SHORT COMMUNICATIONS

Dipper Nestlings Fed by a Gray Wagtail

SONJA I. YOERG[1] AND JOHN O'HALLORAN[2]
[1]*Department of Psychology, University of Massachusetts, Amherst, Massachusetts 01003 USA, and*
[2]*Catchment Research Group, National Rivers Authority, Penyfai House,*
Llanelli, Dyfed SA15 4EL, United Kingdom

There are many published reports of interspecific feeding among birds (see Shy 1982 for review). One of the most commonly observed types of interspecific feeding, exclusive of nest parasites, involves one species feeding the nestlings of another (Shy 1982). The absence of a genetic relationship between caretaker and young poses obvious difficulties for adaptive explanations of this behavior. Previous observations have been brief because the sporadic and unpredictable nature of cross-specific fostering typically precludes systematic study. Nevertheless, if explanations are to be found, more detailed accounts are essential. We report extensive observations of a male Gray Wagtail (*Motacilla cinerea*) feeding Eurasian Dipper (*Cinclus cinclus*) nestlings. A pair of Gray Wagtails had previously been seen feeding dipper nestlings (H. Mayer-Gross pers. comm. *cited in* Tyler 1972), but details are unavailable.

In 1989 as part of a larger study (Ormerod and Tyler 1987, Yoerg in prep.), we observed a dipper nest from a blind 5 m away. A Gray Wagtail nest was 1 m from the dipper nest. Because these species use similar sites, it is not unusual for dipper and Gray Wagtail nests to be close together (e.g. Tyler 1972). Both nests were on a vertical ledge above a narrow (1.5 m wide) tributary of the River Edw, Powys, Wales (52°07'N, 03°15'W). During the first sessions (18 May 1989, 0515–1300 and 1500–1900), the dipper nestlings were 6 days old. Subsequent observations were made on 23 May (0450–1300 and 1500–1900) and on 24 and 26 May (0930–1130). The dipper nest was destroyed by a predator on 27 or 28 May.

We recorded all activities at the dipper nest including aggressive interactions between the species. Deliveries by the Gray Wagtails to their own nestlings were noted first beginning at 0800 on 23 May. The adult dippers were uniquely color-banded. The wagtails were sexed by plumage differences.

During the 11.75 h of observation on 18 May, we observed no cross-specific feeding. The first instance was recorded on 23 May. We probably observed the behavior develop. When the male wagtail fed his own young, he usually flew directly in front of the dipper nest, then perched on top of this nest before flying laterally to his own. The movement of the wagtail across the dipper nest hole always elicited begging from the dipper nestlings. The first time we observed the male wagtail feed the dipper nestlings, he landed at the opening of the nest, instead of on the dome, and fed the begging nestlings. Closeness of nests is the most common proximal reason for interspecific fostering (Shy 1982) and was clearly a factor in this case. Begging by the nestlings, although rarely identified as an elicitor of interspecific feeding, was almost certainly contributory.

During the next 20 min, the Gray Wagtail fed the dipper nestlings nine times. The proportion of all deliveries to the dipper nest made by the wagtail increased significantly during the morning ($r^2 = 0.732$, df $= 6$, $P < 0.05$), rising to 75.0% of all deliveries (Fig. 1A). The wagtail made more deliveries than the dippers combined during 3 of the 4 h of afternoon observation (mean = 64.8% of all deliveries). His contribution declined slightly during the two subsequent observation periods (24 May, 54.1%; 26 May, 52.8%). During 15 h of observation over 3 days, the wagtail fed the dipper nestlings 176 times, making 4 more deliveries than the dippers combined. (Load sizes of the two species, calculated directly from wagtail nestlings with neck collars and indirectly from load composition in adult dippers [Ormerod unpubl. data], are comparable.) The wagtail also contributed in another way: three times he removed feces from below the dipper nest.

