

BEHAVIORAL DIFFERENCES IN NEST VISITS BETWEEN MALE AND FEMALE NORTHERN MOCKINGBIRDS

RANDALL BREITWISCH,¹ NATASHA GOTTLIEB, AND JULIA ZAIAS²

Department of Biology, University of Miami, Coral Gables, Florida 33124 USA

ABSTRACT.—Male Northern Mockingbirds (*Mimus polyglottos*) behaved differently from females during feeding trips to nestlings. We monitored several aspects of behavior of parents within a 20-m radius of nests during 1,005 feeding trips, and timed durations of trips within this radius. During the first half of the 12-day nestling period, females—because they were brooding—spent more time per feeding trip to nestlings than did males. However, when nestlings were older than brooding age, females took less time per trip than did males. Males did not change their behavior in nest visits during the nestling period. Throughout the nestling period, males used more time per trip in approaching and leaving the vicinity of nests than did females. Males also used more perches during both nest approach and departure, although the sexes used perches of similar heights and distances from nests. More frequently than males, females flew directly to the nest without first perching within 20 m of the nest. A previously undescribed call was given almost exclusively by arriving males during nest exchange and food delivery to young nestlings being brooded by females. We interpret these behavioral differences as indicative of male predominance in vigilance against nest predators, at least in the vicinity of nests. Received 12 December 1988, accepted 4 June 1989.

PREDATION on eggs and nestlings is a major selective force shaping the nesting behavior of birds (Tinbergen et al. 1963, Ricklefs 1969, Skutch 1976). The demands of provisioning altricial nestlings can be substantial. It is not unusual for parents to make several hundred feeding trips to their nestlings each day for a one- to two-week nestling period. Parent birds with altricial nestlings are in danger of revealing to predators the location of their helpless young. There are several parental defenses against nest predators, and most individuals probably use a combination of tactics. First, many birds conceal nests or build them in locations that are relatively inaccessible to predators (reviewed in Skutch 1976, Collias and Collias 1984). Second, parent birds move cryptically while attending to nestling needs, especially when delivering food (Skutch 1976). Third, if nesting activities are discovered, parents may distract the predator (Simmons 1955, reviewed in Skutch 1976). Fourth, if a predator approaches a nest, parents may engage in active defense (Kruuk 1964, Andersson et al. 1980, Greig-Smith 1980,

Curio et al. 1985, Knight and Temple 1986, Regelman and Curio 1986, Breitwisch 1988).

Cryptic movements of parents caring for young have not been studied rigorously, but general patterns are known. Many birds delay food delivery to nestlings while predators are in the vicinity of the nest or nesting territory (Skutch 1976). Parents may also eat the food they are carrying to the nestlings (R. Breitwisch pers. obs.). This eliminates a potential cue to visually oriented predators that nestlings are nearby. However, the behavior of parent birds approaching nests on feeding trips has not been quantified. For example, Hann (1937) and Nolan (1978) both reported differences between the sexes in their approaches to active nests, but neither presented analyzed data.

We investigated nest-visiting behavior by Northern Mockingbirds (*Mimus polyglottos*) caring for nestlings. This species nests in shrubs and low in trees (Bent 1948, Laskey 1962, Means and Goertz 1983, Breitwisch 1988). Nests vary in concealment from those well-hidden in vegetation to nests rather conspicuous in sparse foliage (Joern and Jackson 1983, Means and Goertz 1983). Males defend eggs and, especially, nestlings from potential predators more strongly than do females (Breitwisch 1988). Further, both males and females care for fledglings. The males defend fledglings more strongly against potential predators and provide them

¹ Present address: Department of Biology, University of Dayton, 300 College Park, Dayton, Ohio 45469 USA.

² Present address: Department of Ecology, Ethology, and Evolution, 606 East Healey Street, University of Illinois, Champaign, Illinois 61820 USA.

with more feedings (Zaias and Breitwisch 1989). Also, males and females share equally in the provisioning of nestlings, although on different schedules (Breitwisch et al. 1986). In addition, Breitwisch et al. (1986) found that females made more trips delivering unidentified food items than did males. Their impression was that the primary reason for this difference was rapid approaches to nests by females.

