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ONTOGENY OF FORAGING AND OTHER BEHAVIOR IN FLEDGLING NORTHERN MOCKINGBIRDS

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Abstract.—We observed the behavior of fledgling Northern Mockingbirds (*Mimus polyglottos*) in order to test predictions of hypotheses concerning the schedule of the ontogeny of adult behavior. Soon after leaving the nest, fledglings displayed foraging behavior. During the first three weeks post-fledging, they significantly increased the time spent both foraging on the ground and pecking at vegetation. Fledglings continued to utter the nestling begging call during this period, and they first gave adult chat calls about a week after fledging. Young mockingbirds first displayed wing-flashing behavior between one and two weeks after fledging. Development of chat calling and wing-flashing appears to be retarded as brood size increases, supporting the sibling competition hypothesis. Exploratory pecking at vegetation continues unabated in growing fledglings, in contrast to previous findings for carnivorous passerines, and this difference may reflect the advantages of investigative foraging for omnivorous species such as mockingbirds.

The fledgling period is the least studied phase in the life history of altricial birds (Zaias and Breitwisch 1989). Fledgling birds are much more difficult to observe than adults in many species, primarily because fledglings remain hidden in vegetation while still dependent on parental care. Nestlings are easier to observe than fledglings, but various aspects of adult behavior are not displayed by nestlings. For these reasons, relatively little is known about the ontogeny of adult behavior in many species of altricial birds.

Recent study of the parental care of fledglings by Northern Mockingbirds (*Mimus polyglottos*) has shown that parent mockingbirds provide both food and protection for fledglings three weeks or more after the young fledge (Zaias and Breitwisch 1989). The parent more responsible for care during most of the fledgling stage is the attending male. Mockingbirds are multi-brooded, and sequential nesting efforts frequently overlap. For broods followed by another nesting effort, males usually continue to feed their fledglings until the day the younger nest-

lings hatch. Then, often abruptly, the male ceases fledgling care and begins to feed nestlings (Zaias and Breitwisch 1989).

Breitwisch et al. (1987) found that independent juveniles are relatively inefficient in capturing insects while foraging along the ground, the common method of insect capture by mockingbirds. The general pattern of high mortality in juvenile birds seems likely to be at least partially due to such foraging inefficiency (Breitwisch et al. 1987, Marchetti and Price 1989, Sullivan 1989, Weathers and Sullivan 1989). The juvenile period thus may contribute substantially to differential fitness, and behavioral ontogeny during the fledgling period should influence the welfare of vulnerable juveniles.

On what schedule do fledgling mockingbirds begin to display various aspects of behavior important to their survival? Several hypotheses make predictions about the schedule of behavioral ontogeny. First, sibling competition for parental care may negatively affect this schedule, and this hypothesis predicts a slowing of ontogeny with increasing brood size. Alternatively, parents may match brood size to their own quality (Smith 1981), with high quality parents producing large broods, in which case the schedule of ontogeny of behavior in fledglings would be independent of brood size. The same prediction of no brood size effect follows if ontogeny of behavior is strongly determined genetically, with minimal influence from either social interactions or varying levels of nutrition beyond some physiological threshold. Finally, parents may behave differently toward fledglings as a function of brood size (K. C. Derrickson, pers. comm.), perhaps in relation to the different profitability of different brood sizes (Zaias and Breitwisch, unpubl. ms.). The first and last hypotheses are perhaps the more interesting because, under such conditions, the number of siblings—a variable almost beyond the control of the young bird's genes—may influence the probability of survival of newly independent individuals.

We documented the appearance of foraging behavior by fledglings, both during the early fledgling period when they remained in trees and shrubs, and later as they began to descend to ground level and initiate the characteristically adult mode of foraging. We further documented the ontogeny of maintenance behavior and vocalizations. Because we focused on fledgling behavior, we could not address the hypothesis of differential adult behavior. However, our observations allowed us to test predictions of the first three hypotheses. A retardation in appearance of aspects of behavior in larger broods would support the first hypothesis. No differences in the behavior of fledglings in broods of different sizes would support both the second and third hypotheses.

STUDY SITE AND METHODS

We observed fledgling mockingbirds on the main campus of the University of Miami, Coral Gables, Dade County, Florida. The campus habitat is suburban lawn sparsely planted with a wide variety of trees and shrubs. Mockingbirds typically forage for arthropods on lawns and for ripe fruit in trees (Breitwisch et al. 1984, Breitwisch et al. 1987).

