Parental Behavior of a Bigamous Male Northern Mockingbird

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The Northern Mockingbird (*Mimus polyglottos*) is a typically monogamous passerine (Bent 1948, Verner and Willson 1969) in which male bigamy has been documented occasionally (Laskey 1941, Logan and Rulli 1981, Merritt unpubl. data). Hypotheses for the infrequency of polygyny in mockingbirds and other monogamous passerines center on a relatively small variance in (1) quality of territories established by males, (2) quality of male parental care or other aspects of male behavior important in raising young, or (3) male traits strictly related to mating success. We here provide information pertinent to the latter two hypotheses.

Verner and Willson (1969) considered North American passerines to be polygynous only if >5% of males in a population have two or more mates simultaneously. However, even single instances of polygyny in typically monogamous species are interesting because they may clarify the reasons for the relative infrequency of polygyny in these species. We assume that bigamy is not the result of an error in mate choice by a female mating with an already-mated male and that such a female knows she is pairing with a mated male and is choosing the best mating option available to her at that time (cf. Alatalo et al. 1982). In the case reported here, for instance, the second female to arrive paired with a mated male that shared a territorial boundary with an unmated male. It is reasonable to assume she made a choice between at least these two males.

We observed the behavior of a single bigamous male mockingbird for 98.5 h in the 1984 breeding season and quantified this male's behavior with regard to feeding nestlings and fledglings, defending eggs and nestlings, and consorting with mates. We also compared his behavior with that of monogamous males in the same population. The overall framework for comparative analyses of these data is an inquiry into the consequences of bigamy for both females mated to a bigamous male mockingbird.

This population of individually color-banded mockingbirds inhabits the main campus of the University of Miami in Coral Gables, Dade County, Florida (Merritt 1985) and has been under continuous study since 1979. The birds are largely habituated to humans and allow observers to approach as close as 5–10 m (Breitwisch et al. 1984). Male 867, the subject of this study, was banded in March 1980, at an age of at least 1 yr. Prior to 1984, he was monogamous. In 1980 he produced two fledglings but only one survived to independence (= ca. 2 weeks after fledging). There was one fledgling in 1981 that died before reaching independence. Male 867 apparently was unmated in 1982. In 1983, he and female 105 (female

1) paired, raising at least one fledgling to independence. Female 105, of unknown age, was banded in November 1982. Female 246 (female 2) was at least 1 yr old when banded in early May 1984. We suspect she was the same unbanded bird we observed in late March 1984 on male 867's territory but on the side opposite most of female 1's activity. By 29 March, it was clear that male 867 had accepted female 2's settlement on his territory; they were seen repeatedly within 1 m of one another without apparent aggression.

Between 29 March and 19 June, we observed male 867's interactions with his mates during 71 sampling periods on 60 different days ($\bar{x}$ = 59 min, total = 69.8 h). We quantified male feeding of young during an additional 30 sampling periods on 24 days between 30 April and 19 June ($\bar{x}$ = 57 min, total = 28.7 h). Observation of nestling feeding was facilitated by frequent placement of the open cup nests in sparse vegetation. Sampling was distributed throughout daylight hours. Using binoculars, RCR and JZ observed from exposed locations. RB, having handled nestlings of this male, observed from a blind (see Merritt 1984). In each period, the observer maintained visual contact with male 867.

Twice in the breeding season, male 867 had two sets of young simultaneously requiring feeding. A third time, he had three sets of young on his territory, all begging for food (Fig. 1). In each case, he fed only one set of young. In the first overlap (6–11 June), the male fed female 1's fledglings and ignored the food needs of female 2's nestlings. In 659 min of observation between 29 May and 11 June (when female 1's fledglings were 3–16 days out of the nest), the male fed the fledglings 119 times vs. 1 feeding by female 1 (and 8 feedings by an unidentified parent). Female 1 had a new clutch of eggs for most of this time (Fig. 1). The male fed the first brood of female 2 (13 feedings vs. 17 feedings by female 2, in 180 min on 30 April and 1 May). He also fed female 1's nestlings (40 feedings vs. 97 feedings by female 1, in 489 min between 16 and 25 May). Between 6 and 11 June, with only female 2 feeding her nestlings, they grew very slowly (Breitwisch unpubl. data). The nest was not kept clean, and the young were plastered with dried feces. One of the three emaciated nestlings died, almost certainly from starvation. From 6 to 11 June, the male fed female 2's nestlings 1 or 2 times vs. 33 feedings by female 2 (in 300 min); the feedings by the male were on 10 and 11 June when he was still feeding female 1's fledglings. On 10–12 June, when the two remaining nestlings were 4–6 days old and female 1's fledglings had been out of the nest for 15–17 days, the male abruptly