We tested the hypothesis that there are behavioral differences in nest visits between male and female mockingbirds beyond those associated with females brooding young nestlings (see Breitwisch et al. 1984). We predicted these differences would appear in some combination of number and location of perches used during nest visits and time spent on these perches. Such differences could result from dissimilar behavioral demands on the time available to males vs. females. These may include, for instance, disparate levels of vigilance against predators or intruding conspecifics (Ydenberg 1987). Additionally, we asked whether there are particular calls given by one or both sexes that could serve to coordinate activity at the nest.

METHODS

We observed color-banded mockingbirds on the main campus of the University of Miami, Dade County, Florida, from late May to late July 1986. This is the latter half of the breeding season in southern Florida. The habitat is sparsely wooded, suburban lawn. Mockingbirds in this population are habituated to humans and are relatively easy to observe. One of us (Breitwisch) had handled nestling and fledgling mockingbirds earlier in the breeding season and was recognized as a potential predator (Merritt 1984) and forced to observe from a blind.

We observed 14 pairs of mockingbirds that fed nestlings in 19 broods during 95 one-hour observation periods between 0600 and 1800 EST. Our choice of pairs for study was partially based on visibility of nests. In order to be certain of numbers and locations of perches used during feeding trips, we restricted our observations to pairs with nests that were at least partially visible from several vantage points at distances of at least 20 m. We sampled feeding throughout the nestling period, from the day of hatching (day 0) to fledging (usually day 12). Sample sizes used in analyses differed slightly because not all values for variables could be estimated for each feeding trip.

During each observation period, we recorded every feeding trip by both parents, whether each food item delivered was fruit or arthropod, and whether the

item was small (fit within the margins of the bill) or large (extended beyond the margins of the bill).

We defined a *feeding trip* as an instance when a parent brought food to the nest and left without food. The duration of a trip (*total trip time*) was the interval between the time a parent flew within 20 m of the nest and the time, after feeding, when the parent flew beyond 20 m from the nest. Total trip time was divided into time at the nest (*nest time*) and the remaining duration of the trip (*non-nest time*). The 20-m radius included the largest area surrounding the nest we could expect to monitor. When a parent occasionally foraged within 20 m of the nest, we measured trip duration from the time the parent flew toward the nest with the food item until the parent flew beyond 20 m from the nest after feeding.

We recorded each perch used within 20 m of the nest on both the approach and departure during a feeding trip. All data were spoken into tape recorders and later transcribed onto data sheets for computer entry. We used five categories of perch location: (1) perch not in the nest tree, used on approach; (2) perch in the nest tree, used on approach; (3) perch was the nest itself; (4) perch in the nest tree, used on departure; and (5) perch not in the nest tree, used on departure.

Perches chosen when near the nest may be chosen to allow vigilance against predators (see Ydenberg 1987 for a similar influence of vigilance against territorial intruders on choice of feeding perches). We assume that higher perches allow wider visual scanning of the area surrounding the nest than low perches allow. Second, we assume that perches used in locations other than the nest tree are useful for such vigilance before and after delivery of food to nestlings. We recorded perch height (nearest 0.5 m) relative to nest height and horizontal distance between the nest and each perch (nearest 1.0 m). We also recorded the time (s) a parent sat on each perch, and the time it was at the nest. We practiced estimating heights and horizontal distances before and during this study.

We noted every instance a parent removed a fecal sac. In removing a fecal sac, a parent mockingbird flies directly away from the nest (Breitwisch pers. obs.). We asked if there is a sex bias in removal of fecal sacs, because such a bias could affect the perch used after food delivery.

We noted the time of each bird's vocalization and the bird's location in relation to the nest when vocalizing. Parent mockingbird vocalizations during the nestling stage include several types of calls; song is infrequent (Logan 1983, Merritt 1985). Call types include a harsh, rasping, drawn-out Hew Call (Logan and Fulk 1984), a short, explosive, wide-frequency Chat Call (Logan et al. 1983), and a high-frequency cry of variable length (Breitwisch 1988). Calls commonly are given when a predator is visible (Breitwisch 1988), and we noted whenever a potential pred-

TABLE 1. Parental behavior on feeding trips to nestling Northern Mockingbirds. Nestling ages are in parentheses.

