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BIGAMY IN NORTHERN MOCKINGBIRDS: CIRCUMVENTING FEMALE-FEMALE AGGRESSION[1]

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Key words: Northern Mockingbird; bigamy; opportunistically polygynous; female-female aggression; behavioral options.

Polygamy based on males opportunistically acquiring a second mate is rare among passerine species and probably reflects a conflict between the sexes (Orians 1969, Wittenberger and Tilson 1980). Selection should favor polygyny in males whenever the benefits of a second concurrent clutch exceed costs to his primary clutch. In contrast, if bigamy decreases female reproductive success through reduced survivorship of fledglings, selection might increase female-female aggression. This aggression would represent an additional cost to any other female being courted by her mate and could limit the number of additional females her mate could attract.

Obviously, a male must attract a second female in order to become bigamous. Then, he must invest time in courtship and defense of the second female while keeping his mated status hidden (Ford 1983). Alternatively, he could reduce the disruptive influence of his first mate to some level tolerable to the secondary female. The tolerance shown by the secondary female is likely to change with her level of investment, being greatest when she has a completed clutch. Several behavioral options are available to the male. Among these are: (1) acquiring a large territory, (2) influencing the females' movements relative to each other, and (3) timing when the second female begins her clutch. How often these behavioral options are used by males to circumvent female-female aggression requires detailed behavioral observations and is still poorly documented for most species.

Northern Mockingbirds (*Mimus polyglottos*) typically are monogamous (Laskey 1935, Verner and Willson 1969, Ford 1983), and pairs commonly remain mated for several nesting attempts during a single breeding season and even through consecutive breeding seasons. Nesting duties generally are shared: both males and females vigorously defend their territory

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(Laskey 1935, 1936, 1962; Michener and Michener 1935; Michener 1951), both sexes build the nest, and although females exclusively incubate the eggs, both members of a pair feed nestlings and fledglings (Laskey 1935, Breitwisch et al. 1986a, Zaias and Breitwisch 1989). However, a few cases of bigamy have been reported (Laskey 1941, Logan and Rulli 1981, Breitwisch et al. 1986b). In fact, Ford (1983) considered mockingbirds to be opportunistically polygynous. Here I report two more cases of bigamy in the Northern Mockingbird. Several observations, including the timing of secondary females' nesting attempts, interactions between primary and secondary females, and circumstances surrounding a secondary female's nest failure, collectively suggest that female-female aggression may constrain the ability of male mockingbirds to become polygynous. Polygyny may occur only when males can circumvent female-female aggression.

Research on mockingbirds was conducted at Tyler Arboretum, Lima, Pennsylvania during the 1980–1983 breeding seasons. Each year six to 10 pairs were studied. Although the study focused on singing behavior, observations were detailed enough on five to seven pairs each year (total of 25 pair-years) to determine reliably if bigamy had occurred. A single occurrence of bigamy occurred in both 1980 and 1981, and involved different territories and different males.

1980 OCCURRENCE

One unbanded male, M1, was observed for 22.5 hr on 41 days from arrival on his territory on 26 March through early September. He had the largest territory during the study. In fact, the next year two males divided it. The primary female, F1, was first observed on 2 April. Forty-eight percent (10.9 hr) of the observations were concentrated during 5 May–13 June when the second female, F2, was present. Nest building began along the eastern edge of the territory during late April, and F1 began incubating a clutch of four eggs on 4 May (see Fig. 1).

The next day, F2 was observed with M1 in the northern portion of his territory. F2 had been associating with M1's territorial neighbor earlier in the day. She moved onto M1's territory and was followed by the neighboring male, who started to sing but quickly retreated to his territory upon arrival of M1. The neighbor remained unmated during all of 1980. Thus, F2's decision to mate with M1 was not due to a lack of unmated, territorial males. M1 chased F2 among trees in the northern and central portion of his territory, typical courtship behavior (Laskey 1935). Within 30 min, M1 was running along branches and occasionally singing quietly from the interior of conifers while F2 foraged nearby, behavior typically associated with the male showing future nest sites to a female (Laskey 1935, pers. observ.). M1 continued courting F2 on 6 May and on 7 May deposited twigs in a Korean pine (*Pinus koraiensis*), the site of their future nest, that was located centrally in the territory and approximately 60 m west of F1's nest. F1 was incubating and chased F2 only once during 2 hr of observation on 6–7 May.

