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Mate guarding tactics used by Great Crested Flycatchers.—To counter female infidelity, male birds have evolved several behaviors which increase their probability of paternity. Mate guarding may be defined as any behavior by a mated male whose principal function is to decrease the likelihood of his mate copulating with other males during the period when her eggs can be fertilized (Birkhead 1979, Beecher and Beecher 1979, Hatch 1987). Most studies of mate guarding focus on following behavior. Mate guarding is inferred from following behavior if males follow their mates more often when the females are fertile than when they are non-fertile (e.g., Gowaty and Plissner 1987). Territoriality may also function as mate guarding. By defending a larger breeding territory during his mate's fertile period, a male increases the distance between his mate and intruding males (Møller 1990; but see Dunn 1992).

We investigated mate guarding in the socially monogamous Great Crested Flycatcher (*Myiarchus critinus*). We predicted that males in this species would attempt to increase their probability of paternity by using one or both of these forms of mate guarding behavior. First, we compared the tendencies of males to follow their mates during vs after the female's fertile period; second, we measured territory size throughout the breeding season to determine whether males defend larger territories when paternity is at stake. Here we present evidence that male Great Crested Flycatchers do guard their mates.

Methods.—We studied six pairs of Great Crested Flycatchers breeding in natural cavities around the Queen's Univ. Biological Station, near Kingston, Ontario, from 16 May to 30 July 1991. We located all nests during nest-building, and monitored each pair until about six days after hatch, when brooding stopped. In this species, only females build the nest, incubate eggs and brood young (Taylor and Kershner 1991), so we could determine the sex of adults through behavioral observations at the nest site. During the breeding season, these birds aggressively defend territories (Bent 1942). Therefore, we were confident that birds seen tending the same nest on different days were the same individuals. As in other studies, we considered females to be fertile during nest-building and egg-laying (Birkhead and Møller 1992). We divided our observations of following and territory size into fertile and post-fertile categories.

We performed watches at each nest site, because it is difficult to track these birds through the forest. Each watch lasted one hour, and was performed between 06:00 and 18:00 h EST, alternating early morning and afternoon watches on subsequent days. During each watch, we recorded visits of the birds to the nest site. For each visit, we determined the sex of the birds, and then categorized the visit into one of three categories: male following, female following, or no following. If the birds visited the nest site, within 5 sec of one another, and flew in the same direction, we considered the second bird to be 'following'. Otherwise, the visit was scored as 'no following'. For each of the six pairs, we observed 16–226 visits in each of the fertile and post-fertile periods.

We measured territory size during playback trials (Falls 1969) to determine whether males defended larger territories during the female's fertile period. The recording used for playback consisted of a loop of Great Crested Flycatcher calls from a commercial recording. We began each playback trial when both birds were observed at the nest site. At this time we played back the recording at a consistent volume, from an initial distance of 10 m, and slowly walked away from the nest at a steady pace. The distance that the male ceased responding to the playback was measured as the response radius. We performed 1–4 playbacks in both the fertile and post-fertile periods to each of three pairs, over four breeding attempts (one pair nested twice). We then calculated the mean radius of response for each male in both the fertile and post-fertile periods. Males' response to repeated playback may