ceased feeding the fledglings and began rapid delivery of food to the nestlings. Between 12 and 17 June, the male fed the nestlings 64 times vs. 47 feedings by female 2 (in 404 min). The growth rate of the young increased dramatically, and they attained typical fledging weights of healthy young. In the second brood overlap (14–18 June), the male continued to feed female 2's nestlings and completely neglected feeding female 1's nestlings. The growth rate of female 1's nestlings was very slow (Breitwisch unpubl. data), and apparently one of her nestlings starved. However, in contrast to his behavior in the first overlap when female 1 had fledglings and female 2 had nestlings, the male stopped feeding female 2's young when they fledged, and he began feeding female 1's nestlings (16 feedings vs. 12 feedings by female 1, in 120 min on 18 and 19 June). From 18 to 26 June, he continued to feed female 1's nestlings and was not observed to feed female 2's fledglings. This neglect of fledglings is in marked contrast to typical monogamous male mockingbird behavior; males provide more food to fledglings than do females (Zaias and Breitwisch MS). It also contrasts with this male's previous rate of feeding female 1's fledglings between 29 May and 11 June.

The male defended his eggs and nestlings vigorously. In the 1983 breeding season, he was known as a notably aggressive mockingbird in the campus population, attacking human intruders when he had young on his territory. In the 1984 breeding season, one of us (RB) quantified male and female behaviors in defending eggs and nestlings against assistants examining eggs and removing nestlings for growth measurements (Breitwisch MS). Male 867 significantly differed from the monogamous males in the population. He approached more closely (Mann-Whitney U-tests for egg defense, $z = 4.53$, $P < 0.05$, and nestling defense, $z = 8.51$, $P < 0.05$), hovered over assistants more closely when defending nestlings (Mann-Whitney U-test, $z = 3.34$, $P < 0.05$), and made closer passes when attacking assistants (Mann-Whitney U-tests for egg defense, $z = 1.91$, $P = 0.05$, and nestling defense, $z = 5.98$, $P < 0.05$). He also more frequently followed assistants off territory ($G = 102.6$, df = 1, $P < 0.05$). He occasionally attacked assistants working at a nest in an adjacent territory and was the only mockingbird (of 24 males and 25 females) to extend defense to a neighbor's nest. Orians (1980) and Wittenberger and Tilson (1980) suggested that polygynous male passerines usually can equally defend more than one nest against predators, and this bigamous male appeared to do so.

Male 867 consorted with each of his mates, even when he neglected to feed her young. In 56 of 71 observation periods (79%) he was seen with female 1; in 40 of 71 (56%) he was seen with female 2. In 30 of these, he was seen with both females within the same observation period. The male's frequencies of consorting with his two females were not different
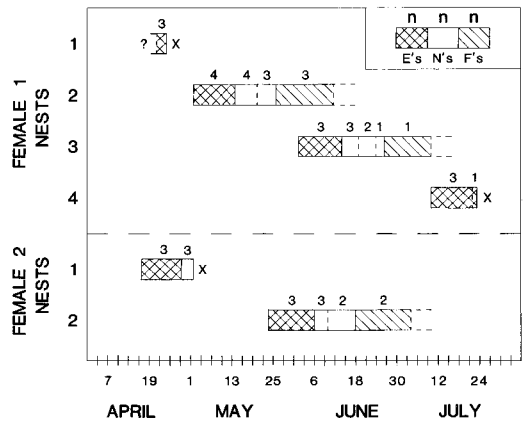

Fig. 1.   Nesting schedule of two female mockingbirds mated to a bigamous male. Numbers of eggs (cross-hatched bars), nestlings (open bars), and fledglings (hatched bars) at each stage of nesting are shown above each nest. Brood reduction is indicated by multiple entry above and a dashed line within the nestling stage for a nest. A predation event is symbolized by an "X." The "?" for nest 1 of female 1 indicates that the clutch was complete upon discovery.

