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SHORT COMMUNICATIONS

MATE GUARDING AND THE ACQUISITION OF NEW MATES IN *CALOPTERYX MACULATA* (P. DE BEAUVOIS) (ZYGOPTERA: CALOPTERYGIDAE)

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The occurrence of guarding of non-mates by males of *C. maculata* appears to be a function of population density. Males in a high density Canadian population regularly defend females with whom they have not copulated, unlike males in a low density Virginian population (cf. J. ALCOCK, 1979, *J. nat. Hist.* 13: 439-446). But males in Canadian and other high density populations that are guarding mates (and non-mates) do occasionally respond sexually to new arrivals on their territories whereas repeat matings between a male and a recent partner are very rare. Both males and females apparently change their receptivity in response to several factors producing a variety of possible interactions between a territory owner and an arriving female. The interchange of signals between a pair leads males to copulate primarily with new partners.

INTRODUCTION

Males of the damselfly *Calopteryx maculata* establish territories on streams at locations that contain plant material at or near the surface of the water (WAAGE, 1973). Territory owners court and mate with females that come to these sites to lay their eggs. After copulation, which takes place on vegetation near the stream, females are released by their mates. The male returns to his territory and after a short delay, the female usually returns to the oviposition substrate that her partner controls. There she will oviposit while the male guards her against intruders who, if not repelled, may bite at the wings of the female, leading her to fly up from the water to the stream edge where she may copulate again. If this happens, the intruder will be able to replace all or most of the sperm stored in the female's spermatheca (WAAGE, 1979a).

At his study sites in Massachusetts, WAAGE (1979b) noted that males that were guarding a mate regularly failed to take advantage of additional opportunities to copulate. Newly arrived females sometimes oviposited in a male's territory without copulating with the owner. In these cases, the resident male guarded non-mates in whom he had no reproductive stake. But in a different (Virginia) population of the damselfly, ALCOCK (1979) found that males rarely guarded non-mates and instead seemed to discriminate between previous partners and newly arrived females. The paper attempts to explain why different conclusions were reached in these studies on mate guarding and "mate--recognition" in *C. maculata.* I will show that in a Canadian population, guarding of non-mates is common for the reasons given by WAAGE (1979b). Second, evidence will be presented that males nonetheless distribute their copulatory efforts so that they mate with a variety of females and rarely copulate again with recent partners. A speculative model of the motivational mechanisms responsible for this outcome will be presented.

METHODS

The study was conducted between 1-12 July 1982 on a small stream that feeds into Lake Opinicon near Chaffey's Locks in southern Ontario, Canada. The stream passed through an open meadow (drained beaver pond) surrounded by deciduous woodland. On 1-4 July, a total of 7 territorial males were given distinctive marks of liquid eraser on the wings or dorsum of the thorax. On any one day, one male was selected for intensive observation with notes made occasionally on nearby individuals. Data were recorded on the nature of the interactions between a male and the females that flew to his oviposition substrate during a period of 1-3 hr in the middle of the day. Whether the male approached an incoming or perched female, landed on her wings, pursued her when she flew or copulated with her was noted. Each female that was mated was also marked on the wings or thorax with liquid eraser while the pair was in copula. This could be done without seriously disturbing the damselflies. As a result, I was able to identify mates and non-mates and to have a record of each male's subsequent reactions to his past mates which could be compared with his treatment of non-mates.

On 8-12 July I staked various amounts of oviposition material at 1.5 m intervals in a straight section of the brook. These patches were quickly claimed by territorial males, enabling me to keep 5 territories under inspection simultaneously for periods of between 4-5 hr daily. Data were gathered on (a) the nature and outcome of all encounters that led to a male pursuit of a female visitor, (b) how many ovipositing females were present in the male's territory at the time he left to chase a new arrival and how many remained when he returned, and (c) how many females were present ovipositing on a territory at 10 min intervals throughout the daily observation period. These data permit an assessment of (a) the probability that a male that pursued a female would actually copulate with her, (b) the probability that unguarded ovipositing females would be lost to intruders while a resident male engaged in sexual interaction with a new female and (c) the pattern of arrivals of ovipositing females at a territory.

RESULTS

THE GUARDING OF NON-MATES

Males of *C. maculata* in the Lake Opinicon population, like those in some New

England locales (WAAGE, 1979b), regularly guarded females with whom they had not mated. It was common for there to be 4-9 ovipositing females in a territory at a time when the resident had copulated with far fewer females (Fig. 1). Because the population density was high and because females were attracted to ovipositing conspecifics (cf. also WAAGE, 1979b), large numbers of females often descended on a territory in a short period (Fig. 1). In the confusion caused by the rapid build-up of ovipositing females, the resident male often missed opportunities to respond sexually to the newcomers (particularly if he was engaged in defence of his territory, a common event).