	Males	Females	T ^a	P	n
Time/trip (s)					
Nest time (≤ 6 days)	42 $\pm$ 11 ^b	177 $\pm$ 31	0	<0.01	11
Nest time (≥ 7 days)	22 $\pm$ 3	30 $\pm$ 7	20	NS	10
Non-nest time (≤ 6 days)	103 $\pm$ 15	56 $\pm$ 10	3	<0.01	11
Non-nest time (≥ 7 days)	92 $\pm$ 15	38 $\pm$ 10	0	<0.01	10
Total trip time (≤ 6 days)	145 $\pm$ 17	233 $\pm$ 32	6	<0.02	11
Total trip time (≥ 7 days)	114 $\pm$ 16	68 $\pm$ 11	1	<0.01	10
No. Perches/trip					
Used in approach	2.6 $\pm$ 0.3	1.6 $\pm$ 0.2	11	<0.05	14
Loc. 1 perches	1.1 $\pm$ 0.2	0.5 $\pm$ 0.1	3	<0.01	14
Loc. 2 perches	1.5 $\pm$ 0.2	1.0 $\pm$ 0.1	15	<0.02	14
Used in departure	1.3 $\pm$ 0.1	0.9 $\pm$ 0.1	21	<0.05	14
Loc. 4 perches	0.9 $\pm$ 0.1	0.7 $\pm$ 0.1	25	NS	14
Loc. 5 perches	0.5 $\pm$ 0.1	0.3 $\pm$ 0.1	19	NS	13
Total used in trip ^c	4.9 $\pm$ 1.2	3.6 $\pm$ 0.9	3	<0.01	14

^a Wilcoxon matched-pairs signed-ranks tests.^b Values are grand means $\pm$ SEM calculated from mean values for individuals.^c Includes nest itself as a perch.

ator was on the focal territory (see Breitwisch [1988] and below for a list of possible predators on young mockingbirds). We restricted our records on predator occurrence to the focal territory because vegetation limited our view onto adjacent territories, and we could not always be certain if a predator was on an adjacent territory.

For some analyses, we divided the data into feeding trips to nestlings ≤ 6 days old vs. trips to nestlings ≥ 7 days old. Previous work in this population (Breitwisch et al. 1984) has shown that females brood nestlings ≤ 6 days old, and female behavior during feeding trips may change between the first and second halves of the 12- to 13-day nestling period.

All analyses were nonparametric, with the exception of ANOVAs testing for brood-size effects. We tested for differences between males and females via Wilcoxon matched-pairs signed-ranks tests (*T*-values reported), where appropriate. We employed Mann-Whitney *U*-tests where Wilcoxon tests were not possible. Correlations were tested as Spearman rank correlations. Tests of association employed the *G*-statistic. We set the level of significance for all tests a priori at $P = 0.05$. Where mean values are reported, these are grand means ($\pm$ SEM) calculated from mean values for individual birds in the sample.

RESULTS

Sample size.—The total sample included 1,005 feeding trips, 406 by males and 599 by females. Each of the 28 adults made at least 10 feeding trips to the nest (for males: $\bar{x} = 29.0 \pm 14.4$ [SEM]; for females: $\bar{x} = 42.8 \pm 26.2$).

Brood size effects.—Brood sizes varied from one

to four nestlings. Of all feeding trips, 2.4% were made to broods of one nestling (by 2 pairs), 12.5% to broods of two nestlings (6 pairs), 50.1% to broods of three (11 pairs), and 35.0% to broods of four (6 pairs). The number of pairs given here exceeds the actual number of pairs studied because some nests suffered brood reduction during the period of observation, and a single nest may thus include feeding trips to broods of smaller size with time. For males and females separately, ANOVAs indicated no consistent effects of brood size on the dependent variables of interest to us. Differences among individual pairs and, as discussed below, age of nestlings very clearly influenced these variables. For this reason, we did not consider brood size in analyses.

