SHORT COMMUNICATIONS

Helping at the Nest in Darwin's Finches as Misdirected Parental Care

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Helping, or the feeding of young birds by nonparental conspecifics, has been reported in more than 150 species across many taxonomic groups (Skutch 1961, Brown 1978). Recent studies have emphasized both kin and individual selection in accounting for the helping behavior (Brown 1978, Emlen 1978, Davies 1982). A different attitude is taken by Lewontin (1979) and Gould and Lewontin (1979), who have stressed that, in general, many traits may simply be unselected consequences of adaptation in other traits. Williams (1966: 208) summarizes such an explanation for helping: "The helper phenomenon can be attributed to selection pressures for the maintenance of a certain pattern of parental behavior with a less than perfect system of timing mechanism for regulating this behavior." Here, we describe the first reported case of helping at the nest in the Darwin's finches *Geospiza scandens* (Cactus Finch) and *G. fortis* (Medium Ground-finch), which was discovered on I. Daphne Major, Galápagos. In view of the cautionary remarks of Williams and Lewontin and Gould, it is appropriate to test hypotheses for the helping behavior against a null hypothesis. Misdirected parental care is offered as a null hypothesis, and we consider explanations invoking natural selection in an attempt to reject it.

The breeding biology of *G. scandens* and *G. fortis* on I. Daphne Major, Galápagos has been under intensive study since 1975 (Boag 1981), and 95% of the finches are now uniquely color banded. In early 1979 we discovered helping at the nest in both species. At this time, hatching success of *fortis* eggs was very low, and all further observations except where specified refer to *scandens*. We conducted full-day nest watches, 1 in January and 10 in March, at 11 of a total of 21 *scandens* nests on the island, all containing young between 7 and 13 days old. All 11 were visited by at least one additional conspecific male, who fed the nestlings. All the helpers were unpaired adult males (at least 3 years old), and they all held territories. No first- or second-year males have ever been recorded helping. Four nests had 2 helpers and each of 4 helpers was known to visit 2 nests concurrently. Altogether at least 11 individuals were identified as helpers. Seven of these had been banded before 1977, and 5 of these 7 were known to have bred in 1976 or 1977. In all but two cases the helper held a territory adjacent to the nesting pair he visited; one bird, however, crossed two territories to visit a nest 300 m away while also attending a nest 60 m in the opposite direction in a territory adjacent to his own.

Daily visits by helpers at nests varied from one to 10 ($\bar{x} = 5.0 \pm 0.48$ SE). This contrasts with 15–32 visits by the paternal male ($\bar{x} = 24.0 \pm 0.26$) and 16–26 by the female ($\bar{x} = 21.7 \pm 0.17$). The number of times a helper regurgitated food for nestlings during a visit ($\bar{x} = 8.6 \pm 0.58$, $n = 36$) is indistinguishable from that of the paternal males ($\bar{x} = 8.6 \pm 0.76$, $n = 128$) but significantly lower than the number for females ($\bar{x} = 10.7 \pm 0.42$, $n = 112$, t-test, $P < 0.001$). Between 1.7% and 24.9% of all regurgitations at a nest in a day were made by helpers, and these values provide an estimate of their relative contribution of food. This estimate is only approximate, because Downhower (1978) (also pers. obs.) has shown that the amount of food brought per visit can vary substantially. As no nests were known without helpers and fledging success in general was very low we are unable to assess the impact of helpers on fledging success.

The response of parents of both sexes to helpers varied according to when helpers were first seen. Helpers were chased if they were seen away from the nest ($n = 17$ for males, $n = 7$ for females), but if these same individuals were encountered at the nest by the parents, they were usually allowed to feed the nestlings ($n = 3$ for males, $n = 1$ for females). The behavior of helpers also varied. Five birds flew quickly and directly to the nest and always spent less than 20 s at the nest feeding nestlings. This is a much shorter stay than that of the parents ($\bar{x} = 55 \pm 1.7$ s, $n = 218$). Six other helpers spent a similar amount of time at the nest to that of the parents, and four of these removed fecal sacs, as the parents did. These six helpers often took different routes to the nest from those of the parents, kept closer to the ground, and traveled less directly, suggesting an avoidance of the parents.

Although fledged young may be entirely dependent on adults for food for several weeks, helpers did not feed them. We have observed more than 1,000 feedings of fledged young by the parents and just one by a nonparental male, when a chick wandered into its territory. This male had helped but not at the nest from which the chick had fledged.

The skewed sex ratio in favor of males, caused by differential survival during the drought year of 1977 (Grant and Grant 1980), provided conditions conducive to helping. The drought also prevented successful breeding in that year (Boag 1981). Of the 90 adult *scandens* in January 1979, 69 (76.6%) were males. The proportion of unpaired adult males fell from 60%

in January to 29% in May 1979, however, and then to 19% in March 1980, as a result of recruitment from the 1978 cohort. The incidence of helping also appeared to decrease. In May 1979 2 out of 4 nests (50%) watched for whole days had helpers, and in January to April 1980 2 out of 6 nests (33%) had helpers. The two helpers in 1980 were the only remaining unpaired birds of those known to help in 1979.

In *G. fortis*, which had a similarly skewed sex ratio, we found helpers at 2 of 6 nests watched for full days in 1979, and they made 1 and 4 visits respectively. During less extensive observations in 1981, we recorded one case of a *G. scandens* male attending a *G. fortis* nest. The *fortis* male parent at this nest, however, was unusual morphologically and was possibly of hybrid origin. Helpers have not been recorded in nest watches with these and other *Geospiza* species on other islands or on Daphne before the drought (Downhower 1978, Grant and Grant 1979, unpubl. obs.; Boag 1981).