F2 laid her first egg by 17 May. The previous day three eggs had hatched in F1's nest and both F1 and M1 fed the nestlings. During the latter part of May, F1 repeatedly chased F2 when F2 was off her nest, effectively restricting F2's movements to the west and northwest of F2's nest. On 28 May, the nestlings were fed primarily by F1 while M1 sang quietly and associated with F2. Three nestlings fledged on 29 May but only one was located on 4 June. F1 was observed to chase F2 twice during 75 min of observation on 30 May. Each time F1 began to fly in F2's direction, M1 flew towards F1, but she evaded him and three-bird chases arose with F1 chasing F2, and M1 trailing further behind.

F2 was feeding four nestlings while F1 had moved into the northern portion of the territory with her fledgling on 4 June. The male did not feed any young on 4 June during 86 min of observation. F1 and F2 cared for their respective young. In fact, M1 did not feed F2's young during 4 hr of observation between 4–13 June. Four young fledged from F2's nest on 11 June, but only a single fledgling was located the next day. The young from both nests and the secondary female were last observed on 13 June. Subsequently, M1 and F1 initiated two more nests which were successful (see Fig. 1).

Thus, in this case of bigamy, a secondary female arrived on territory the day after the primary female initiated incubation. The secondary female's activity was concentrated in areas away from the primary female's nest. Only one chase was observed between the females while the primary female was incubating. Their frequency increased throughout the nestling and fledgling periods. The male was attentive to both nests. He fed the primary female's nestlings but not F2's young. This pattern might be due to limited sampling.

1981 OCCURRENCE

Several unsuccessful attempts at bigamy occurred during 1981, all involving the same male. Behavior observed during these attempts suggests several factors that facilitate a male becoming bigamous. Events summarized here are based on 53.9 hr of observation on this pair over 66 days from 25 March–10 August. Thirty-five percent (18.9 hr) of these observations were concentrated during 27 May–30 June when secondary females were present intermittently. One unbanded male, M1, was observed repeatedly with a banded female, F1, during the winter and early spring. A banded pair neighboring to the south returned to their breeding territory in early March. The female disappeared and the male paired with another banded female that wintered approximately 300 m northeast of this territory. They began nesting on 30 March. The male could not be located on 3 April, and M1 chased this female throughout the territory. The annexing of the neighboring territory resulted in him occupying the second largest territory recorded during my study. The female excluded F1 even though F1 made many intrusions into the territory. For about 1 month M1 was observed with both females and had initiated a nest with his "new" mate (see Fig. 1). The nest was found destroyed on 25 April and she disappeared by 27 April. The next day F1 moved throughout both territories accompanied by M1. They attempted to nest twice (see Fig. 1), but both nests were depredated.

