Helping, or the feeding of young birds by non-
parental 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, Da-
vies 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 attrib-
uted to selection pressures for the maintenance of a
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 (Me-
dium 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 be-
behavior against a null hypothesis. Misdirected paren-
tal care is offered as a null hypothesis, and we con-
sider 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 in the nest at both species.
At this time, hatching success of fortis eggs was very
low, and all further observations except where speci-
fied 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 help-
ers was known to visit 2 nests concurrently. Alto-
gether at least 11 individuals were identified as help-
ers. 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 op-
posite direction in a territory adjacent to his own.

Daily visits by helpers at nests varied from one to
10 (x̄ = 5.0 ± 0.48 SE). This contrasts with 15–32 vis-
its by the paternal male (x̄ = 24.0 ± 2.26) and 16–26
by the female (x̄ = 21.7 ± 0.17). The number of times
a helper regurgitated food for nestlings during a visit
(x̄ = 8.6 ± 0.58, n = 36) is indistinguishable from
that of the paternal males (x̄ = 8.6 ± 0.76, n = 128)
but significantly lower than the number for females
(x̄ = 10.7 ± 0.42, n = 112, t-test, P < 0.001). Be-
tween 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 sub-
stantially. 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 (x̄ = 55 ± 1.7 s,
66 = 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 depen-
dent 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 con-
ducive to helping. The drought also prevented suc-
cessful 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 possibility 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 (Passerculus 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 (χ^2 = 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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**Literature Cited**


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