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ASSOCIATION OF MALE AND FEMALE AMERICAN ROBINS (*TURDUS MIGRATORIUS*) DURING THE BREEDING SEASON: PATERNITY ASSURANCE BY SEXUAL ACCESS OR MATE-GUARDING

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ABSTRACT.—Male American Robins (*Turdus migratorius*) behave in ways consistent with the protection of paternity hypothesis. During nest building and egg laying when females are fertilizable, males are with females significantly more often than they are during incubation when females are assumed to be nonfertilizable. Males are significantly closer to females and follow them significantly more often during fertilizable than nonfertilizable periods. Our data suggest that neither reduction in the risk of predation or other direct advantages to females select for the observed variation in the behavior of males. We therefore conclude that male behavior is a probable result of selective advantage gained through paternity assurance, though not necessarily through mate-guarding. *Received 15 Jan. 1986, accepted 4 Sept. 1986.*

Sperm competition probably occurs in at least 26 avian families (McKinney et al. 1985); most of the species are sociographically monogamous (Wickler and Seibt 1983), i.e., males and females consort in pairs, confirming the prediction that mixed reproductive strategies among avian males are common (Trivers 1972). When care of offspring is costly to males, selection against males who care for nonlineally related offspring should occur, and behavior consistent with functional interpretations of protection of paternity should arise.

Protection of paternity can be inferred from differential distribution of parental resources to lineal and nonlineal offspring (implying kin recognition) and from other behavior that increases the probability that females produce offspring sired only by a given male. Mate aggression (Barash 1976), differential responsiveness to courtship cues (Erickson and Zenone 1976), and so-called "mate-guarding" or surveillance of females (Lumpkin et al. 1982) all have been interpreted as behavior increasing the probability that offspring are biologically sired by the males performing the behavior.

Functional interpretations of protection of paternity are often based on predictable variation in behavior. For example, if protection of paternity takes the form of male attendance of females, behavior that could vary includes following of females by males, proximity of males to females,

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and interference by males in interactions of females with other males (e.g., Beecher and Beecher 1979, Birkhead 1979, Mumme et al. 1983). Assessment of the existence and function of aggression between females and males, or courtship differences in wild bird populations is dependent on chance observations of rare events or experimental manipulation of rare events (Erickson and Zenone 1976, Gowaty 1981). In contrast, assessment of existence of attendance depends on relatively easily collected behavioral samples of free-ranging individuals.

American Robins (*Turdus migratorius*) are sociographically monogamous, and males and females cooperate in feeding and defense against predators of nestlings and fledglings (Verner and Willson 1969). We asked if males behaved towards females in ways consistent with protection of paternity through attendance. If so, we expected that (1) males would be with fertilizable females more frequently than with nonfertilizable females, (2) males would stay closer to fertilizable females than to nonfertilizable females, and (3) males would follow fertilizable females more than they followed nonfertilizable females. In this paper we document variability in behavior of male robins consistent with these predictions. We conclude, however, that the functional significance of these attendance patterns remains in question.

METHODS

We watched robins on the lawns and gardens of the Cornell University campus primarily in the experimental garden of the Cornell Plantations. Focal individuals were females with whom we could associate a particular nest. Females, associated with 27 nests, are included in these samples. Ten of the focal females were color banded; others were not. Three males that were seen with females were also color banded. We sampled behavior during nest building, egg laying, and incubation stages of the nest cycle at irregular intervals always before 12:00 EST. For the analyses presented here we considered nest building and egg laying stages to represent *fertilizable* periods for females and the incubation stage as a *nonfertilizable* period. Twenty-five observation bouts were conducted during nest building, 10 during egg laying, and 29 during incubation. Observation bouts yielded 31 samples: females from 4 nests were sampled during both periods, 27 were sampled during only one period. Total minutes of observation were 429 for nest building, 237 for egg laying, and 704 for incubation; thus sample time was almost evenly distributed between fertilizable (666 min) and nonfertilizable (704 min) females. Observation bouts were terminated if we lost track of focal females. Observation bouts lasted 19 ± 9 min [SD] for fertilizable periods; and 24 ± 8.4 min during nonfertilizable periods.