Kin selection has been invoked as part of an evolutionary explanation for many observed cases of helping behavior. Close kinship between helpers and helped is unlikely in these cases, however, even though relatedness among adult males is unknown. First, only one of the 58 young (a male) of known birthplace has settled in a territory adjacent to that of the parents, and of the 16 nests fledging more than one young in 1978 there is only one instance of siblings (two brothers) settling in territories adjacent to each other. Yet nine of the 11 cases of helping in our study involved helpers from adjacent territories. Even though we do not know the relatives of the helpers, the evidence argues against relatives settling in adjacent territories and helping one another. Second, known first- and second-year offspring (which were not breeding, $n = 18$) were never discovered helping their parents. Third, the only helper who sang the rarer of the two song types present on the island helped at three different nests where the paternal male sang the commoner type. Because sons copy their father's song type (in 20 out of 20 cases), this evidence shows that the helper was not assisting his male relatives. Fourth, several helpers attended more than one nest, and these nests were also receiving visits from other helpers. Any scheme of close relationships between subsections of the population would have to be extremely complicated to account for this pattern.

We consider several hypotheses proposing that the behavior evolved through individual selection. Because five, and possibly all, of the helpers had bred successfully before 1979, we rule out the often advanced argument (e.g. Emlen 1978) that they gained experience preparatory to breeding.

Helpers may gain by increasing the chances of securing a mate in following breeding seasons from among the birds they helped to raise. This did not occur. Breeding success in 1979 was poor, and only two females from observed nests with helpers survived to breed. They paired with males not known to help. Furthermore, no females ($n = 28$) have been known to settle in territories adjacent to their birthplace, whereas all helper males retained the same territory in successive breeding seasons. Helpers may also gain by attracting the females they helped. Only three females have changed mates during the study, and none of these paired with a bird known to help at her nest, although all of these helpers remained unpaired and nearby.

A second possiblity is that helper males "stole" copulations (Bray et al. 1975, May and Robertson 1978) from females on adjacent territories and therefore, potentially at least, fed their own offspring. We have never observed selective feeding of chicks by helpers at any nest, however. We have other evidence that argues against uncertain paternity as being a general explanation for helping. Of more than 200 copulations observed in the field, all have been between individuals of mated pairs. On six occasions females have been observed refusing a displaying intruder, then copulating with their mate upon his return. Where uncertain paternity is implicated, we have failed to detect helping. P. T. Boag (1981) has evidence from studies of the population of *G. fortis* in 1978 that females that raised second broods with different males were inseminated by their mates of the first brood. In our study two female *scandens* from watched nests raised second broods with new males, but their old mates did not help. Incidentally, both the newly mated males had previously helped but not the pairs from which their females originated.

These observations, combined with the cessation of helping when the young fledged, do not point to any obvious selective advantage to helping. Therefore we accept the null hypothesis stated earlier that the helping reported here is a case of misdirected parental care, possibly stimulated by the loud vocalizations of the nestlings. Misdirected care is the generally accepted explanation for many unusual cases of helping, which may often arise after the helper has lost its own brood (Brown 1978, Brown and Brown 1980; see Perrins 1979 for cases of interspecific helping arising in this way). In 1980 a *G. fortis* helping a conspecific fitted this category. The widespread occurrence of brood parasitism (Payne 1977) shows that parental care can easily be misdirected (Coyne and Sohn 1978). Misdirected care has also been proposed as the explanation for nonparental feeding of fledglings in communally breeding Gray-breasted Jays (*Aphelocoma ultramarina*) (Brown and Brown 1980) and for nest attendance by stranger male Savannah Sparrows (*Paserculus sandwichensis*) after experimental removal of the parental male (Weatherhead and Robertson 1979). In general, however, selective explanations have been invoked for helping even when nonkin are involved (e.g. Woolfenden 1975, Reyer 1980, Birkhead 1981, Emlen 1981).

Hypotheses of selection are usually based on the assumption that there is some cost to helping (Brown 1978, Emlen 1978). In this study, and others, breeding is not an alternative (because of mate shortage), and selection pressure against helping may be very weak. In fact, we were unable to detect any disadvantage to helping with regard either to future survival or to breeding. Only two males disappeared between January 1979 and January 1980; neither was a known helper. Ten of the 11 helpers (19%) had secured mates by March 1980, whereas only 20 of the 29 unmated adult males not known to help (69%) had done so. The difference is not significant ($\chi^2_1 = 1.9$, $P > 0.1$).

We have postulated a positive association between parental feeding and helping that results in the expression of helping behavior because of the adaptiveness of parental feeding. This postulate has further implications for selection on the helping behavior. Selection against helping may be weakened because of possible maladaptive consequences for parental behavior. If there is selection for helping, by contrast, the helping behavior should rapidly spread in the population. This leads to the expectation that there should not be large variation in expression of the behavior among equivalent members of the population if helping is adaptive. If we assume that nonbreeding males in this study are equivalent with respect to potential selection pressures, then the observed variance in behavior (with several males apparently not helping at all) adds support to a nonadaptive hypothesis.

To summarize, the costs and benefits of the helping behavior we have described seem to be small or nonexistent. Although our study is unusual in some respects, it does suggest the possibility that costs and benefits in other species may be insufficient to cause significant selection for or against the helping behavior. We hope that other workers will be encouraged to give more serious consideration to this possibility in studies of helping behavior.

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