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# THE MATING SYSTEM OF *ORTHETRUM CALEDONICUM* (BRAUER), WITH SPECIAL REFERENCE TO VARIATION IN COPULATION DURATION (ANISOPTERA: LIBELLULIDAE)

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Males of the common Australian libellulid *O. caledonicum* defended small territories at a pond in areas where there was open water at the shoreline. The density of males at the pond edge and the proportion of time spent in flight was greatest at midday. Females visited open shoreline to oviposit in shallow water for a period of about one minute. Males captured incoming females and copulated for periods ranging from 6 s to about 20 min. Unlike some other spp. of *Orthetrum*, prolonged copulation was apparently not practised exclusively by subordinate males unable to secure a territory. Alternative hypotheses on the variation in copulation duration are presented.

## INTRODUCTION

Previous studies of *Orthetrum* dragonflies (ITO, 1960; HEYMER, 1969; PARR, 1980, 1983a, 1983b; MILLER, 1983; SIVA-JOTHY, 1984, 1987) have revealed some interspecific variation in the degree of territoriality by males and, especially, intraspecific variation in the duration of copulation. Here I describe the behavior of *Orthetrum caledonicum*, a previously unstudied Australian species, as a contribution to the body of information available for the genus. I shall describe how males distribute themselves in relation to opportunities to encounter receptive females, and I shall document that in this species too, copulation times vary a great deal. This latter topic has recently been explored fruitfully in the context of sperm competition and alternative mating tactics. MILLER (1983), SIVA-JOTHY (1984, 1987) found that some non-territorial males of *O. chrysostigma* and *O. cancellatum* may copulate for prolonged periods. In contrast, territorial males copulate briefly. Lengthy copulations in *O.*

*cancellatum* permit the male to remove nearly all the sperm stored in his mate. Short copulations result in the removal of fewer rival sperm but they save time that the male may use to defend his territory and interact with other females. I shall show that in *O. caledonicum* variation in the duration of copulation does not appear to be correlated with differences in the primary reproductive tactics employed by males.

## MATERIAL AND METHODS

The study was conducted from 19 February to 7 March 1986 at a small, reedy pond in a park in Nedlands, Western Australia. Data were collected by the author and by an advanced entomology class from the University of Western Australia.

The circular pond was divided into four sectors each with approximately the same length of shoreline. We measured the amount of shoreline in each quadrant in which open water reached the pond border versus the shoreline that was covered with tall reeds. A total of 65 censuses were made on 8 days between 20 February and 7 March. A minimum of 30 min separated two censuses. As the observer walked slowly around the pond, he or she noted the location of each male seen, each ovipositing female, and each copulating pair.

Fifty males were captured in an insect net and given a distinctive color combination on the wings using Liquid Paper Typewriting Correction Fluid or enamel paints. Between 28 February and 6 March, 36 records of male activity were gathered at various times during the day by observing a marked individual for 20 min; activity was measured as the duration of all flights during the period.

Statistical analyses were performed with the Epistat Statistical Package. All means are presented ± 1 S.D.

## SPATIAL DISTRIBUTION OF MALES

Males perched at the pond edge where there was open shallow water. They avoided areas of dense reeds. From their perches they launched patrol flights back and forth over the water along the edge of the pond. The density of males in each quadrant of the pond was a simple function of the availability of shoreline with exposed water in each sector (Tab. I).

The spatial distribution of males corresponded to the availability of females. The number of females seen ovipositing or copulating in the four quarters of the pond was also a function of the length of open shoreline per sector (Tab. I).

Most males (23 of 27 marked individuals seen on more than one day) exhibited site fidelity returning to the same 2-5 m stretch of pond edge on two or more days. Many males, however, occupied more than one segment of pond edge over the course of the study; the mean for the sample of 27 males was 2.6 ± 1.2 sites with an average of 7.3 ± 3.3. days between first and last sighting.

Although males had a tendency to return to the same location for a few days, they then usually shifted their perch-patrolling sites.

Table I

The relationship between the length of open shoreline in the four quadrants of a pond and the number of females and males of *Orthetrum caledonicum* recorded during censuses of the pond (20 Feb-7 Mar)

| Quadrant of pond | NW | NE | SW | SE |
|---|---|---|---|---|
| Open shoreline (m) | 33.5 | 14.5 | 38.9 | 54.1 |
| Mean maximum number of males[1] | 12 | 5.8 | 13.2 | 16.8 |
| Total number of females[2] | 14 | 7 | 10 | 22 |
| Ratio of females/males | 1.2 | 1.2 | 0.7 | 1.3 |

[1] Mean maximum = the average of the five highest counts of males recorded during all censuses of a particular quadrant

[2] The total number of females counted on all 65 censuses during the study

## TEMPORAL DISTRIBUTION OF MALES

Male density varied over the course of the day, peaking between 1030-1430 (Fig. 1). The rather broad peak of male activity at the pond reflects the more or less even temporal distribution of females over the day (Fig. 1).

