

ON THE SIGNIFICANCE OF HELPING BEHAVIOR IN BIRDS

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ABSTRACT.—In cooperatively breeding birds, the feeding of nestlings by nonbreeding helpers may be derived from a general stimulus-response interaction, widespread among altricial species. It has been suggested that adaptationists have overinterpreted this helping behavior. Two distinct points can be recognized here: evolutionary origin and current functional significance. The significance of helping behavior to the helper appears to vary on a species-to-species basis. However, the evidence overall does not support a unitary, nonfunctional or nonadaptive interpretation of avian helping behavior. *Received 1 February 1989, accepted 2 June 1989.*

THE IMPETUS for this essay was a paper by Ian Jamieson and John Craig (1987), "Critique of helping behavior in birds: a departure from functional explanations." More recently, Jamieson (1989) reiterated and qualified Jamieson's and Craig's major arguments. Jamieson and Craig make some important and previously unstated points that merit the attention of the ornithological community. Their nonadaptive or "unselected" explanation of helping behavior in cooperatively breeding birds, specifically the feeding of nestlings by nonbreeders, requires a response from function-oriented students of avian cooperative breeding. Jamieson and Craig address two major issues. We present each of these issues as a direct statement and offer replies to them.

1. *Feeding nestlings by nonbreeding helpers is not a unique behavior that sets cooperative breeders apart from other avian species.*—The view that avian cooperative breeding is a subject apart from other areas of ornithology is based both on the existence of nonbreeding helpers and on the interpretation of their significance. Nonbreeding helpers define cooperative breeding, and early in the modern study of this subject, emphasis was placed on the concept of "altruism" by helpers (e.g. Brown 1970, 1974, 1975). Brown and Brown (1981) and Brown (1987) later urged caution in the use of the term "altruism." However, the perception had been established that feeding behavior by nonbreeding helpers was a costly behavior in terms of personal reproductive success and that helpers were repaid by gain in the indirect component of their inclusive fitness. This dichotomy—species with altruistic helpers and species without helpers—tended to foster the view that avian cooperative breeding is fundamentally distinct from other

aspects of avian reproductive biology, which are based on male-female and parent-offspring interactions and can be accounted for solely by direct gains in inclusive fitness.

In contrast, Jamieson and Craig (1987) argue that the feeding of nestlings by helpers basically is no more than a manifestation of a general trait among altricial birds, namely an "automatic" response (placing food) to a stimulus (the gaping mouth of a vocalizing nestling). They point out that nonbreeding birds of a variety of species (including individuals too young to be "hormonally primed") will respond to this stimulus. Other lines of evidence also support a stimulus-response interpretation of feeding behavior. For example, many cases of interspecific feeding of nestlings have been recorded (Shy 1982), and a wild bird even fed fish (see Welty and Baptista 1988: fig. 17-7). Perhaps the best evidence for the stimulus-response nature of feeding nestlings comes from the phenomenon of avian brood parasitism. Certain species, such as many cuckoos and the Brown-headed Cowbird (*Molothrus ater*) in North America, specialize in exploiting the general gaping-feeding interaction. These points led Jamieson and Craig to propose "that the feeding of nestlings in communal breeders is maintained by the same stimulus-response mechanism that results in parents feeding their own young or host species feeding parasitic young..." (Jamieson and Craig 1987: 80).

Jamieson and Craig argue that the feeding of nestlings by nonparents is not a uniquely evolved character that distinguishes cooperatively breeding species from other birds. Rather, it is the nondispersal of young birds that provides these nonbreeders with access to the stimulus of begging nestlings (also see Wool-

fenden and Fitzpatrick 1984: 345). Jamieson and Craig conclude that no evolutionary change based on selection for helping behavior per se has occurred in cooperative breeders. By this view, cooperative breeding is no more than the outcome of ecologically based natal philopatry, which provides the opportunity for the stimulus-response feeding interaction between nonbreeding helpers and nestlings.

A question that arises is whether Jamieson and Craig have confounded two separate issues: origin of a trait and current utility or functional significance of that trait (Tinbergen 1963, Sherman 1988). This leads to their second and more controversial point.