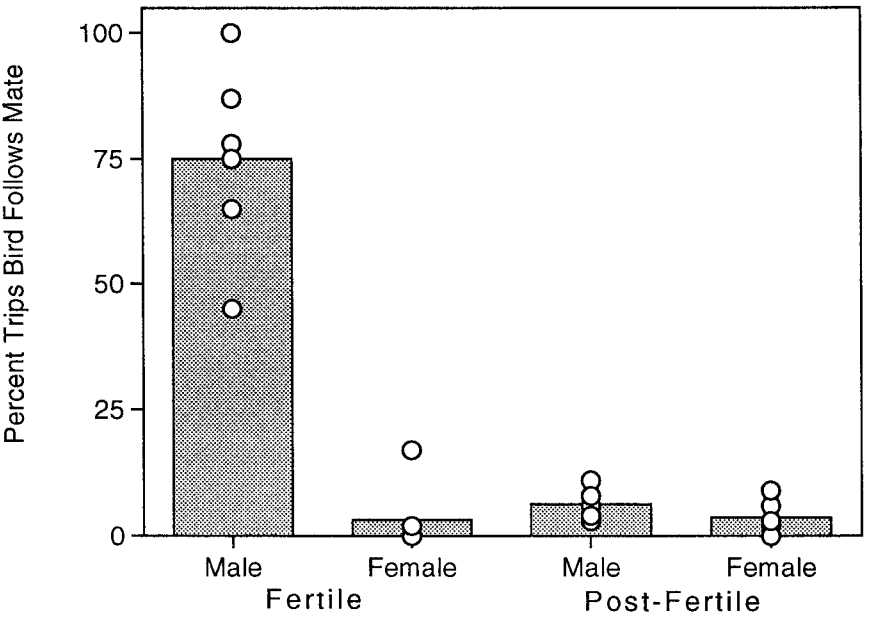

FIG. 1. Percentage of visits to the nest in which six male and six female Great Crested Flycatchers followed their mates, during the fertile and post-fertile periods. Open circles represent individual tendencies to follow a mate; bars indicate group means.

change independently of territory size due to learning, either decreasing (Verner and Milligan 1971) or increasing (Knight and Temple 1986). To reduce these effects, we performed playback trials at least four days apart.

Results.—Males were more likely to follow their mates during the fertile period than during the post-fertile period (Fig. 1). As well, males followed females more often than females followed males during the fertile period (Fig. 1). For each period (fertile and post-fertile), we calculated the proportion of visits that males followed females or females followed males. These proportions are independent because during a number of visits, neither bird followed. A two-way repeated measures ANOVA on the arcsine-transformed data revealed a main effect of sex (F = 33.7, df = 1,10, P = 0.0002), a main effect of period (F = 30.2, df = 1,10, P = 0.0003), and a significant interaction (F = 30.0, df = 1,10, P = 0.0003). That is, males followed females more during the fertile period than during the post-fertile period, or than females followed males at all.

Territory size tended to decrease from the fertile period to the post-fertile period. That is, the radius of response to playback decreased from the fertile to the post-fertile period in three of four nesting attempts (Fig. 2). Although the decrease in response radius was statistically significant (one-tailed paired t-test, t = 2.42, df = 3, P = 0.047), this analysis includes observations made on a pair which renested after their first nest failed. During the second nesting attempt, the territory dynamics matched the general trend observed; response radius increased during the second fertile period, and subsequently decreased. Exclusion of this second nesting attempt reduces our sample size to the point where inferential statistics are unwarranted.

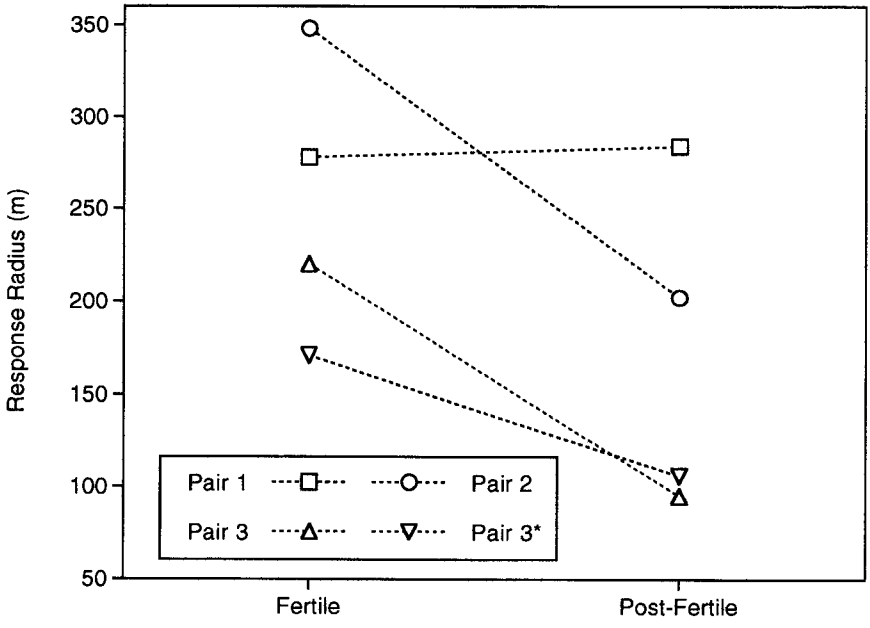

FIG. 2. Mean radius of response to playback (distance from the nest at which male Great Crested Flycatchers stopped responding to song playback), during the fertile and post-fertile periods. 'Pair 3*' refers to the second nesting attempt by pair 3.