Despite the substantial and increasing contribution by the male wagtail during the morning of 23 May, the total number of deliveries by both species to the dipper nest remained constant ($r^2 = 0.315$, df $= 6$, $P > 0.05$). That is, the dippers made fewer deliveries as the wagtail made more (Fig. 1A). Delivery rates on 24 and 26 May were comparable to those observed at this nest on the first observation day and at other nearby nests that year (Yoerg unpubl. data).

On the morning of 23 May, as the male wagtail fed the dipper nestlings more often, his contribution to his own nest declined sharply, falling to 11.1% of the total (Fig. 1B). During that evening, however, the male made more than half of the deliveries to the wagtail nest. His contribution fluctuated between these extremes on 24 and 26 May. The female wagtail compensated somewhat for the behavior of her mate. For example, the hour during which she made the most deliveries ($n = 16$; 23 May, 1100) followed the hour during which her mate brought food only once.

The female dipper chased both the male wagtail (18 chases) and the female (6 chases) wagtail. Seven of the 18 chases of the male occurred on 23 May from 0800 to 0900, shortly after the first observed inter-

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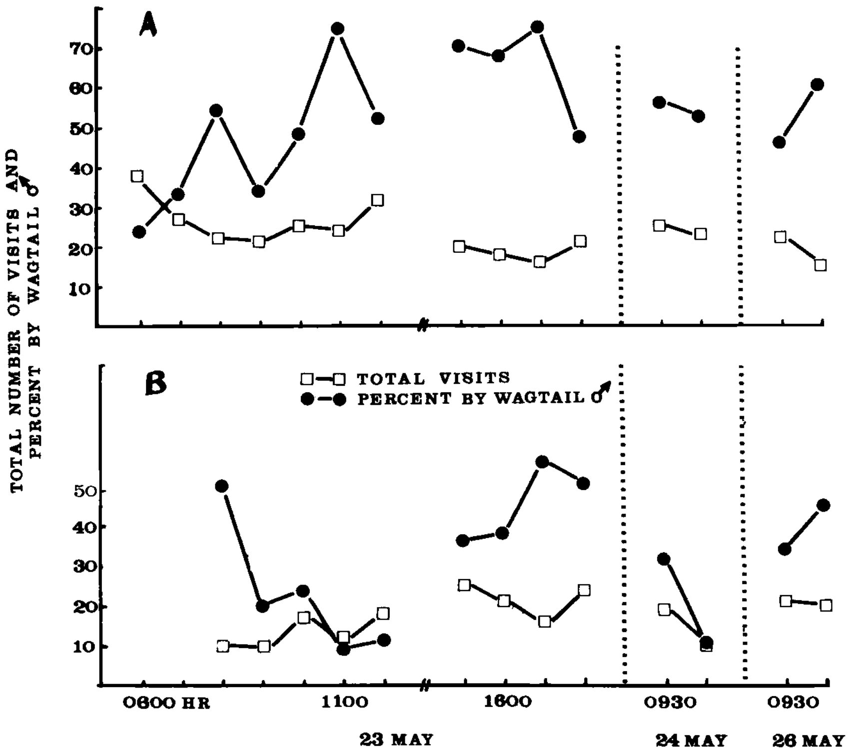

Fig. 1. Total number of visits and the percent contribution by the male wagtail during each hour of observation at the dipper nest (A) and the wagtail nest (B).

specific feeding. The chases usually followed approaches by the male wagtail to the dipper nest. This bout of aggression and the sharp increase in the interspecific feeding rate strongly suggests the behavior had developed that morning. Because aggression did not deter the wagtail, the stimuli (probably the proximity of loudly begging chicks) that motivated him to feed alien young must have been very potent.

Beginning at 1500 on 23 May, we noted whether the dipper parents were present when the wagtails brought food to either nest. When a dipper was present, the male wagtail fed the dipper nestlings only once but fed his own nestlings 15 times. A dipper was also more likely to be present when the male wagtail fed his own nestlings (24.5% of 61 deliveries) than when the female fed them (10.4 % of 96 deliveries). We believe that the presence of dippers, and presumably the threat of aggression from the female, may have partly determined which nestlings the male wagtail fed. Indeed, after the bout of chasing early on 23 May, if a dipper was near when the male wagtail arrived with food, the wagtail usually delayed delivery until the dipper left. However, the dippers were present less frequently as the wagtail fed their nestlings more frequently, presumably because the nestlings were not as hungry and begged less. The male wagtail was therefore increasingly able to feed the dipper nestlings without risk of aggression. This feedback relation may have occasioned the sharp rise in interspecific feeding rate and maintained it at a high level.