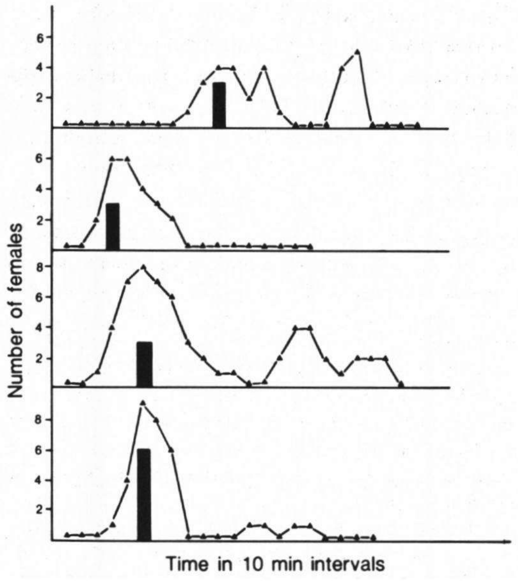

Fig. 1. Four records of the total number of females of *C. maculata* ovipositing in a male's territory; counts made at 10 minute intervals (line graph). The vertical bars indicate the number of females the male had mated by that time.

Moreover, as WAAGE (1979b) has suggested, males that are guarding several females appear less strongly motivated to mate than males without any ovipositing females in their territory. This response may be adaptive because males that leave their sites to pursue new females to streamside vegetation often lose any females that are ovipositing in their territory to intruding males. Thus there is a trade-off between (a) the probability of acquiring a new mate and (b) the probability of losing a previous partner to a rival. The likelihood of success in pursuing a new female was 56% (88 of 156 pursuits recorded from 8-12 July resulted in copulation). During the study, 37 records were collected in which a male that was guarding 1-6 females (mean = 2.5) left to mate successfully with a new female. Of the 94 ovipositing females that were abandoned temporarily, 40 (44%) were driven off invading males. These data are similar to results collected by WAAGE (1973). To the extent that the guarded females were the territorial male's sexual partners, their loss represents a loss of egg fertilization opportunities for that male. Females that are chased off before laying their clutch of eggs often mate again with consequent sperm replacement (WAAGE, 1979a).

MALES GENERALLY MATE WITH NEW FEMALES

Despite the fact that males do guard females with whom they have not copulated, when they do respond sexually to a female she is usually a new individual and not a previous mate of the day. Even while guarding one or more ovipositing mates or non-mates, males will sometimes pursue and copulate with a newcomer. Of 102 copulations recorded on 4, 8-12 July, 13 occurred when a male left a single ovipositing female to mate with a new arrival and 21 took place when the male left from 2-6 egg-laying females to copulate with a newcomer. Thus guarding males of *Calopteryx* remain sexually responsive and acquire additional mates as a result (HEYMER, 1973; ALCOCK, 1979; WAAGE, 1979b).

Further information on the response of males to non-mates versus previous mates comes from the data collected on 1-4 July on the reaction of males to females as they landed in a territory. Interactions between male and female involved the following steps: (1) the male approached the perched female and whirred his wings in hovering courtship flight (WAAGE, 1973) while facing her, (2) the male might then land on the female's wings to bite and pull at her, (3) if at any stage, the female flew from the water, the male could pursue her, and (4) if the female landed on vegetation, a male in close pursuit could give the courtship display and then copulate with the perched female. A male-female encounter could end at any stage if for example, the male ceased to interact with the female, or if the female refused to fly up from the water, or if a pursued female escaped or was lost because of interference from other males.

Table I

Difference in the response to recent mates and non-mates by territorial males of *Calopteryx maculata*

Female category	Interaction terminates after male approaches[1] female	bites wing of female	pursues female	copulates with female
Recent mate	49	7	7	3
Newly arrived non-mate	9	9	11	33

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[1] Male flies toward female and often performs wing-whirring display in front of her and then leaves female to perch nearby.

$\chi^2 = 53.9$, df = 3, $p < 0.001$

Table I shows that encounters were much more likely to end after an initial approach/courtship flight by the male if the female were a previous mate than if she were a non-mate. Included in the 49 records in this category are 31 cases in which the interaction occurred shortly after a copulation (usually within 60 seconds after release of the female). When a female arrived shortly after the male had copulated he almost never did more than approach the female before permitting her to oviposit. This is true even if the female was not his mate but by chance happened to come to the site before his actual partner had returned (N = 5). This indicates that males do not recognize their mates as individuals but are in some way programmed to experience reduced sexual motivation immediately after a copulation. (But if the newcomer flies up from the oviposition substrate, the resident will follow. I collected 11 records of males that mated twice within 5 minutes).