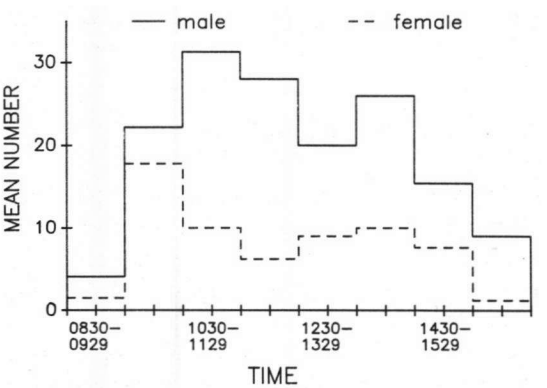


Fig. 1. The mean number of males (solid line) and females (X10) (dotted line) seen on censuses made between 20 February and 4 March. The number of censuses per hour ranged from 4 to 8.

There is some evidence that males are most likely to be at the pond edge when females are most likely to be coming to the pond to oviposit. In the period from 20 February to 4 March, there were 11 censuses in which the census taker saw at least two ovipositing or mating females; the mean number of males at the pond on these censuses was 27.7 ± 6.7. Fot the 15 censuses in which only one female was detected the mean number of males was 22.8 ± 9.7. For the 24 censuses in which no female was counted, the mean of males was only 18.3 ± 12.4 ($F_{2,47} = 4.42$, $P < 0.02$).

## TEMPORAL CHANGES IN MALE ACTIVITY

Not only did the number of males vary temporally over the course of the day,

Table II
The proportion of time spent in flight by marked males observed for 20 min periods

| Time of day | 0830-1030 | 1031-1230 | 1231-1430 | > 1431 |
|---|---|---|---|---|
| Mean proportion of flight (± SD) | .12 ± .08 | .40 ± .21 | .26 ± .17 | .08 ± .08 |
| Sample size | 3 | 9 | 11 | 13 |
| $F_{3,32} = 8.52$; $P < 0.01$ | | | | |

but also the amount of time males spent in flight changed. Males were most likely to patrol the pond edge or chase other dragonflies in the middle of the day (Tab. II). Males of *O. caledonicum* rarely spent more than 50% of any 20 min observation period in flight, and so like other members of the genus can be categorized as perchers (CORBET, 1962).

## MALE-FEMALE INTERACTIONS

Males pursued all passing conspefics, and attempted to capture females. Succesful captures leading to copulation were observed 28 times; 19 involved females that were grasped while ovipositing at the pond edge, 6 involved females that were flying over the land toward the pond edge, and 3 females were flying over the water when taken in mid-air.

Following aerial capture and the formation of a tandem pair, the dragonflies usually landed to copulate. There was great variation in the duration of copulation, which lasted from as little as 6 s to nearly 20 min (Fig. 2).

Following a brief copulation, the female invariably flew directly to the water to resume or begin oviposition. After a long copulation, the female remained perched for several minutes before flying to the water. After both short and long matings, the male accompanied the female when she flew to the water to oviposit on 26 of 41 cases in which the observer recorded the postcopulatory behavior of the male. (Note that these records also include cases in which the pair was encountered already in copula). In all but two of the remaining 15 cases, the male stayed with the female at least

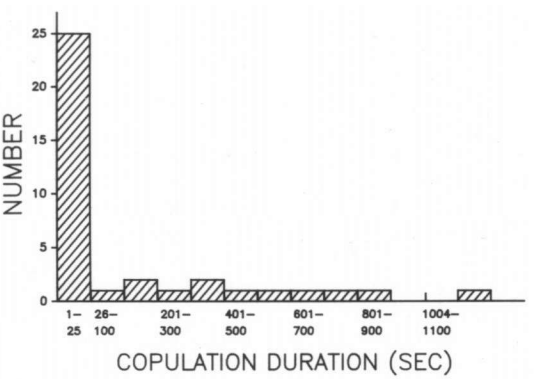


Fig. 2. The number of copulations of different duration by pairs of *Orthetrum caledonicum*.

briefly before flying off after an intruder, leaving the female unguarded when she oviposited.