2. *It is inappropriate to interpret helping behavior in cooperative breeding systems in an adaptive framework* ("We therefore advocate a complete departure from increased fitness-type arguments to explain the occurrence of so-called helping behavior." Jamieson and Craig 1987: 92).—Jamieson and Craig's view of helping behavior as a single stimulus-response interaction has a certain appeal in that it hypothesizes a single explanation for the feeding of nestlings. For example, in a variety of cooperatively breeding species, no positive effect of feeding behavior on reproductive success or survival of group members has been observed; in some cooperatively breeding species, helpers unrelated to the young occur regularly; and in some well-studied cooperative breeders, there is no relationship between degree of genetic relatedness and feeding effort by helpers (e.g. Rabenold 1984, 1985; Emlen and Wrege 1988). At one level these facts appear to support Jamieson's and Craig's unitary, nonadaptive explanation of helping behavior. However, this diversity of observations also suggests an alternative interpretation.

The relevant data on cooperative breeders suggests to us that Jamieson and Craig have overextended their nonadaptive view of the helping phenomenon. Although we agree that early in the study of cooperative breeding too much emphasis was placed on kinship or indirect fitness as an adaptive explanation for helping, we believe also that the way to understand helping behavior is to recognize and appreciate the variation among cooperative breeders in both the circumstances and the effects of helping. We concur with Jamieson and Craig that the feeding response of helpers probably occurs in a proximate sense because nonbreeders are in close proximity to begging nest-

lings and therefore have access to them. This factor probably is shared by all cooperative breeders (Fig. 1). However, developments subsequent to this common starting point are the ones of special interest to most students of adaptation (e.g. "... adaptation should be defined by its effect rather than by its causes . . .," Clutton-Brock and Harvey 1979, also see Mayr 1983). As Sherman (1988) pointed out, hypotheses about the evolutionary origin of a trait and its current significance are at different "Levels of Analysis" and thus are not alternatives. Few students of cooperative breeding have confounded origin of helping with its current functional effects (*contra* Jamieson 1989).

It is likely that no adaptive benefit to helpers, direct or indirect, will be detectable in each and every cooperatively breeding species. We are looking at a variety of birds through a single slice in time; and the time elapsed since the initiation of group-living via natal philopatry, as well as the ecology and intensity of subsequent selection, almost certainly will vary from species to species (Fig. 1). In cases where cooperative breeding has been the rule for a long time, we may be able to document a benefit of some sort to the helpers. This provides a feedback system that can reinforce the feeding behavior and fine-tune the entire nestling-helper interaction.

If helping behavior is costly to the helper, and if it persists, we would expect a compensating benefit. However, with one possible exception (Reyer 1984), no cost of helping in terms of direct fitness has been detected for any cooperative breeder. In addition, the stimulus-response feeding behavior probably will nearly always be maintained by natural selection because of its overwhelming importance in parental care (Jamieson 1989), because all birds hatch with the possibility of becoming parents (i.e. the cost of responding to a nearby gaping mouth rarely will exceed its benefits), and because production of offspring is by far the primary means of maximizing individual fitness.

Interactions with nestlings (e.g. feeding and grooming) can potentially increase the direct or personal fitness of helpers. Because of the large number of social relationships that may be modified to the helper's advantage by virtue of its feeding and other cooperative behavior, development or strengthening of personal bonds with the young birds can benefit greatly both helper and nestlings. For example, in Green Wood-

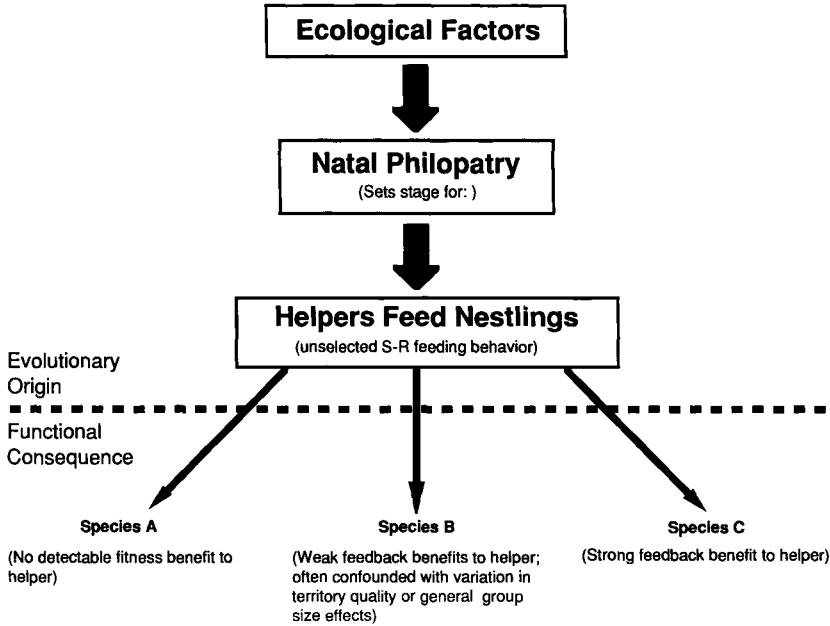


Fig. 1. The relationship between (1) ecological factors and natal philopatry (constraints, Emlen 1982, or benefits, Stacey and Ligon 1987, in press), and (2) the natal philopatry of helpers and the expression of the stimulus-response (S-R) interaction (Jamieson and Craig 1987).