We sampled motor patterns in three ways consistent with Mumme et al. (1983): (1) At minute intervals during sample periods (of a maximum 30 min), we recorded on check sheets whether females were within 30 m of other robins and, if so, the sex of the other robin(s). (2) At each minute interval we also recorded the estimated distance apart in meters of focal females and of the individual(s) within 30 m of her. (3) Whenever a focal female or her male "attendant" moved by flying away, we recorded both which individual initiated the movement and whether the other followed within 30 sec.

Sexes of robins were assigned on the basis of hood color and head and nape contrasts (e.g., see Gochfeld and Burger 1983), and behavior. We determined the sex of color-banded individuals by the presence of a brood patch in females or a cloacal protuberance in males. We assumed that unbanded individuals were females if they carried nesting material, built nests, or incubated eggs, activities usually confined to females among robins (Verner and Willson 1969).

Statistical tests are from Sokal and Rohlf (1981) and Siegel (1956); all tests were one-tailed.

RESULTS

Males were seen within 30 m of focal females in 87% of the 31 samples. During fertilizable periods 100% ($N = 16$) of females were with males (also called "attended by males") during some part of the sample; in contrast, during incubation 73% ($N = 15$) of females were with males during some part of the sample ($G = 6.444$, $df = 1$, $P < 0.01$). Similarly, the total time that females were or were not attended by males was associated with fertilizability. Females were attended by males for greater proportions of each sample time during fertilizable periods than during nonfertilizable periods (for arcsin transformed data $t = 3.7828$, $df = 29$, $P = 0.00035$). The mean percent of each sample during which a female was attended was 77% during fertilizable periods and 28% during nonfertilizable periods.

The mean distance apart for males and females was 6.3 m during fertilizable periods and 9.6 m during the nonfertilizable periods ($t = -1.5198$, $df = -25$, $P = 0.07$).

Females initiated 74% of all movements and were followed by males 53% of the time. The likelihood that a female was followed by a male was associated with fertilizability ($G = 19.672$, $df = 1$, $P < 0.001$). Males followed females at least once in 93.7% of samples during fertilizable periods but in only 20% of observations during the nonfertilizable periods. When counts of following of females by males are examined for association with fertilizability, the hypothesis of independence is clearly rejected. During fertilizable periods females were followed by males more often than expected (88 out of 142 female initiated movements), and not followed less than expected (54 out of 142 female initiated movements). During nonfertilizable periods females were followed by males less than expected (8 of 38 female initiated movements) and not followed more than expected (30 of 38 female initiated movements) ($G = 20.9852$, $df = 1$, $P < 0.001$). When males initiated movements, females followed them at least once during 37.5% of fertilizable periods but only during 6.7% of nonfertilizable periods ($G = 4.6$, $df = 1$, $P = 0.032$). However, when counts of following of males by females are examined for association with fertilizability, the hypothesis of independence cannot be rejected ($G = 3.2054$, $df = 1$, $P < 0.10$).

DISCUSSION

The behavior of male robins is associated with fertilizability of females. Predictions of the uncertainty of the paternity hypothesis are met by these data: compared to nonfertilizable females, fertilizable females were attended by males more frequently than were nonfertilizable females, and males followed females more frequently than the reverse.

What evolutionary hypotheses can explain the close attendance and following of females by males and are consistent with these data?

(1) Variation in close affiliation by males of females may be the result of selection for "mate-guarding," defined as behavior by males that inhibits or interrupts sexual advances of other males to females with which the "guarding" male associates. Mate-guarding has been inferred from similar data in a variety of species (e.g., Beecher and Beecher, 1979; Birkhead, 1979, 1982). Our data, however, are inadequate to claim mate-guarding among robins. Roughly a third of the females, but only a tenth of the males we observed were marked individuals. Thus we cannot comment on the duration of the associations we did observe; we do not know if all of the males we watched attending females were bonded to them and thus their mates. Secondly, it seems difficult to differentiate guarding from alternative explanations (see (2) below) for variation in the behavior of males we observed.