We observed fledgling mockingbirds in their natal territories for a total of 63 h of focal sampling on individual fledglings between 19 June and 17 July 1987. Sample periods were 30 min in duration and spread throughout daylight hours, although we avoided early afternoon because fledglings are generally inactive at that time. We watched 11 individually color-banded fledglings in 6 broods (2 broods of 1 fledgling, 3 broods of 2, and 1 brood of 3). Age of fledglings ranged from 4 to 24 days post-fledging. The nestling period is ca. 12 days, so ages from hatching are approximately 12 days older than those discussed here. For 10 of these 11 fledglings, we obtained reasonably large samples of their behavior, with a mean (\pm SD) of 300 ± 105 min of observation per fledgling (range: 133 - 468 min). For these 10, our sampling of their behavior spanned a mean period of 15 days, from 6 to 20 days post-fledging, inclusive. For some analyses, we could use all 10 fledglings, while for other analyses, we had reliable data on a smaller number, as indicated for the particular analysis.

During each minute, we recorded whether the focal fledgling foraged in vegetation or on the ground. We arbitrarily chose 3 pecks/min as a minimal rate of activity to qualify as foraging. We noted that fledglings pecking in vegetation appeared only infrequently to obtain food by this behavior. We thus tentatively classify this as "exploratory" pecking. For fledglings perched in vegetation, we noted whether a fledgling was exposed to view or hidden (partially or completely) in foliage and its height in vegetation. We also recorded whether the focal fledgling preened or "wing-flashed" (Hailman 1960). We noted begging and chat calls by fledglings (see Derrickson and Breitwisch 1992).

In assessing changes in behavior with age, we grouped observations on fledglings into several age classes in order to yield sufficiently large sample sizes for statistical comparisons (n 's ≥ 20 samples). These classes were 4-9, 10-12, 13-15, 16-17, and 18-24 days post-fledging. Ten fledglings were represented in each of the first four age classes, and eight of these fledglings in the fifth age class.

All statistical analyses are non-parametric due to moderately small sample sizes and unknown underlying distributions of variables. We report Spearman correlation coefficients, H values for Kruskal-Wallis one-way ANOVAs, and G values for tests of independence. Finally, we are aware that fledglings within broods may not behave truly independently from one another. The difficulty of focally sampling the behavioral ontogeny in individual fledglings necessarily limited the number of fledglings we could observe. Although our impression was that brood members did behave independently from one another, this remains an assumption that warrants future testing.

RESULTS

Foraging on the ground for arthropods is a primary technique used by adult mockingbirds to capture prey. Time fledglings spent in this behavior increased with fledgling age ($r_s = 0.90$; $P = 0.05$; $n = 5$ age classes; Fig. 1). Fledglings initially spent about 8% of their time foraging on the ground, and this increased to more than 15% as they aged. There were too few records for analysis of brood size effects.

Fledglings pecked at vegetation, including foliage, bark, flowers, and unripe and ripe fruit. Single fledglings did this in 13% of the min spent

in vegetation, fledglings in pairs in 12%, and 3-fledgling broods in 7%. Young fledglings (all brood sizes together) spent 7% of the time in vegetation pecking in this manner, and this increased to 14% as fledglings aged ($r_s = 1.00$; $P = 0.01$; $n = 5$ age classes; Fig. 1).

Fledglings spent 89% of their time perched in vegetation, but there was no relationship between this percentage and fledgling age. We also tested whether fledglings were more hidden in vegetation when young than when they were older, but we found no such relationship. Overall, fledglings spent 31% of the time they were in vegetation partially to completely hidden from view (24% for single fledglings, and 33% for pairs and trios). Heights at which fledglings perched in vegetation were similar to those of previous findings (Zaias and Breitwisch 1989), typically within several meters of the ground.

Fledglings preened their plumage in 22% of the min in which they were visible. There was no relationship between preening frequency and age ($r_s = 0.10$; $P > 0.05$; $n = 5$ age classes). Fledglings in the youngest age class preened in 23% of the min observed, in the second age class in 25%, in the third age class in 22%, in the fourth age class in 11%, and in the oldest age class in 27%. There was heterogeneity among brood sizes in preening frequency ($G = 8.91$; $P < 0.05$; $df = 2$), although no pattern with increasing brood size. Single fledglings preened in 23% of the min,