hoopoes (*Phoeniculus purpureus*), helpers can gain breeding status in a new territory via cooperative group emigration. In this way younger, subordinate allies are critically important to the helper (Ligon and Ligon 1983). The same is true for Acorn Woodpeckers (*Melanerpes formicivorus*; Koenig 1981, Hannon et al. 1985), and Arabian Babblers (*Turdoides squamiceps*; A. Zahavi pers. comm.). In the babblers and the woodhoopoes, helpers may compete among themselves to feed nestlings and young fledglings by stealing food from each other and taking it to the young birds. Feeding behavior may help to cement personal bonds in a manner similar to alloparental care and grooming in primates. Thus, helping can produce a variety of positive fitness effects for a helper which can be viewed as adaptations based in part on the feeding response.

Thus far, we have emphasized adaptive extensions of the basic stimulus-response behavior. The feeding response can be modified in other ways. Apparently, it can be repressed by selection. Stacey (1979) found in the polygamous Acorn Woodpecker that individuals that joined a group after egg laying (thus they could not be parents) declined to feed the nestlings. Koenig (MS) has experimentally corroborated

and extended this finding. Immigrants also sometimes killed young birds if re-nesting was possible (Stacey and Edwards 1983). These negative responses provide important evidence (different in kind) that selection has operated on the basic feeding response in this species.

As pointed out earlier, indirect fitness benefits have often been viewed as critical payoffs to helpers. We have placed a few selected cooperative breeders into one of three categories to document the variation among species in indirect fitness effects (Table 1). Additional examples could be added.

Species in Category A (Table 1) fail to demonstrate a positive relationship between helpers and number of related young birds produced (the first prerequisite for an adaptive, indirect fitness interpretation of helping behavior). Three cases illustrate this point: (1) Bednarz (1987) found that pairs and groups of Harris' Hawks (*Parabuteo unicinctus*) showed no difference in clutch size, number of young produced per successful nest, or number of offspring fledged per year. (2) For the Pygmy Nuthatch (*Sitta pygmaea*), Sydeman (1989: 154) concluded that "... helpers appear to be selectively neutral in relation to feeding rates and enhancement of reproductive success." Also,

TABLE 1. Selected examples of indirect fitness effects on helpers. Sources follow scientific names.

| A. No correlation between helpers and number of fledglings | B. Correlation between presence of helpers and young birds produced | C. Increased productivity due to helping behavior ¹ |
|---|--|---|
| Harris' Hawk <i>Parabuteo unicinctus</i> Bednarz 1987 | Acorn Woodpecker <i>Melanerpes formicivorus</i> Stacey & Koenig 1984, Koenig & Mumme 1987 | Pied Kingfisher <i>Ceryle rudis</i> Reyer 1984 |
| Pygmy Nuthatch <i>Sitta pygmaea</i> Sydeman 1989 | Stripe-backed Wren <i>Campylorhynchus nuchalis</i> Rabenold 1984 | White-fronted Bee-eater <i>Merops bullockoides</i> Emlen 1984 |
| Superb Blue Wren <i>Malurus cyaneus</i> Nias 1987; Nias & Ford MS | Gray-backed Fiscal Shrike <i>Lanius excubitorius</i> Zack & Ligon 1985 | |

¹ Feeding of nestlings.

helpers do not enhance the survival of the breeders. (3) Similarly, in the Superb Blue Wren (*Malurus cyaneus*), "the presence of helpers did not increase the number of fledglings produced per nest by breeding pairs or the annual reproductive output of breeders" (Nias 1987, Nias and Ford in press). Many of the Australian species that Dow (1980) referred to as "opportunistic cooperative breeders" may also fall into this category. For these species, the feeding of nestlings may not provide any measurable, indirect fitness benefits to the helpers, and this appears to support the arguments of Jamieson and Craig.

Species in Category B (Table 1) represent the most common situation and the one most difficult to interpret. In these, there is a positive relationship between numbers of helpers and number of young fledged; however, all of these species are territorial and territory quality may affect reproductive success. A causal relationship between number of helpers (group size) and production of young birds is therefore questionable (e.g. Koenig and Mumme 1987: 165). Various studies (e.g. Zack and Ligon 1985) have attempted to separate statistically these effects, but there is no unequivocal evidence that helpers rather than some aspect of territory quality drive the positive relationship between group size and productivity (Stacey and Ligon 1987).