($\chi^2 = 2.67$, df = 1, $P > 0.05$). Furthermore, he used the two parts of his territory equally. He was observed on female 1's half (although not necessarily with the female) in 68 of 71 periods (96%) and on female 2's half in 54 of 71 periods (76%); these frequencies were not different ($\chi^2 = 1.61$, df = 1, $P > 0.05$). However, he sang with different frequency in the two halves of his territory. He sang on female 1's half in 43 of 71 periods (61%) and on female 2's half in 23 of 71 periods (32%) ($\chi^2 = 6.06$, df = 1, $P < 0.05$). If song in mockingbirds functions primarily in male-female interactions (see Merritt 1985), this difference may indicate signaling by this male to his first mate in preference to his second mate.

Mockingbird breeding territories are all-purpose territories, although birds in this population will leave territories to forage from nearby fruiting trees (Merritt 1980, Breitwisch et al. 1984). We did not assess the quality of territories held by mockingbirds in this population, but the male's territory was not obviously different from territories of monogamous males. Mockingbirds are ground foragers, taking large numbers of terrestrial arthropods; the area of lawn available for foraging may be an important aspect of territory quality (see Roth 1979). Male 867's territory was among the larger territories, as Merritt (unpubl. data) found for a previous bigamous male in this population, but it was not uniquely large.

The bigamous behavior of male 867 suggests that individual quality apart from territory quality may be important in determining instances of bigamy in mockingbirds (cf. Borgia 1979). In the 1984 breeding

season, for 23 monogamous pairs, 15 of 67 nests with eggs (22%) were preyed upon, and 26 of 52 nests with nestlings (50%) were preyed upon. Both egg and nestling periods of mockingbirds in southern Florida are ca. 12 days, and these predation rates correspond to loss rates of 0.0187 nests with eggs lost per day and 0.0417 nests with nestlings lost per day. Only 26 of 67 nests (39%) produced fledglings, and only 18 of 67 nests (27%) yielded independent young. In contrast, 3 of the 6 nests (50%) of the two mates of male 867 together produced 6 fledglings, and all young reached independence. As an additional measure of success, we can compare the number of independent young produced per female. In 1984, the mean number of independent young produced by females in monogamous pairs was 1.2 (SD = 1.28) from a mean number of 3.0 nests per pair ($n = 23$ pairs) (Breitwisch unpubl. data). Female 1 nested 4 times and produced 4 independent young from 2 nests. Female 2 nested twice and produced 2 independent young from 1 nest. Each of these females produced at least as many independent young as the average female in the monogamous population.

The male's high level of defensive behavior may have contributed to his success in producing independent young. This would argue against the hypothesis that female choice of male traits strictly related to mating success accounts for male bigamy (Weatherhead and Robertson 1979). Presumably, a newly settling female could estimate a potential mate's level of defensive behavior by observing his overall level of aggression, perhaps toward both potential predators and conspecific intruders, perhaps toward herself. In the breeding season, mated male mockingbirds had higher attack rates against intruding conspecifics than had unmated males (Merritt 1985). In the nonbreeding season, mated males in this population were more aggressive than unmated males, as estimated by frequency of involvement in conspecific chases (Breitwisch et al. 1986a).

Monogamous male mockingbirds in this population provide as much food to nestlings as do females (Breitwisch et al. 1986b), and male 867's schedule of feeding young illustrates one of the potential costs to females mated to a bigamous male. He neglected feeding a brood of young when he had another set of young on his territory, and two of the neglected nestlings starved to death, while others grew at slow rates. More complete staggering of broods could reduce this potential cost (Verner 1964). Nonetheless, our data on nest success and production of independent young suggest that, despite the potential for starvation of nestlings not fed daily by a bigamous male, bigamy may still be advantageous to females.