Even if we exclude the 31 cases in which a male only approached his recent mate shortly after copulation, the response of males to mates versus non-mates is statistically different ($G = 25.8$, d.f. $= 3$, $p<0.001$). Eighteen records were gathered in which a male only displayed to a returning mate that had left after a period of oviposition on his territory (females departed because of a naturally occurring disturbance on the stream or because they were experimentally removed by the observer).

In contrast to the usual approach/display response to old mates, newly arrived females often elicited a strong response from the territory owner and were often pursued and mated. Of the 36 matings achieved by the 7 males under observation, only three involved females with whom the male had copulated earlier in the day. Moreover, the three rematings occurred after 21, 41, and 43 minutes had passed since the first mating; a result similar to that recorded by ALCOCK (1979) and WAAGE (1979b).

DISCUSSION

WAAGE (1979b) and ALCOCK (1979) almost certainly reached different conclusions on the frequency of guarding of non-mates because the populations they studied differed in density. The maximum number of females seen ovipositing simultaneously in the Virginian population was only 5 whereas WAAGE (1979b) observed males with as many as 16 females on a territory. In the Canadian population the record was 11, with 9 females seen together in a territory on several occasions. Further evidence that population densities differed comes from the records on the maximum number of copulations for one male in one day (Virginia - 9, New England - 11, Ontario - 14). When population density is high, as in the New England and Ontario study sites, female visits are more closely spaced temporally and male intruders more numerous. Thus resident males are less likely to detect new arrivals, more likely to become sperm-depleted (WAAGE, 1979b), and more likely to have ovipositing mates stolen by intruders if the territory were left unguarded. As a result, guarding of non-mates is common in high density populations whereas males in low density populations are less likely to be swamped by arriving females, so that they rarely guard non-mates.

But under conditions of both high and low density, males seldom copulate with females with whom they have mated that day. My observations and those of WAAGE (1973, 1979b) suggest that the sexual receptivity of females and males varies depending on a number of factors. Females signal a readiness to mate in several ways (Waage, manuscript), ultimately by flying from the male's territory to streamside vegetation. If they refuse to do this, the probability of copulation is almost nil (on two occasions, a male secured the tandem position with an ovipositing female and eventually succeeded in pulling her far enough out of the water to induce her to copulate). But females vary in their readiness to fly from the water to mate. In some cases the only interaction between a male and female at the oviposition site is the male's cross-display (WAAGE, 1973). Females that fly up in response to the cross-display, without landing at the oviposition site, are very likely to copulate (13/15 cases - 87%), indicating that they are highly receptive. But most females land and require at least a hovering courtship display before leaving the stream with the male in pursuit. In these cases, the likelihood of copulation is reduced (43/67 - 64%), perhaps because some of these females have recently mated and are more likely to fly long distances or attempt to escape. This increases the probability of male-male conflict and the loss of the female for the resident male. Females in a third category appear even less receptive. Those that do not fly up until they have been bitten on the wings are even less likely to copulate (32/74 - 43%) ($\chi^2 = 12.85$, df = 2, $p<0.01$).

Presumably females alter their receptivity depending upon how recently they have mated or how sperm depleted they are or how difficult it is to gain access to a guarded oviposition site. Likewise males that have just mated or that are guarding a mate seem to be less receptive because they sometimes fail to perform courtship flights to perched females or to bite at the wing of a newly arrived female. In effect males have a graded series of reactions (the cross-display, the hovering courtship display, and the wing bite attack) that announce their degree of receptivity and readiness to harass an ovipositing female. The interaction between variation in female readiness to respond to these signals and variation in male readiness to provide them leads males to mate primarily with newly arrived non-mates. Recently mated females not only are less likely to respond to male signals but males are less likely to give them when they have just returned to their territory after a copulation. But those newly arrived females that have not mated are highly receptive to male signaling. They will often be pursued and mated by the resident male, particularly if he is not engaged in mate-guarding or has not mated for some time and gives strong indicators of his sexual readiness (through courtship and wing biting). Thus there is sufficient congruence in the reproductive interests of males and females to reduce the likelihood of quick repeat matings between a pair and to increase the probability of copulation between non-mates. As a result, when males do invest in a copulatory attempt, they are likely to do so with an individual that offers considerable potential for egg fertilization gain.

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