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SHORT COMMUNICATIONS

Acquisition of food by fledgling Egyptian Vultures *Neophron percnopterus* by nest-switching and acceptance by foster adults

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In a dense population of Egyptian Vultures *Neophron percnopterus* in northern Spain, nest-switching occurred between nearby nests. Fledglings obtained more feeds by intruding and pirating than by remaining in their own nests during the same period. Intruder fledglings showed the same behaviour with Foster adults attacked intruder fledglings significantly less than they attacked alien adults and immatures but more frequently than they attacked their own fledglings. Effective rejection behaviour by foster adults to intruders may not have evolved as Egyptian Vultures usually nest at lower densities than that found in the study area.

The adoption of alien young by adult breeding birds has been reported in several species. In raptors, adoptions are the consequence of nest-switches or intrusions of fledglings into another territory or nest (Kussman 1976, Poole 1982, Wyllie 1985, Newton 1987, Lett & Bird 1987). In general, nest-switching seems to be an adaptive strategy overall since the survival of young may be increased through obtaining extra food (Poole 1982, Wyllie 1985, Newton 1987) and/or a level of parental investment higher than that received in their own nest (Pierotti & Murphy 1987, Pierotti 1988, Hébert 1988). However, in the Cape Vulture *Gyps coprotheres* the intrusion of fledglings into alien nests seems to be a maladaptive behaviour, potentially leading to the death of the chick rejected by its foster parents (Robertson 1985). This study reports nest-switching in a dense population of Egyptian Vultures *Neophron percnopterus* and examines the ultimate factors which may favour this behaviour.

Study area and methods

The study was undertaken in the Bardenas Reales region of the Ebro valley, Navarra, northern Spain. The terrain is predominantly flat and below 650 m a.s.l., and has a cold mediterranean climate. The Egyptian Vulture population (40 pairs) living in this region is one of the densest in Europe (14·5 km^2/pair) the average spacing between nests being 1400 m (range 260–4000 m; pers. obs.).

Observations were made during July, August and September 1986 and 1987. Eight fledglings from six nests were studied, six of them (two broods with two fledglings and two broods with one fledgling) for more than six days; the total number of days of observations at these six nests was 58. All observations refer to the post-fledging period which starts approximately 75 days after hatching (range 68–80; pers. obs.). Fledglings were wing-tagged (Kochert *et al.* 1983) and fitted with radiotransmitters fixed with backpack harnesses so they were individually identifiable and their movements could be followed. The adults were either identified by wing tags or by distinctive plumage characteristics.

Observations started at dawn and ended at dusk. Two teams of observers worked simultaneously observing each nest and recording the behaviour and movements of the fledglings and events in the natal territory. Statistical differences were tested by means of Student *t*-tests (percentages were previously log-transformed).

Results

Frequency of intrusions

Two of the six fledglings studied intruded at other nests. They were siblings (nest VE86) and both regularly visited two nests situated at 260 m and 670 m from their own nest. The siblings made their first intrusions when they were 89 (oldest) and 80 (youngest) days old. The age of the young in the most frequently invaded nests was not exactly known but they made their first flights shortly after the first flight of the oldest young studied. Of a total of 190·5 hours of observation for each fledgling 16·7% (older sibling) and 8·5% (younger sibling) of this time was spent in another territory. None of the other four fledglings followed during the post-fledging period made intrusions; the neighbouring Egyptian Vulture nests were more than 1000 m away from the natal nests.

Intrusions occurred in three of the four nests studied. No significant correlation appeared between the percentage of time spent by intruder fledglings in the territory studied and the distance to the nearest active nest ($r_2 = -0{\cdot}050$, n.s.) as some territories, despite having active nests very close by, did not receive visits from other fledglings.

Factors affecting nest-switching

The factors causing intrusions were investigated using the pair of siblings that showed this behaviour. The intrusions tended to occur early in the day (Fig. 1).