Trip times.—Total trip times to nestlings ≤ 6 days old by females were longer than those by males (Table 1). In contrast, feeding trips to nestlings ≥ 7 days old were longer for males than females. Total trip times for males did not differ between the halves of the nestling period ($U = 43$, $P > 0.05$, $n_1 = 11$, $n_2 = 10$), but did for females ($U = 6$, $P < 0.02$, $n_1 = 11$, $n_2 = 11$).

The decrease for females in total trip times was due to time spent brooding. The mean nest times per trip for the first six days of nestling life were much longer than those for the second half ($U = 1$, $P < 0.001$, $n_1 = n_2 = 11$). Males displayed no change in nest times ($U = 32.5$, $P > 0.05$, $n_1 = 11$, $n_2 = 10$). Mean nest times for females in the first half of the nestling period

TABLE 2. Heights and distances from nests of perches used on feeding trips to nestling Northern Mockingbirds.

Perch location	Males	Females	T ^a	P	n
Height (m)					
1	3.9 ± 0.39 ^b	4.1 ± 0.47	37	NS	14
2	2.7 ± 0.32	2.9 ± 0.35	30	NS	14
3 ^c	3.0 ± 0.30				
4	2.8 ± 0.30	2.9 ± 0.33	27	NS	14
5	3.3 ± 0.41	3.8 ± 0.41	21	NS	13
Distance (m)					
1	9.5 ± 0.82	9.5 ± 1.05	50	NS	14
2	1.1 ± 0.20	0.7 ± 0.07	33	NS	14
4	1.0 ± 0.24	0.8 ± 0.14	30	NS	14
5	9.8 ± 0.83	10.2 ± 1.06	30	NS	13

^a Wilcoxon matched-pairs signed-ranks tests.

^b Values are grand means ± SEM, calculated from mean values for individuals.

^c Loc. 3 perches are nests.

were longer than male nest times in all 11 pairs.

Non-nest times were longer for males than for females in both the first half and second half of the nestling period. Neither males nor females changed non-nest times from the first to second halves (males: $U = 45$, $P > 0.05$, $n_1 = 11$, $n_2 = 10$; females: $U = 44$, $P > 0.05$, $n_1 = n_2 = 11$).

Mockingbirds may fly to the vicinity of the nest tree, pause, and scan the immediate area visually and auditorily before proceeding with food delivery. The sexes (male $\bar{x} = 19 \pm 1.9$ s vs. female $\bar{x} = 12 \pm 1.9$ s, $T = 12$, $P < 0.01$, $n = 14$) spent different lengths of time on the first perch used in a feeding trip when birds perched within 20 m of the nest before delivering food.

Number of perches used on feeding trips.—In 13 of 14 pairs, the mean number of perches used by the male per feeding trip was greater than the mean number used by the female (Table 1). Differences also existed in the use of perches in approaching and departing from the nest (Table 1). Males used more perches when approaching. This was the case both for perches not in the nest tree and for perches in the nest tree. Males also used more perches after departing from the nest. However, when the latter were divided between perches in the nest tree and others, males and females did not differ significantly.

More females than males flew directly to and from the nest without perching within 20 m either way. Twelve of 14 (86%) females did this at least once, but only 4 of 14 (29%) males did

so ($G_{adj} = 7.52$, $P < 0.01$). Concerning approach only, 8 of 14 (57%) males made feeding trips without perching before landing at the nest ($n = 18$); all 14 females made this type of feeding trip ($n = 75$), and the difference between the proportions for the sexes was significant ($G_{adj} = 6.02$, $P < 0.02$).

There was no correlation between age of nestlings and number of perches used on feeding trips, for either males ($r_s = -0.132$, $P > 0.05$, $n = 13$ days of age) or females ($r_s = 0.418$, $P > 0.05$, $n = 13$).

Perch heights and distances from the nest.—There were no differences between mates in either the heights of perches or the distances of perches from the nest (Table 2). Perches used in locations other than the nest tree were higher than those used in the nest tree on both approach and departure.