Between the efforts of the male wagtail and the dippers, the nestlings were adequately fed. The bodyweights and tarsus-lengths were similar to dipper nestlings of the same age at other nearby sites 36 h after the first feeding (Yoerg unpubl. data). We could not evaluate longer-term effects of interspecific feeding because the dipper nest was lost to a predator. It is unknown whether the predation was related to the interspecific feeding per se, although the proximity of the nests and the aggression between the species may have made the nests more conspicuous.

Data on other species suggest that had the dippers survived, their behavior might have been altered. For example, female Zebra Finches (*Poephila guttata*) raised by Bengalese Finches (*Lonchura striata*) did not choose conspecific mates (Sonnemann and Sjolander 1977). It is possible that dippers fed chronically by a Gray Wagtail would not develop normal mate preferences. Furthermore, although the diets of dippers and Gray Wagtails overlap considerably, differences exist. For example, wagtails eat many more dipterans and emerged insects than do dippers (Ormerod and Tyler 1987). Because early dietary experience can affect later choice (e.g. Rabinowitch 1968), the dietary preferences of dipper nestlings fed by wagtails might be atypical.

We do not understand what benefit, if any, accrued to the wagtail from feeding the dipper nestlings. Dawkins (1976) suggested that birds adopting alien young might benefit in gaining experience as a parent. Although this explanation might account for inexperienced birds feeding heterospecific nestlings, it seems unsuitable for the behavior of this Gray Wagtail, given that he simultaneously fed his own brood, at least one of which fledged. Instead, the prolonged investment in the dipper nestlings was more probably a maladaptive response to the proximity of loudly begging chicks. Strong responsiveness to stimuli associated with dependent young may have advantages that compensate for the rare instances in which that responsiveness results in maladaptive behavior. It may be significant that wagtail nestlings are much quieter than dipper nestlings. The dippers' calls may have acted as a "super-normal" stimulus (Tinbergen 1948) to trigger feeding of the alien young as the male passed en route to his own nest with food. One prediction of this hypothesis is that noisy nestlings would be more likely to be fed by heterospecifics than quiet nestlings, especially if the young of the adopting species are quiet.

A significant aspect of our observations is that spontaneous interspecific feeding, once initiated, may be self-perpetuating. First, increased feeding by the heterospecific reduces the parents' contribution and, consequently, their activity near the nest. The interspecific aggression that might deter the adopting bird is therefore less likely to occur. Second, the sign stimuli that initially occasioned the interspecific feeding (e.g. begging calls, gaping mouths) may become associated with the sight of the alien nest and with approaches to it, thus increasing the probability that the adopting bird will return to the alien nest. A comprehensive understanding of the proximal mechanisms underlying interspecific feeding, and any ecological and evolutionary consequences, awaits additional data.

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Mate Attraction by Autumnal Song in the Northern Mockingbird (*Mimus polyglottos*)

CHERYL A. LOGAN AND LAURA E. HYATT
Department of Psychology, University of North Carolina, Greensboro, North Carolina 27412 USA

The Northern Mockingbird (*Mimus polyglottos*) is perennially territorial in the southeastern United States. Both mated and unmated males defend autumnal territories, and both sing throughout the months of September and October (Breitwisch et al. 1986, Logan 1987). In the spring, unmated males sing more than mated males (Breitwisch and Whitesides 1987), and mockingbird song appears to function in mate attraction. Merritt (1985) removed females from the territories of mated males in the spring; the song production of males whose females were removed was greater than that of mated males and approximated amounts of singing produced by unmated males. Autumnal song is produced from early September to November, and mockingbirds have been observed to form pairs in autumn (Logan unpubl.