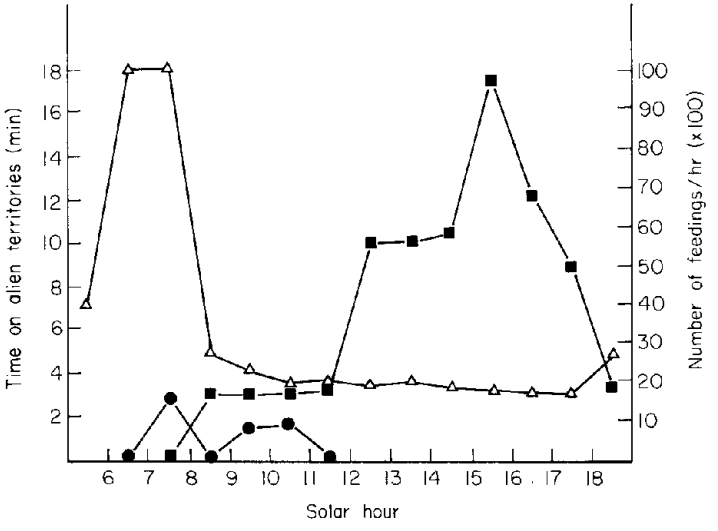

Figure 1. Hourly feeding frequency pattern (number per hour of observation) of Egyptian Vultures in the most studied nest (which contained the siblings making intrusions). The hourly percentage of time spent by both siblings in other territories is also shown. The data are means of daily values through the whole post-fledging period. △ Time on alien territories; ● Feeds stolen in alien territories; ■ Feeds in the natal territory.

During intrusions the foster parents were present in their territories for a significantly greater percentage of the time than the parents of the intruder fledglings were on the natal territory (both fledglings together: means = 71·8% *v.* 17·8%, $t_{38} = 5{\cdot}71$, $P < 0{\cdot}001$; older sibling: means = 72·2% *v.* 13·5%, $t_{24} = 5{\cdot}64$; $P < 0{\cdot}001$; younger sibling: means = 71·2% *v.* 25·8%, $t_{12} = 2{\cdot}28$, $P < 0{\cdot}05$). The intrusions seemed to be influenced by the relative likelihood of getting food from natal and alien parents since the highest frequency of intrusions occurred in the hours in which the rate of food delivery by the parents was the lowest (correlations: both fledglings together $r_{12} = -0{\cdot}366$, $P < 0{\cdot}05$, older sibling $r_{12} = -0{\cdot}731$, $P < 0{\cdot}01$, younger sibling $r_{12} = -0{\cdot}731$, $P < 0{\cdot}01$) and the number of feeds stolen from alien adults was maximum (see Fig. 1).

Over the study period the older sibling managed to obtain one feed from another nest but it lost another at its own nest because it was absent when its parent arrived with food. The younger sibling obtained three feeds from other nests and only lost one (in the same way as its sibling) at its own nest. Of these four stolen feeds two were obtained on entering the nest after the departure of the adults and the other two by waiting for the arrival of the adult at the nest itself together with the resident fledgling. When food was delivered the alien adults were not seen attacking the intruders, but at least one delivery was contested with the resident fledgling. The possibility that intruding birds managed to steal more food than this cannot be dismissed as the nest most frequently invaded was an extensive and very dark cavity, so that they could have eaten food stored there without this being visible to us. The feed lost by the older sibling while it was intruding was eaten by its brother which remained at the natal nest. The feed lost by the younger sibling was eaten by the parent which brought the food, since the older sibling was absent from the natal territory (but not intruding). At the time these feeds were lost none of the siblings could have realised that their parents were bringing food since the natal nest was out of their sight.

Relationships between adults and young on invaded nests

Finally, we studied the interactions between adults and fledglings in relation to the following variables: (1) daily number of movements by the adult towards the fledgling per hour of observation in which adults and fledglings were simultaneously in the territory; (2) daily number of movements of the fledgling towards the adult per hour of observation in which adults and fledglings were simultaneously in the territory; (3) daily percentage of time the fledgling spent begging for food (calculated from the time for which adults and fledglings were simultaneously in the territory); (4) daily percentage of time spent by the fledgling in the territory with at least one adult (calculated from the time for which adults and fledglings were simultaneously in the territory). For variables 1, 2 and 3 we only considered movements and time in which birds encroached within pecking distance.