Vocalizations.—Four types of calls but no songs were given during nest visits. In addition to hews, chats, and cries, we detected a fourth call. We labelled this a Soft Peep Call, a low-amplitude, high-frequency, short call.

There were no differences between the sexes in the numbers of birds that gave any of the first three calls. Hew Calls were given by enough birds (13 males and 12 females) to allow testing for an association between the number of birds giving the call and the location of perch. There was no association for either males ($G_{adj} = 2.26$, $df = 4$, $P > 0.05$) or females ($G_{adj} = 0.74$, $df = 4$, $P > 0.05$).

More males (7 of 14 = 50%) than females (1 of 14 = 7%) gave the Soft Peep Call ($G_{adj} = 4.63$, $P < 0.05$). Further, it was given only at the time of exchange at the nest. The male arriving with food gave the Soft Peep Call from a perch away from the nest tree, and the female, if at the nest, immediately departed. Then the male flew to the nest. Use of this call was also restricted temporally to the first half of the nestling period, when females brooded. Six of 7 males heard to call did so when nestlings were ages 0–3 days. Only 2 males gave the Soft Peep Call after day 5 (days 7 and 8).

Food brought to nestlings.—Males and females fed nestlings food items of similar size ($T = 34$, $P > 0.05$, $n = 14$). For males, $74 \pm 18.6\%$ of feeding trips yielded large items; for females, $81 \pm 12.4\%$. Males delivered a higher percentage of arthropods ($\bar{x} = 97 \pm 4.7\%$) than did females ($\bar{x} = 83 \pm 15.6\%$) ($T = 3$, $P < 0.01$, $n = 14$; but see Breitwisch et al. 1986). Last, females

delivered a larger percentage of unidentified food items than did males ($44 \pm 13.8\%$ vs. $26 \pm 11.5\%$; $T = 10$, $P < 0.01$, $n = 14$).

Fecal sac removal.—Nine males removed 18 fecal sacs, while 10 females removed 57 fecal sacs. Parents removed fecal sacs in proportion to time spent at the nest ($G_{adj} = 1.37$, $P > 0.05$). However, in the large majority of nest departures after feeding, birds did not carry fecal sacs. This indicates that they ate most of these.

DISCUSSION

To our knowledge, this is the first study to quantify in detail differences in the behavior of male and female birds delivering food to nestlings. Female behavior changed markedly from the first half of the nestling period (when brooding was common) to the second half, and this change in female behavior appears to account for differences in trip duration between the sexes in both halves. Throughout the nestling period, males both spent more time and used a greater number of perches than females did on both approach to and departure from nests. There were no differences, however, in either the heights or the distances from the nest for perches used by the sexes. As in a previous study (Breitwisch et al. 1986), females delivered more unidentified food items than males delivered. It now seems clear that our inability to identify food items is a function of female behavior (in particular the rapid approach to the nest by females). It is possible also that females carry food items deeper in their bills, making identification more difficult.

We suggest that these behavioral differences reflect a greater role for males than females in vigilance against predators of nestling mockingbirds (including birds, mammals, and snakes), at least in the vicinity of nests. Although data are insufficient for analysis, we witnessed several instances in which a male remained in the vicinity of the nest tree after feeding, and a potential predator (Fish Crow [*Corvus ossifragus*], human, dog, or cat) then entered the territory. In these cases, the male was silent until his mate returned bringing food. He then called (Hew or Chat call), and the female interrupted her nest visit and perched nearby until the predator left. She then resumed her feeding trip. Such episodes further support the suggestion that males are the more vigilant sex in the vicinity of the nest, although

this hypothesis needs to be tested experimentally.