F1 laid the first egg in their third nest, located in a

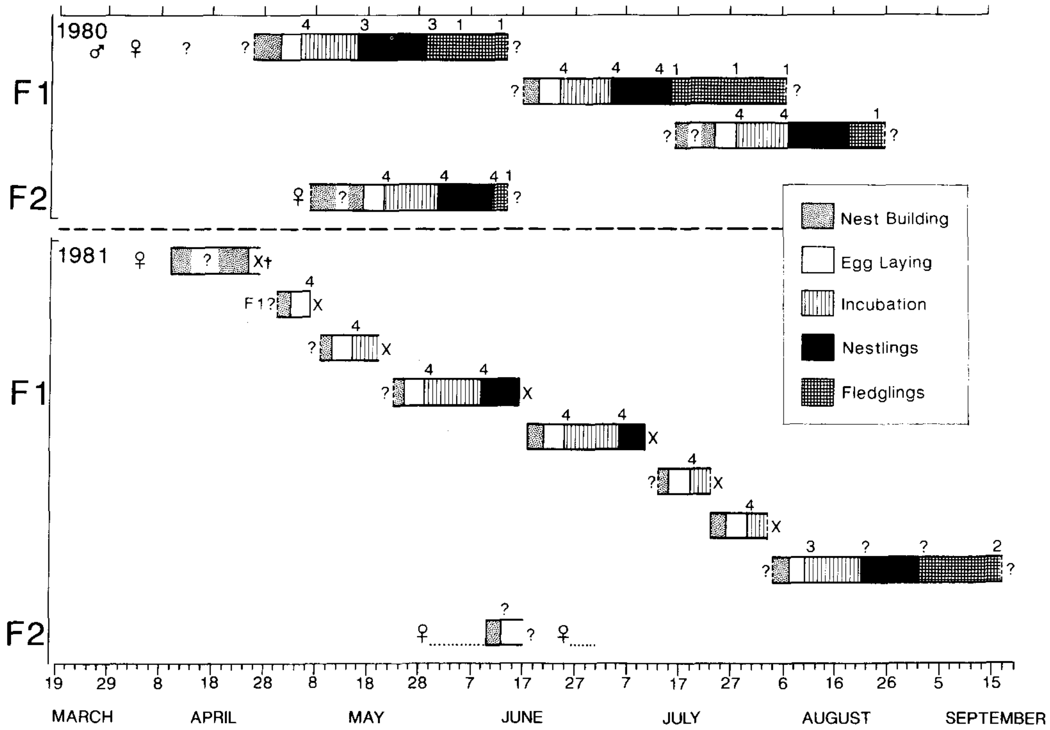

FIGURE 1. Chronology of nesting activity during two cases of bigamy in Northern Mockingbirds. The numbers of eggs, nestlings, and fledglings at each stage of nesting are shown above each nest. Intermittent incubation began with the laying of the third egg. A predation event is symbolized by an X. The ? indicates exact initiation date of nest building was unknown or the number of eggs, etc. was not determined. The ♂ and ♀ indicate when birds first appeared on the breeding territory. In 1981, the male was already present. † indicates disappearance of the female.

Douglas fir (*Pseudotsuga menziesii*) in the northern section of their "enlarged" territory, on 25 May. A copse of white pines (*Pinus strobus*) just to the south of this nest divided the territory and limited the view of the remainder of the territory. F1 laid her fourth egg on 28 May and began incubating.

M1 sang extensively along his southern border throughout the morning of 28 May. He sang during repeated short flights and sang quietly while running along perches in the interior of conifers, behavior associated with showing a nest site to a female. This continued on 30 May when I noted a new female on his neighbor's territory. Between 1–10 June, M1 divided his time between perching silently near his active nest and singing intensively along the southern portion of his territory. The eggs hatched in F1's nest on 9 June. The next day a secondary female, F2, was observed on his territory. M1 was observed three times to collect and deposit twigs as a foundation for a nest in a Colorado blue spruce (*Picea pungens*) along the southern edge of his territory. Concurrently, F2 made eight trips to the nest with lining materials such as dry pine needles and rootlets over a 93-min period. M1 followed F2 on these trips. After returning to the nest under construction, M1 typically sang from a neighboring cedar (*Thuja* sp.).

Several times on 10 and 12 June, while feeding nestlings, F1 left her nest, flew south through the copse of white pines and chased F2. Whenever F1 appeared under the pines, M1 flew rapidly towards her. She dodged M1, continued south, and chased F2. These chases extended over the entire territory south of the white pines. Both females vocalized extensively with the rasping hew call (Logan and Fulk 1984) during these chases but did not fight. Typically, M1 trailed the females by 3–5 m and accompanied F1 back to her nest when she stopped chasing F2. Generally, M1 resumed singing from the vicinity of F2's nest within a few minutes.

No nest building by M1 or F2 was observed on 12 June, and I speculated F2 might have started her clutch. Unfortunately, the nest was too high to determine its contents. M1 sang intermittently from the southern portion of his territory, further suggesting that F2 had initiated her clutch (see Logan 1983). He also spent time in the vicinity of F1's nest where he repeatedly mobbed and chased American Kestrels (*Falco sparverius*) that were hunting in the northern portion of his territory. I did not observe M1 feed the nestlings during 98 min of observation, except possibly once when I noted him leaving the fir as F1 approached with food.

F1's nest was depredated before my next visit on 16

June. M1 sang loudly and continuously, and F1 foraged throughout the territory. F2 was not located.

M1 and F1 began another nest, along the west side of the territory, by 18 June, and the first of four eggs was laid on 21 June. On 24 June, when F1 began incubating, M1 sang near another female. F1 repeatedly chased this female and she left the territory. A similar situation occurred 6 days later while F1 was still incubating. Again, the additional female did not remain. M1 and F1 repeatedly fed nestlings on 6 July. However, the nest was again lost. M1 and F1 initiated three more nests, only the last being successful (see Fig. 1b). In total, F1 produced 27 eggs during 1981! She bred again with M1 in 1982.

Thus, secondary females were observed on this territory on three separate occasions. Each time the primary female was incubating. In the first instance, the secondary female was in the process of completing her clutch when the primary female lost her nest and possibly evicted the secondary female. In the second and third instances, no nesting attempts were discovered.