Discussion.—The pattern of following by males, during their mates' fertile and post-fertile periods (Fig. 1), strongly suggests that male Great Crested Flycatchers use close surveillance to guard their mates. Several alternative hypotheses have been proposed for close male attendance during the fertile period (e.g., Power 1980, Lumpkin et al. 1982, Gowaty and Plissner 1987), but our results do not support the predictions derived from these hypotheses. If males escort their mates to guard them from predation (Power 1980), or if male surveillance results from pair bonding (Lumpkin et al. 1982), following should increase as the season progresses. Instead, we found that male following was most frequent during the fertile period. If males follow females primarily for copulatory access (Gowaty and Plissner 1987), most following should occur in the early morning, when copulation is most likely (Birkhead et al. 1987); instead, male following was consistently high throughout the fertile period, although we performed half the nest watches after 11:00 h. Male surveillance may, of course, serve more than one function (e.g., Power 1980), but our findings are most consistent with the mate guarding hypothesis: males attempt to defend paternity by closely following their fertile mates (Beecher and Beecher 1979, Birkhead 1979).

We found evidence that male Great Crested Flycatchers defend larger territories while their mates are fertile. This evidence should be interpreted cautiously, however, in light of the small sample sizes. The idea that territoriality functions as a form of mate guarding (Møller 1990) is more controversial than that of close following. Although a large territory should increase the average distance between the resident female and intruding males, by patrolling a large territory a male also increases the distance between himself and his mate

(Dunn 1992). Furthermore, if female Great Crested Flycatchers solicit extra-pair copulations outside the territory (e.g., Smith 1988), territoriality is unlikely to have a mate-guarding effect. In some species, there appears to be a trade-off between mate guarding and territory defense (Sherman and Morton 1988, Meek and Robertson 1994); mate guarding by close following may preclude mate guarding through territoriality. It is clear that male Great Crested Flycatchers closely follow their mates during the fertile period. It remains to be determined, however, whether males also use territory defense as a mate guarding tactic. At this time, the relationship between defending territories and defending mates per se is an open question.

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Red imported fire ant predation on Crested Caracara nestlings in south Texas.—In 1989 I observed two instances of red imported fire ant (*Solenopsis invicta*) predation on newly hatched nestlings of Crested Caracara (*Caracara plancus*) in the vicinity of the Attwater Prairie Chicken National Wildlife Refuge (APCNWR), Colorado County, Texas (29°40′N, 96°15′W). The refuge encompasses 3232 ha of prairie, marsh, cropland and riparian forest and is kept in secondary succession for habitat for the endangered Attwater's Prairie Chicken (*Tympanuchus cupido attwateri*).

A lone caracara chick hatched in Nest 1 and two chicks hatched in Nest 2 on 16 July and 23 July 1989, respectively. Both nests were built 20 cm below the canopy in Macartney rose (*Rosa bracteata*), approximately 2 m above the ground. On the morning of 16 July I checked Nest 1. The male was perched on a nearby Macartney rose and the female was on the nest. Both adults flew when I climbed the nest tree. I found one live day-old chick and the remains of what appeared to be an unfertile egg (egg yolk, shell fragments) at 08:30 h CST. I observed fire ants on shrub branches near the nest. The adults returned to the nest as soon as I left the area. I returned to the nest in the late afternoon and observed the adults in the same positions as in the morning. I climbed the nest tree again and found the chick dead in the nest covered with fire ants at 16:00 h. I retreated to my truck and at 17:00 h CST saw the female fly to the nest. In a few minutes shew flew off with the dead chick in her bill and dropped it approximately 100 m from the nest. The adults remained in the natal area for another five days, usually perched on shrubs near the nest tree. After 21 July the adults were not seen again. On the afternoon of 23 July I checked Nest 2 for hatching. I found two dead one-day-old chicks in the nest covered with fire ants. The adults perched near the nest but did not appear to enter the nest that day. I returned to the nest on July 24, but was not able to locate the adults. Later observations suggest that the adults abandoned the nest.

I observed five caracara pairs hatch first clutches during the period January–March, 1989, but I found only two clutches in June. Both of these were preyed upon by fire ants. Fire ants apparently were not active during the colder weather in January, February, and March (maximum temperatures of 18.7°C, 14.6°C, 21.8°C, respectively), and cold probably restricted the ants' movements. Porter and Tschinkel (1987) found red imported fire ant workers foraged from 15° to 43°C, with maximum rates between 22° and 36°C. Porter (1988) reported red imported fire ant colony growth ceased below 24°C.

Predation by red imported fire ants on newly hatched chicks has been reported for Northern Bobwhite (*Colinus virginianus*) (Stoddard 1931), Wood Ducks (*Aix sponsa*) (Ridlehuber 1982), Cliff Swallows (*Hirundo pyrrhonota*) (Sikes and Arnold 1986), and colonial water-