We can argue for the efficiency of such a division of labor. The alternative—given that some vigilance is necessary—is for the sexes to be equally watchful. Insofar as the demands for provisioning nestlings compete with the need to avoid nestling predators, the question of the more efficient compromise is not trivial. By remaining in the vicinity of the nest longer than females, males can more readily detect predators. Male vigilance allows females to provision nestlings without first pausing on a nearby perch or perches before delivering food. This suggests that nest predators may be foiled largely through the activities of one individual, if that pair member (here, male) can forego foraging to perch longer near the nest. That is, two pairs of eyes are not significantly better than one pair, at least if the addition of a second pair imposes a cost. This is different from flocking behavior, where it appears that benefits to individuals increase with the number of vigilant flock members (Pulliam 1973, Caraco et al. 1980, Elgar et al. 1984). The differences between behavior of mates vs. behavior of flock members may reflect cooperation by mates (Zaia and Breitwisch 1989) that is absent among flock members.

Male mockingbirds spend more time at nests and provide stronger defense of eggs and nestlings (Breitwisch 1988) and fledglings (Zaia and Breitwisch 1989) than do females. We suggest that it is most efficient to combine early detection of predators with strong defense by the same individuals, although a pattern of female vigilance and male defense theoretically could occur (Logan pers. comm.). Second, perched males can simultaneously watch for conspecific intruders and monitor the activities of their mates. Such vigilance would also allow detection of predators on adult mockingbirds. Thus, males could simultaneously offer some protection for their mates. Mate protection would, in turn, be favored by a male-biased sex ratio of adults in this population (Breitwisch et al. 1986; Breitwisch 1988, 1989), making females a limiting resource.

The Soft Peep Call given by males (also heard in the same behavioral context by Derrickson [pers. comm.]) may be a signal that prevents mates from being at the nest simultaneously. Presumably, simultaneous nest visits would make the nest site more apparent to predators. Alterna-

tively, a brooding female surprised by the arrival of her silent mate might bolt from the nest, risking injury to herself or nestlings. The Soft Peep Call was given most frequently when nestlings were young, and females were likely to be brooding. The probability of overlapping presence at the nest was therefore greatest during this period. The Soft Peep Call may function similarly to song given by arriving male Prairie Warblers (*Dendroica discolor*) in similar circumstances (Nolan 1978). If our reasoning as to function is correct, it also seems possible that similar, almost inaudible (to investigators) vocalizations may be given by a variety of birds in the context of nest exchange.

There appear to be no comparable data on nest-visiting behavior for any other bird, although there is anecdotal evidence of sex differences in other species. Nolan (1978: 276) noted in Prairie Warblers that "males tended to approach more slowly and gradually than females, usually landing 20–30 m from the nest and singing 1–3 min before going to it." Male warblers usually made 2–3 additional stops before arriving at the nest. After feeding, they tended to remain in the nest tree, hopping about, for 15–20 s before departing. Female warblers, in contrast, frequently flew away directly after landing. Hann (1937) noted similar differences between male and female Ovenbirds (*Seiurus aurocapillus*).

Future studies should include nest-visiting behavior during nest-building and incubation. Generally, only one parent works on the nest at a particular stage of nest-building, and the differences observed in this study may not occur under those conditions. Second, circumstances led us to conduct this study during the latter half of the breeding season. Early nests should be monitored also, especially because mockingbirds tend to build nests higher in vegetation as the breeding season progresses (Laskey 1962, Derrickson pers. comm.). Finally, because Joern and Jackson (1983) found that well-hidden mockingbird nests had greater success than those less hidden, it would be instructive to monitor the behavior of adults visiting such nests.

Parental investment theory (Trivers 1972, Maynard Smith 1977) does not clearly explain differences in aspects of behavior between mates as found in our study. Nestlings should be equally valuable to the parents, insofar as mockingbirds are monogamous, and mates tend to

remain together year after year (Breitwisch unpubl. data). There is no indication that males and females experience different longevities. Thus, if behavioral differences in nest visits entail different levels of investment (perhaps in association with defense against predators), investment theory must be modified to account for this (Breitwisch 1989). If the differences in nest-visiting behavior do not reflect disparate levels of investment, existing theory of parental investment does not predict such a distinctive difference between the sexes. It seems likely that cooperation between mates (Zaias and Breitwisch 1989) results in these differences, but such cooperation in monogamous birds has thus far received very little attention.

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