BIGAMY: WAYS TO CIRCUMVENT FEMALE-FEMALE AGGRESSION

Bigamy can occur in mockingbirds even when unmated territorial males are present (Laskey 1941, Breitwisch et al. 1986b, both cases reported here). Logan and Rulli (1981) reported that bigamy could be precipitated by the disappearance of a male territorial neighbor. A similar situation almost occurred in the 1981 case described herein. In both of these instances, the females were able to maintain their respective territories through female-female aggression. Breitwisch et al. (1986b) noted that two females subdivided a male's territory in half, although no aggression was witnessed during approximately 100 hr of observation (Breitwisch, pers. comm.). In the instances reported by Logan and Rulli (1981) and Breitwisch et al. (1986b), both females nested repeatedly. In the instance reported by Laskey (1941) and both cases described here, the second females disappeared after their first attempt. I suggest that the low incidence of bigamy in mockingbirds and whether or not second females renest are due to the high level of female-female aggression. Yasukawa and Searcy (1982) and Zaias and Breitwisch (1989) suggested that this aggression helps ensure the male's continued parental investment.

Several behavioral options were used by male mockingbirds to circumvent female-female aggression. Among these were: (1) acquiring a large territory, (2) attempting to influence the movements of females relative to each other, and (3) timing when the second female begins her clutch. By acquiring a large territory, a male, in effect, maintains two smaller territories, one for each female. The two males which attracted secondary females had the two largest territories during my study. Female movements often are associated with the nest site, and because the male initiates the nest he can restrict a female's movement by showing nest sites and constructing nest foundations in a portion of his territory away from the other female. A large territory facilitates positioning nests away from one another. Finally, by courting the secondary female when the primary female is occupied with incubation and feeding of nestlings, a male can reduce the interference of his mate when he attempts to attract a second female (Orians 1969). Laskey (1941) reported that the secondary female nested approximately 70 m from the primary female's nest and began incubating while the primary female was occupied with her nest. The 1980 case reported here is very similar both in the distance between the nests and timing. The 1981 case might have failed due to a combination of circumstances. The secondary female had not begun incubating and did not tolerate the elevated incidence of chases by the primary female which occurred because of "spare time" brought on by the loss of her nest.

The behavioral options used by male mockingbirds to circumvent female-female aggression are observed in many other species that are opportunistic polygynists. In several species males are polyterritorial, attracting mates to separate territories (see review by von Haartman 1969, also Freed 1986), and, thereby potentially deceiving females about their mated status (Alatalo et al. 1981). Commonly, second females are attracted and begin to nest only after the first female has finished egg laying or is incubating (Marsh Wren, *Cistothorus palustris,* Verner 1964; Scrub Jay, *Aphelocoma coerulescens,* Woolfenden 1976; Marsh Warbler, *Acrocephalus palustris,* Dowsett-Lemaire 1979; Great Reed Warbler, *A. arundinaceus,* Dyrcz 1986; Least Flycatcher, *Empidonax minimus,* Briskie and Sealy 1987; Willow Flycatcher, *E. traillii,* Prescott 1986; Northern Mockingbird, see references cited above). This may account partially for why males commonly do not assist in incubation. Another way males potentially could circumvent hostilities between females is to locate the two nests as far away from each other as possible. This partially could account for why males assist in nest building, especially the early stages of nest construction, in many species. I predict that, in comparison to monogamous species, more species classified as opportunistically or facultatively polygynous will be typified by males assisting in nest building and avoiding all incubation duties. Further elucidation of the occurrence and timing of social and behavioral factors leading to bigamy in opportunistically polygynous species will require detailed behavioral observations.

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OLFACTION IN SUBANTARCTIC SEABIRDS: ITS PHYLOGENETIC AND ECOLOGICAL SIGNIFICANCE[1]

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Key words: Olfaction; seabirds; procellariiforms; feeding ecology.

Early studies of olfaction in birds concentrated on the anatomy of olfactive structures (Bang 1966, 1971; Bang and Cobb 1968; Cobb 1960). More recently, authors have emphasized physiological aspects of olfaction (Smith and Paselk 1986, Clark and Mason 1987). Nevertheless, our field knowledge of the role of seabird olfaction remains poor (Grubb 1972, 1974; Hutchison and Wenzel 1980; Wenzel 1980; Hutchinson et al. 1984; Bang and Wenzel 1985).

The aim of this paper is firstly to use a well-established method to test the olfactory capacities of several species belonging to different seabird families. Olfactory guidance to a source of food-related odor has never

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