Intruder fledglings behaved towards foster adults as with their own parents. Their movements towards adults, the time spent begging, and the time that adults and fledglings spent in the territories did not show significant differences. However, foster adults showed significantly less interest in intruder fledglings than did their own parents, making very few movements towards them (means = 0·22 *v.* 2·66, $t_{46} = 3{\cdot}32$, $P < 0{\cdot}05$). Moreover, we compared the daily percentage of time spent by owner adults and fledglings chasing intruding Egyptian Vultures of different ages. To avoid the effect of the frequency of intrusions the percentage was calculated on the total time that the intruders remained on the territory. The results showed that owner adults spent more time chasing intruder adults and immatures than chasing

intruder fledglings (means 27·4% *v.* 0·3%, $t_{56} = 3{\cdot}17$, $P < 0{\cdot}01$), and more time chasing intruder fledglings than chasing their own fledglings (means = 0·3% *v.* 0·0%, $t_{93} = 2{\cdot}89$; $P < 0{\cdot}01$). Fledglings on their natal nest spent a similar amount of time chasing adults and immature intruders as they did chasing intruder fledglings (means = 0·3% *v.* 0·1%, $t_{99} = 0{\cdot}85$; n.s.) but spent more time chasing intruder fledglings than chasing their own siblings (means = 0·1% *v.* 0·0%, $t_{88} = 2{\cdot}89$; $P < 0{\cdot}01$). These results suggest that owner adults and fledglings recognized intruder fledglings, although they tolerated their intrusions more than those of adults and immatures.

Discussion

Our results suggest that nest-switching could be advantageous for intruders and for their parents, but possibly detrimental for the fostering adults and their fledglings. The benefit obtained by the switchers is the stolen food, as has been observed in other raptors (Ellis & Groat 1982, Poole 1982, Wyllie 1985, Newton 1987). This may explain why the intruders appear to make a similar effort to maintain contact both with the foster adults and their own parents, since this behaviour may increase the possibility of obtaining food. In fact, the pursuit of adult Egyptian Vultures during the post-fledging period appears to be aimed at obtaining extra investment during the period of reduction of parental care (pers. obs.). The parents of switchers obtain a double advantage; acquisition of extra food for their offspring and ingestion of the food not consumed by their fledglings. On the other hand, the adoption and feeding of alien fledglings must prove detrimental to the adults visited by intruders if their inclusive fitness is thereby reduced.

The adoption of fledglings by foster adults was only transitory and was not reciprocated. We consider nest-switching in Egyptian Vultures to be a special type of food piracy (see also Ellis & Groat 1982). Intraspecific kleptoparasitism by Egyptian Vultures of food left in other nests is frequent (pers. obs.) and piracy on nests of other vultures is also well known (Cramp & Simmons 1980). This kind of piracy would not always be advantageous for fledglings, but only when food deliveries occur at different times in natal and alien nests. For the two siblings studied in most detail, food deliveries at their natal nests were at a maximum in the middle of the afternoon but in other nests the maximum occurred in the morning or early afternoon (see Ceballos & Donázar 1988). In addition, the nests must be sufficiently close for the fledglings to monitor feeding rates in other territories, as otherwise they might lose feeds brought by their parents. For this reason, in our study area, the fledglings that made frequent intrusions were those that had alien nests very close to their own, as has also been reported in other populations of raptors (Poole 1982).

Our results on the aggressiveness of adults and fledglings towards intruder young showed that tolerance of intrusions cannot be explained by misrecognition. Forbearance could be due to the absence, in normal circumstances, of opposing selective pressures. The Egyptian Vulture nests in which nest-switching was observed were very close to one another, probably due to the exceptional availability of nest-sites and food resources in the study area (Ceballos & Donázar 1989, pers. obs.). However, in European and African populations the nest-density is, in general, markedly lower except in areas where food is abundant due to human activities (see Garzón 1973, Bergier & Cheylan 1980, Cramp & Simmons 1980). As a result, effective rejection behaviours towards alien fledglings would not evolve as in true colonial species, which usually show a strong parental defence against intruding chicks (Stoddard & Beecher 1983, Robertson 1985, Pierotti & Murphy 1987, Pierotti 1988, Bustamante & Hiraldo 1990).

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