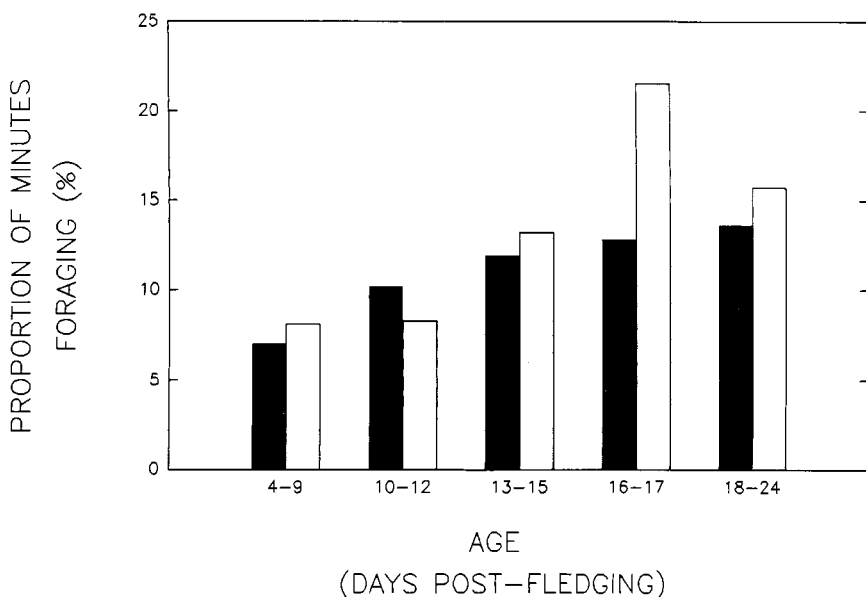


Figure 1. Proportion of time spent foraging by fledgling mockingbirds as a function of age. Open bars refer to foraging (exploratory pecking) in vegetation, and shaded bars refer to foraging on the ground.

members of pairs in 19%, and members of trios in 27%. Even though fledglings in pairs and trios frequently perched near one another throughout the fledgling period, they did not preen one another.

Wing-flashing is a stereotypical display characteristic of mockingbirds; adults display wing-flashing when foraging on the ground and in situations of apparent conflict (Hailman 1960, Derrickson and Breitwisch 1992). Fledglings were first observed to wing-flash between 6 and 13 days post-fledging ($\bar{x} = 10.2 \pm 2.9$ days; $n = 8$ fledglings). Two single fledglings first did this at 6 days post-fledging, the three fledglings we could observe in broods of two at 10, 10, and 11 days, and the three fledglings in a single brood of three at 13 days each. Fledglings in smaller broods first displayed wing-flashing earlier than did fledglings in larger broods ($H = 6.73$; $P < 0.011$; $n = 8$ fledglings). Most wing-flashing was done while on the ground. We observed wing-flashing in 2% of the min fledglings spent in vegetation and 33% of the min they spent on the ground ($G = 308.3$; $P < 0.001$; $df = 1$). There was no relationship between age and frequency of wing-flashing in vegetation; on the ground, fledglings were not seen to wing-flash before 10 days of age. Frequencies remained similar from that age through the oldest age classes.

Chat calls are vocalizations given by adult mockingbirds in territorial defense, as well as in other aggressive interactions (Derrickson and Breitwisch 1992). Chatbursts are short series of rapidly repeated chat calls also given by adults in these contexts (Logan et al. 1983; Logan 1985). Fledglings were first heard to give chat calls between 4 and 12 days after fledging ($\bar{x} = 8.3 \pm 2.4$ days; $n = 7$ fledglings). Two single fledglings did this at 4 and 8 days post-fledging, four fledglings in broods of two at 8, 8, 8, and 12 days, and one fledgling for which we had this information in a brood of three at 10 days. First chat calls were given earlier by fledglings in smaller broods ($H = 9.44$; $P < 0.057$; $n = 7$ fledglings). Fledglings were not heard to give chatbursts.

Fledglings give a characteristic begging call that sounds similar to that given by nestlings. Fledglings were heard to give begging calls in 37% of the min they were observed, and frequencies were similar for begging calls given from vegetation (36%) and from the ground (38%) ($G = 0.45$; $P > 0.05$; $df = 1$). There was no clear relationship between incidence of begging calls and age. Three weeks and more after fledging, young mockingbirds were still fed by their fathers (Zaias and Breitwisch 1989) and still gave begging calls. Begging rate was marginally associated with brood size ($H = 4.72$; $0.057 < P < 0.091$; $n = 10$ fledglings). Single fledglings gave begging calls in 57% of the min they were observed, fledglings in pairs in 35%, and fledglings in trios in 26%.

We occasionally observed fledglings following their male parent. Such following occurred both in vegetation and on the ground. In 12 instances of this behavior, the mean age of fledglings following males was 17.1

days, whereas the mean age of fledglings sampled was 13.6 days. Although these data are few, they suggest that fledglings engage in this behavior more frequently as fathers become less attentive to begging calls of such older fledglings (Zaias and Breitwisch, unpubl. ms.).

