult and a new clutch was laid in the same nest. No replacement clutch was initiated after the death of nestlings. Overall 3 of the 20 (15.0%) replacement clutches were successful in fledging young (Table 1), and only 0.56% (3 of 533) of the pairs that failed in their initial breeding attempt were successful in their renesting. This contrasts with the proportion of successful initial clutches (ranging between 47% in 1992 and 57% in 1997). Of the fledged young, 0.48% (3 of 620) were from replacement clutches.

When combining the data of all years, there was no differences in the proportion of adults and subadults renesting or not renesting after failure ($X^2_1 = 0.19, P = 0.65$ with Yates correction), nor between each class of pairs ($X^2_2 = 0.02, P = 0.98$). Laying dates of inital clutches did not differ between years (Kruskal-Wallis test H = 1.37, P = 0.71, n = 1115). Pairs involved in clutch replacement laid their initial clutches before (median 10-day period = 11–20 January) pairs that failed and did not replace clutches (median 10-day period = 21–30 January; Mann-Whitney U-test U = –4.17, P = 0.00003, n = 530). Most vulture pairs involved in a renesting attempt lost their initial clutches in the middle of the incubation period (42.1%, between 20–40 days n = 19). The period between failure and renesting was typically around 25 days (73.7% between 10–40 days after failure). There was no difference between adult and mixed pairs in the dates of loss of initial clutches before renesting (Mann-Whitney U-test, U = 0.40, P = 0.68, n = 13) nor in the dates of replacing (Mann-Whitney U-test, U = 1.04, P = 0.29, n = 13). The three chicks succesfully raised from replacement clutches fledged in the first half of September (n = 2) or October (n = 1).

Table 1. Number of breeding failures and replacement clutches of Griffon Vultures from central Spain.

Years	Pairs studied	Pairs laying eggs	Failures	Replacement clutches(%)	Succesful replacements(%)
1991–92	32	32	17	1 (5.9)	0 (0.0)
1993–94	307	268	121	5 (4.1)	0 (0.0)
1994–95	336	275	141	7 (5.0)	2 (28.4)
1995–96	358	288	131	4 (3.1)	0 (0.0)
1996–97	359	290	123	3 (2.4)	1 (33.3)
Total	1392	1153	533	20 (3.8)	3 (15.0)

4. Discussion

The rate of clutch replacement after the loss of the initial egg was relatively low (3–4%) as expected according to the large body size, large duration of the breeding period and high adult survival of Griffon Vultures (Newton 1979, Donázar 1993). Nest predation is the primary source of nesting mortality in birds (Martin 1995), although there are no precise data for vultures (Blanco et al. 1997b). The source of nesting failure may probably influence the rate of clutch replacement between species, but the difficulty of obtaining such data in vultures prevents any analysis of this effect.

The period between failure and renesting was typically around 25 days. These results are consistent with the intervals of 20 and 28 days between the induced failure by removing the first clutch and the laying of a replacement clutch in two nests of southern Spain (Fernández & Fernández 1974), and with observations in captivity (Mendelssohn & Leshem 1983). The fledging success from replacement clutches was very low compared with the success of initial clutches. Therefore, renesting is not expected to be compensated for by a net fitness benefit in terms of production of young. Given their long life expectancy, vultures may gain less by investing in renesting if this affects negatively their survival and future breeding success (Linden and Moller 1989), or the survival of their offspring. The late fledging dates of young raised from replacement clutches may negatively affect their survival prospects, as occurs in late initial attempts (e.g. Brouwer et al. 1995), and may, therefore, represent an additional parental cost. The three young raised from the replacement clutches fledged as late as two and three months before the first clutches were laid in the following breeding season (unpubl. data), when most fledglings from the inital breeding attempts were already independent and had started their southward dispersive migration (Elosegi 1989, Donázar 1993). Early laying may increase the probability of a successful repeat clutch after initial breeding failure. In fact, vultures involved in clutch replacement laid their initial clutches earlier than the pairs that failed and did not renest. Furthermore, adult vultures were not more likely to lay replacement clutches than subadult vultures. However, among pairs that failed with early laying dates there was also a low proportion of pairs that renested. This suggests that only a small proportion of vultures laying early in the season may invest in a renesting attempt, and may eventually be successful in raising young.

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Selostus: **Uusintapesyeiden määrä, ajoitus ja menestys hanhikorppikotkalla**

Kirjoittajat tutkivat vuosina 1991–97 hanhikorppikotkien pesintää Keski-Espanjassa yhteensä liki 1400 pesällä. Keskimäärin yli kolmannes (533 pesää) aloitetuista ensi pesinnöistä epäonnistui (Taulukko 1). Vain 20 kertaa kirjoittajat havaitsivat parin aloittaneen uusintapesyeen tuhoutuneen tilalle. Uusintapesyeistä vain 3 (15%) tuotti lentopoikasia, eli pesänsä menettäneistä pareista vain 0.56% (3/533) onnistui tuottamaan poikasia. Ensipesyeistä 47–57 % tuotti poikasia. Uusintapesyeiden tuottaneet parit olivat aloittaneet ensipesyeen munimisen aikaisemmin (mediaani 11.–20. tammikuuta) kuin ensipesyeensä menettäneet parit, jotka eivät tehneet uusinatpesyettä (mediaani 21.–30. Tammikuuta). Kirjoittajat päättelevät, että vain pieni osa aikaisin ensipesintänsä aloittaneista pareista pystyy investoimaan uusintapesyeeseen aikarajoitteiden takia.

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