This instance of mockingbird bigamy is in agreement with that reported by Logan and Rulli (1981) and verified by Merritt (unpubl. data) in that each bigamous male fed only one set of young when he had more than one set at the same time (but note in

this case very minor feeding of female 2's neglected nestlings on 10–11 June as the male switched from feeding fledglings to feeding nestlings). However, this case differs from Logan and Rulli's (1981) instance in two ways. First, the latter arose through disappearance of a male from a pair and usurpation of the widowed female's territory by a neighboring male. The widowed female and the male later paired. Second, when faced with two broods of young, the bigamous male of Logan and Rulli always fed the older set of young. In contrast, male 867 stopped feeding female 2's young when they fledged and switched to feeding female 1's nestlings. This behavior departs from Trivers's (1972) prediction that parents should favor older over younger offspring in conflict situations. We suggest that male care may be more important for mockingbird nestlings than for fledglings. Such a difference should be entered into any equation predicting parental investment patterns with respect to ages of offspring competing for parental care (Maynard Smith 1977).

Polygyny in birds frequently has been explained by differences in quality of male territories (e.g. see Orians 1980, Oring 1982), and without doubt this explanation fits many cases. We suggest, however, that variability in male behavior, particularly in aspects of parental care, apart from variability in quality of territories warrants careful investigation.

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Stomach Pumping: Is Killing Seabirds Necessary?

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Many seabird species regurgitate when handled, allowing diet assessment without killing birds (e.g. see Ashmole and Ashmole 1967, Harrison et al. 1983). Other seabirds, notably penguins (Wilson 1984) and petrels away from their breeding grounds (Harrison et al. 1983, pers. obs.), are less willing to regurgitate. A quantitative, but nonlethal, sampling technique is needed for diet studies on these seabirds, particularly in view of the growing opposition toward the killing of animals for biological research.

Emetics and stomach pumps have been used to obtain stomach contents from seabirds, but results have been unsatisfactory (Wilson 1984, Duffy and Jackson MS). Wilson (1984) described a simple technique for sampling stomach contents in seabirds, but it has been suggested that it does not always recover the entire stomach contents (Lishman 1985; but see Horne 1985) and is less effective on birds that have full stomachs with tightly packed contents (Lishman 1985). We tested the efficiency of Wilson's stomach pump on four species of petrel and review its use in other birds.

Seven White-chinned Petrels (Procellaria aequinoc-tialis) (mean mass 1,250 g) from Marion Island (46°52'S, 37°51'E) each were fed a large meal (125 g) of squid (Loligo sp.), lightfish (Maurolicus muelleri), and antarctic krill (Euphausia superba) in equal proportions, then pumped and killed after varying intervals. The amount (mass and number of prey items) of food recovered by stomach pumping was expressed as a proportion of the total stomach contents (determined by dissecting out the oesophagus and proventriculus) and compared with the total stomach contents. In addition, single Cape Petrels (Daption capense), Salvin's Prions (Pachyptila vittata salvini), and Wilson's Storm-Petrels (Oceanites oceanicus) were collected at sea off southern Africa, then similarly tested.

Mean pump efficiency (the proportion of food recovered by a single pumping) was 89.2% (SD = 13.3) by mass and 99.1% (SD = 2.0) by number of prey items ($n = 10$). The proportion of food (by mass) recovered by a single pumping was negatively correlated with total stomach content mass in the 7 White-chinned Petrels examined (Fig. 1; $r = -0.85$, $P < 0.01$ on arc-sine transformed data). The proportion of prey items recovered was also negatively correlated with the total number of items present ($r = -0.67$, $P < 0.05$, $n = 10$). Approximately equal masses and numbers of the three prey types were recovered, irrespective of stomach fullness. When stomachs were less than 20% full, the entire contents were removed by a single pumping. The three other petrel species tested all yielded 100% of their stomach contents.