DISCUSSION

These data demonstrate that several aspects of behavior typical of adult mockingbirds appear in fledglings still dependent on parental care and less than 36 days old (12 days as a nestling plus 24 days as a fledgling). We recorded ground-foraging, exploratory pecking at vegetation, preening, wing-flashing, and chat calling by fledglings. Nestlings also preen and beg, but the other aspects of behavior apparently first appear in fledglings. However, hew calls and high-pitched cries—two calls given by adult mockingbirds in conflict situations (Breitwisch 1988, Derrickson and Breitwisch 1992)—were not heard from fledglings (nor were chatbursts). Apparently, neither is given by juveniles, either (R. Breitwisch, pers. obs.), although chatbursts are (C. A. Logan, pers. comm.). Not surprisingly, fledglings did not sing. Juvenile males first sing in early autumn (Derrickson and Breitwisch 1992).

Fledglings increased the time they spent ground-foraging as they aged. Foraging techniques further develop in independent juveniles (Breitwisch et al. 1987). Younger juveniles forage from the ground, but older juveniles increase their use of an aerial attack technique, in which a mockingbird flies from a perch in vegetation to the ground, where it attacks insects (Breitwisch et al. 1987). Although it seems likely that the increased use of this foraging technique may be due to the lifting of prior developmental constraints (Marchetti and Price 1989), this question has not been investigated for this species.

Fledglings increased the frequency of pecking at foliage, flowers, and fruits with time. They did so despite our impression that most of this behavior was apparently exploratory and unrewarding nutritionally. This finding is in contrast to other studies that have demonstrated a decline in such exploratory behavior soon after fledging (Smith 1973, Davies 1976, Davies and Green 1976, Moreno 1984). We hypothesize that this difference among species reflects dietary differences among adults of the species studied. Loggerhead Shrikes *Lanius ludovicianus* (Smith 1973), Spotted Flycatchers *Muscicapa striata* (Davies 1976), Reed Warblers *Acrocephalus scirpaceus* (Davies and Green 1976), and Northern Wheatears *O. oenanthe* (Moreno 1984) are all highly insectivorous or, more generally, carnivorous. In contrast, mockingbirds are notably omnivorous, and fruit is an important component of the diet of adults, as well as of nestlings and fledglings (Breitwisch et al. 1984, Breitwisch et al. 1986, Zaias and Breitwisch 1989). Fledglings of carnivorous species begin to specialize in foraging techniques at rather young ages, whereas

fledglings of omnivorous species may well be frequently rewarded by their continued exploration. This suggestion is reminiscent of differences in neophobia displayed by generalist and specialist bird species (Greenberg 1983, 1990).

Wing-flashing and chat calling were displayed by single fledglings earlier than by members of broods of two or three fledglings. This observation supports the brood competition hypothesis, predicting a slowing of behavioral ontogeny with increasing brood size. It also counters the prediction of no brood size effect by both the quality matching and genetic determination hypotheses. Insofar as our findings suggest a parental trade-off between number of offspring and behavioral development in these offspring, it clearly argues for further study on both a larger sample of fledgling mockingbirds and on other bird species.

Although we could not address the differential parental behavior hypothesis, it should be noted that, as hypothesized by Zaias and Breitwisch (unpubl. ms.), this predicts that smaller broods that have arisen through brood reduction will be treated as unprofitable by parents. That would be reflected in a retardation of behavioral ontogeny in smaller, reduced broods. We have no indication of such retardation in this study. In general, feeding rates per fledgling to broods of different sizes are not obviously different (Zaias and Breitwisch 1989). Males delay nest-building for the next clutch in relation to the number of fledglings under care (Zaias and Breitwisch 1989), so members of large broods may receive a small benefit in this manner.

Sibling interactions, competitive or otherwise, clearly are possible. Fledglings within broods frequently perched close to one another in vegetation, often within a half meter. When one flew to a new location, sibling(s) sometimes followed. At other times, fledglings within a brood were 15 m or more apart, apparently behaving quite independently from one another. Fledglings perched close together may directly compete for food via begging calls. The influence of fledgling interactions on behavioral development are largely unknown.

Finally, included in this study were broods followed by subsequent nestings. As found by Zaias and Breitwisch (1989), male parents aggressively drove their fledglings from the natal territory on the day that the next clutch hatched. However, some fledglings were able to remain on the natal territory simply by withstanding paternal aggression for one or two days, at which time aggression waned. This persistence resulted in their continued occupancy of their natal territory for an additional week or more. This suggests that fledglings may sometimes be able to experience further behavioral ontogeny while remaining in familiar surroundings. Such familiarity may, in turn, benefit a juvenile once it disperses from its natal territory and becomes fully independent from its parents.

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