Many of these examples also illustrate another potentially confounding problem. If a positive relationship exists between presence or number of helpers and number of young produced per year, a common interpretation is that "helpers help." The simple implication of this interpretation is that this is *why* helpers are present.

Before this interpretation can be accepted, two other points must also be considered. First, this positive relationship may be based on a more general positive group-size effect related to predator deterrence. For example, in Florida Scrub Jays (*Aphelocoma c. coerulescens*), all social categories—breeders, nonbreeding helpers, and immatures—survive better when more birds (i.e. helpers) are present (Woolfenden and Fitzpatrick 1984). Rabenold (1984) found that reproductive success, as measured by fledglings produced, was correlated positively with group size in the Stripe-backed Wren (*Campylorhynchus nuchalis*). This effect was not related to feeding nestlings. Moreover, juvenile survival over the first 6 months was unaffected by group size. Thus it may be misleading to conclude that the evolved function of feeding by helpers is *for* production of younger relatives.

Second, in most cooperative breeders the basic social unit is composed of a breeding pair and their offspring or siblings. In such systems, the only individuals available for a young bird to interact with are its relatives, and it is difficult to identify the evolutionary basis of the observed interactions (Ligon 1983). Some students of cooperative breeding have assumed that a positive relationship between helper numbers and production of young birds was driven by kinship. However, the fact that helpers are usually related to nestlings in and of itself does not necessarily support a kin-selected interpretation of helping behavior. For example, Wilkinson (1988) used both empirical field data and computer simulations to investigate the effects of food-sharing (a similar form of aid-giving) on the probability of survival of vampire bats (*Desmodus rotundus*). An intriguing outcome was

that reciprocal aid-giving contributed more to an individual bird's inclusive fitness than kinship, regardless of relatedness (i.e. cooperation has personal benefits apart from, or in addition to, genes shared by relatives). This conclusion is highly relevant to considerations of the evolutionary significance of avian helpers.

At least two well-studied situations demonstrate a strong increase in production of young, directly as a result of the food delivered by helpers (Table 1: Category C). The striking effect of food delivered by helpers on production of young birds make two colonial species, the White-throated Bee-eater (*Merops bullockoides*) and the Pied Kingfisher (*Ceryle rudis*), the strongest cases known for an adaptive, indirect effect of feeding nestlings (Emlen 1984, Emlen and Wrege 1988, Reyer 1984). Helpers in the nonterritorial Pied Kingfisher fall exclusively into one of two categories, primary (close relatives [$r = 0.5$ or 0.25]) or secondary (unrelated). Because helpers exert such a profound effect on the number of young produced and because territory quality is not a confounding variable, kingfisher primary helpers are the best example of a specific adaptive, indirect effect of helping behavior.

In summary, as Jamieson and Craig (1987) suggest, placing food in the gaping mouths of nestlings seems to be a basic trait of altricial birds. This view is supported by the hundreds of species exploited by social parasites and by the many cases of interspecific feeding. In cooperatively breeding birds, nonbreeding individuals remain in their parents' territory and feed youngsters. This may be due initially to physical proximity and free access to the stimulus of begging nestlings. According to this view, feeding by helpers is not a specially evolved characteristic of cooperative breeders. Among some cooperatively breeding species, however, helping behavior appears to have reliable benefits for the helper at least as often as for the recipients. In these cases, it appears that the basic stimulus-response pattern emphasized by Jamieson and Craig has been affected by natural selection in a number of diverse ways that are to the helpers' benefit (via either direct or indirect fitness gains, or both). If so, the non-adaptive interpretation of feeding by helpers as proposed by Jamieson and Craig is useful to understand the evolutionary background of helping at the nest, but it is insufficient to account for the current significance of the phe-

nomenon. As Sherman (1988) pointed out, two explanatory hypotheses at different levels of analysis (here origin and current utility) can both be correct. With regard to the latter, it appears that the relative costs and benefits of helping behavior for both donors and recipients vary from species to species, and even from situation to situation within a species (e.g. Reyer 1984). The current significance of helping behavior in birds cannot be fully explained by any single adaptive model and in fact for some species no adaptive function has been identified. Thus the overall significance of helping behavior per se will be understood only by investigating the phenomenon on a case-by-case basis. Although this is not a satisfying conclusion, we believe that it is the one best supported by current evidence.

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