## OVIPOSITION

Oviposition females dipped the tip of the abdomen into shallow open water near the pond edge. In the 34 cases for which records of complete oviposition events exist, a bout of egg-laying ended voluntarily when the female flew vertically up from the pond surface (N = 15), or when the female flew away from a male attempting to capture her (N = 9), or when the ovipositing female was recaptured and remated (N = 10). The mean total duration of oviposition for the longest records was 58.5 ± 7.1 s (includes cases in which a female oviposited in two or three bouts with brief interruptions for remating).

## DISCUSSION

### COMPARATIVE ASPECTS OF THE BEHAVIOR OF *ORTHETRUM*

The behavior of *O. caledonicum* resembles that of some other members of the genus (ITO, 1960; PARR, 1980, 1983a). Some males are weakly territorial at the pond edge, patrolling a strip of shallow, open water that is used by females as an oviposition site. Territorial males distribution themselves in spatial and temporal patterns that reflect the availability of receptive females coming to the pond to oviposit. Males of this species, and many other libelullids (PARR, 1983b) employ non-contact guarding of mates even though (a) rivals regularly succeed in capturing and remating females in the midst of oviposition and (b) the duration of oviposition by females is brief. These factors would seem to favor contact (or tandem) guarding by males, a trait that has evolved independently several times in the Libellulidae (UEDA, 1979; PARR, 1983b; SHERMAN, 1983). Tandem mate-guarding would reliably prevent takeovers and the loss of egg fertilization opportunities for males whose mates will copulate again if recaptured in the midst of an oviposition bout; at the same time, the loss of opportunities for contact--guarding males to defend the territory or to capture other mating partners would be very small because the oviposition rarely exceeds one minute. One of the major puzzles of odonate reproductive biology is the widespread evolution of non-contact guarding in species like *O. caledonicum.*

### HYPOTHESES OF VARIATION IN THE DURATION OF COPULATION

In his study of *O. chrysostigma,* MILLER (1983) found that resident territory owners mated on average for about 3 min, whereas satellite or wanderer males copulated for about 50 min. In *O. cancellatum,* there was a strong correlation

between the mate-encounter site and the duration of copulation (SIVA-JOTHY, 1984, 1987). Males copulating with females at the foraging areas away from water tended to be young, non-territorial individuals and they mated for about 15 min on average. In contrast, pairs in copula at the aquatic oviposition site mated only for about 20 sec.

These studies suggest that males excluded from territorial ownership exercise alternative mate-location tactics (searching for females at foraging areas rather than at oviposition resources, or wandering about non-territorially at places where females came to oviposit). When these males copulate, they do so for prolonged periods, presumably in order to remove as much stored sperm as possible from their mates (definitely demonstrated for *O. cancellatum* by SIVA-JOTHY [1987]), and to transfer large quantities of their sperm, the better to withstand sperm removal efforts of their partners' subsequent mates. The time costs of prolonged copulation are thought to be slight for subordinate males who do not have territories to defend and who are not likely to miss additional mating opportunities while in copula with one female, because the frequency of mating for non-territorial males is very low.

In the population of *O. caledonicum* that I studied there was no evidence that long copulations were employed by subordinate males. Both prolonged and very brief copulations took place at the pond edge. Five males known to be residents at the same location for 2 or more days were observed in prolonged copulation with a female. Three of these individuals engaged in both brief ($< 30$ s) and long ($> 2$ min) copulations during the study, and in one case the two types of mating were separated by less than 15 min. Whether mating briefly or for a long time, males usually accompanied their partners to the water and attempted to guard them against rival males (in at least 8 of 15 records of lengthy copulations).

Therefore in *O. caledonicum* the long copulation option appears to be an option used by at least some territorial males, and not just by non-territorial subordinates. Alternative hypotheses to account for prolonged copulation by territorial males include:

(1) Males may be able to determine (a) the probability of encountering another receptive female or (b) the probability of losing their territory to a rival if the site is left undefended for some time. When probability (a) or (b) is low, long copulations may be favored.

(2) Males that have mated several times in the course of a day may become sperm-depleted, leading to brief copulations if the transfer of large quantities of sperm is the time-consuming element of long matings.

(3) Males may detect which captured females are sperm-loaded, with prolonged copulation following when a male attempts to remove most rival sperm before transferring is own gametes to a partner.

(4) If males can detect which females are egg-depleted (either because they are low in fecundity or because they have just laid a portion of their mature

clutch), males may tend to mate briefly with such females because of the low rate of egg fertilizations they offer.

The data needed to discriminate among these alternatives are lacking currently, but it is possible that a complex set of factors may influence male readiness to invest in prolonged copulation, and the female's readiness to permit it. The interaction between partners may affect the duration of copulation in *O. caledonicum*, in much the same way that variation in the internal state of males and females of some other odonates appears to interact in influencing whether copulation will occur at all (ALCOCK, 1983; WAAGE, 1984).

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