(2) Close affiliation of females and males during nest building and egg laying may be the result of selection for the males' opportunities to copulate irrespective of any protection of paternity from competitive sources. This hypothesis predicts that males should affiliate with and follow females only during those times of day when copulations are likely to occur. Because most of our samples were collected before 10:00, we cannot comment further upon this idea. Additional needed data include a frequency distribution of copulations during the day. We observed copulation at all hours of the morning except for the hour after dawn; we do not know if copulations occurred during midday, afternoon, evening, and night. Even with appropriate data on circadian distribution of copulations, variation in attendance patterns attributable to this hypothesis would be difficult to differentiate from variation associated with protection of paternity, an undiscussed difficulty in interpretation of many studies of mate-guarding (e.g., Birkhead 1979, 1982). Ways to differentiate the guarding hypothesis from the copulatory access hypothesis include noting variation in behavior of males with females during a single day. If after copulation

is achieved, males discontinue following and close association with females, the guarding hypothesis would be weakened. Critical evaluation of the existence of mate-guarding also depends on observations of social situations in which more than one male may have access to fertilizable females (e.g., Mumme et al. 1983). Given that the robins we observed were only weakly territorial with as many as 10–12 nests in a few acres, we can claim that more than one male may have had access to a given female. We are unable, however, to offer comparisons of robins under more dispersed, strongly territorial nesting conditions.

(3) Close attendance and following of females by males may be a reflection of the increasing bond concurrent with the pair formation phase of the nesting cycle. This pairbond explanation for close attendance and following predicts that the mechanisms of association will intensify as the breeding cycle continues (Lumpkin et al. 1982). The significant decrease in attendance and following of females by males from fertilizable to nonfertilizable periods allows the rejection of this prediction of the increasing-bond hypothesis.

(4) Close attendance and following of females by males may be the result of selection against predation. If predation has selected for male behavior, i.e., if the risk of predation on females is reduced by the presence of males, males should attend and follow females during nest building and egg laying as well as incubation with about equal intensity, or with greater intensity during incubation when the female and nest are presumably of greater reproductive value to males. Our data do not support this hypothesis. For example, males followed females more during nest building and egg laying and less during incubation rather than the reverse pattern. Reduction in predation risk may contribute some selective advantage; however, reduction in this risk alone cannot account for the observed variation in attendance, following, and proximities to females by males.

(5) Another hypothesis, related to (2) and suggested by consideration of advantages to females in shaping the behavior of males (Lumpkin 1981), is that females gain direct benefits from close attendance of males, e.g., reduction in the probabilities of forced extra-pair copulations or predation. This hypothesis predicts that males initiate movements as frequently as females and that females follow males as often as males follow females. Our data lend little support to the notion that females manipulate the attendance behavior of males, although it should not be overlooked that the frequencies with which females did or did not follow males at least once during a sample is associated with fertilizability. This may mean that females gain benefits such as protection from unwanted copulations with other males or that association may reflect female so-

licitation of copulations. We observed few copulations, and none of these gave evidence of force. Furthermore, females always were able to chase males away from nests when intruder males approached. We therefore suspect that female robins are able to avoid forced copulations and to defend themselves against predators without male help. We are unable to comment further on female "solicitation" because we observed so few copulations.

(6) A final hypothesis states that changes in foraging requirements associated with different periods of the nesting cycle shape attendance and following. While it does seem likely that nutritional requirements for females may vary with nest cycle periods, it seems unlikely that variation in nutritional needs can explain the attendance and following behavior of males unless male robins are less successful than female robins in finding food during early stages of nest cycles.

We conclude that male robins behave in ways consistent with the protection of paternity hypothesis. Based on our observations, we *predict* that male robins engage in a mixed reproductive strategy, cooperating with one female in the care of offspring while taking opportunities to copulate with other females in whose offspring they do not invest. The variation in male attendance behavior suggests that a similar study on a universally marked population of individuals would be profitable.

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