

**OBSERVATIONS ON THE REPRODUCTIVE BEHAVIOUR OF
ORTHEMIS FERRUGINEA (FABRICIUS) (ANISOPTERA:
LIBELLULIDAE)**

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The territorial, copulatory and post-copulatory behaviour at 2 artificial pools in Trinidad are described. Each pool held one territorial resident: when more than one male was present a fight ensued. Territorial disputes can be divided into two types: short (mean duration 16.9 s) or long (mean duration 5.3 min). Diel patterns of female arrival and territorial disputes were similar. Residents always won short disputes; intruders won 41% of long disputes. Non-territorial males were often observed. The temporal pattern of female arrival at the pool was clumped. Thirty-five matings near water were obtained by territorial residents, 7 by non-territorial males and 11 by males of unknown status. Copulation was brief: the mean duration of the wheel position, which occurred in flight, was 11.7 s. Males non-contact guard females during egg-laying. Instances of males copulating with a second female while guarding, and of females being mated by a second male while being guarded are described.

INTRODUCTION

Odonata, both Zygoptera and Anisoptera, exhibit a wide range of reproductive behaviour (CORBET, 1962, 1980; WAAGE, 1984). The full functional significance of the various strategies of mate-finding, sperm displacement and post-copulatory guarding has yet to be determined, but recent detailed studies of adult behaviour (e.g. ALCOCK, 1979, 1982; UEDA, 1979; MILLER, 1981, 1982, 1983; FINCKE, 1982; WAAGE, 1983; BANKS & THOMPSON, 1985) and recent theoretical developments in behavioural ecology (see KREBS & DAVIES, 1984 for a review) have enabled progress to be made. Here we report

results of a field study into aspects of the behaviour of *Orthemis ferruginea* (Fabr.). This species has been studied by NOVELO GUTIERREZ (1981) who described and illustrates copulatory, mate-guarding and oviposition behaviour.

We show, first, that males are strongly territorial, but that a non-territorial role is sometimes used by some individuals; evidence is presented that fewer matings near water are obtained by non-territorial males. After copulation, males non-contact guard females. The adaptive significance of mate-guarding strategies has been widely discussed (ALCOCK, 1979, 1982; UEDA, 1979; WAAGE, 1979, 1984; SHERMAN, 1983) and one suggested advantage is that it enables males to mate other females while guarding. Here we report occasions of males mating with a second female while guarding.

STUDY AREA AND METHODS

Observations of adult behaviour were conducted over a nine day period (27 July - 4 August 1985) at two artificial pools in the garden of Simla Research Station, Arima Valley, Trinidad, West Indies (10°42'N, 61°17'W), during the early part of the rainy season, which had begun during mid-June. Heavy rain fell on all days except 27 July and 2 August, but male *O. ferruginea* were active at the pools for at least three hours on each day of the observation period.

The two pools were approximately 30 m apart and were separated by buildings; the ponds were not therefore, within sight of each other. Pool one (P1) was approximately 2 m long, 1 m wide and 1 m deep. Pool two (P2) was 3 m long, 2 m wide and 60 cm deep and was divided into two halves by a concrete wall 10 cm wide. This wall projected about 10 cm above the water level. Emergent vegetation in the centre of P1 provided perches for dragonflies. A bamboo cane 1 m high was placed at the centre of one of the long sides of P2 which was used as a perch by the resident male. Other perches, mainly garden plants and, in the case of P2, an overhead electricity cable were available around the pond. The garden area of Simla is surrounded by secondary deciduous forest (BEARDS, 1946). The ecology of the area is described in BEEBE (1952).

Observations were conducted from 0630 to 1830 h Local time each day. (During the observation period sunrise and sunset were at 0555 and 1830 h Local Time respectively). One pond was observed at a time. Each day was divided into half-hour periods and the pond to be observed for each period was chosen at random. We thus avoided any bias which a regular switch between pools at the end of each observation period might have created. Individual males were caught with a flight net and were marked uniquely on the wing with a permanent-ink marker pen (Penol 700). This mark could be read easily with binoculars, often when the dragonfly was in flight. Marking of males began on 19 July, eight days before systematic observations commenced. Altogether 20 male *O. ferruginea* were caught and marked.

During each observation period a continuous record of activity and behaviour of *O. ferruginea* was kept. Particular attention was paid to the following:

- (1) The identity of the resident male.
- (2) The identity and status (resident or intruder) of individuals involved in territorial disputes, and the outcome of such disputes.
- (3) The presence, within 5 m of the pools, of males perching for long periods of time but not attempting to fight with the resident for the territory.
- (4) The time of arrival of females and the identity and status of males which mated each female.
- (5) The duration of the wheel position and the number of dips of the abdomen made by the female during egg-laying.

MALE TERRITORIAL BEHAVIOUR

Males of *O. ferruginea* are strongly territorial. Each pond held only one resident male (although one or more non-territorial males may also be present — see below). If two or more males were present at the pool then fights invariably occurred. A maximum of four males were seen at any one pool. One perch site

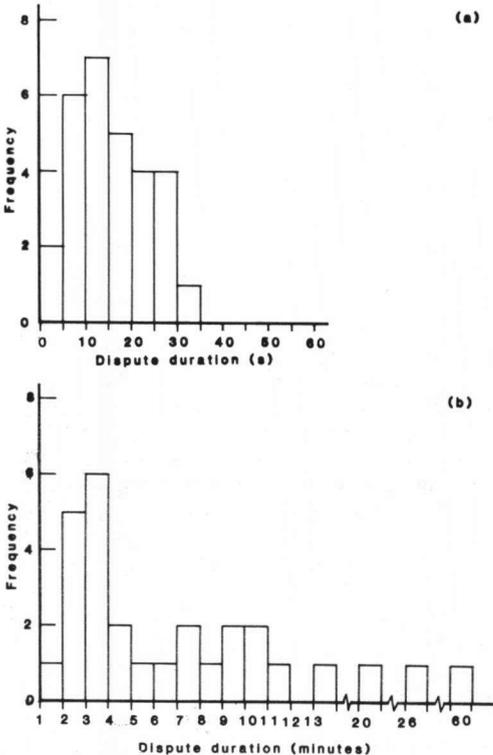


Fig. 1. Duration of short and long territorial disputes between mature adult male *Orthemis ferruginea*: (a) The frequency distribution of duration of "short" territorial disputes. "Short" territorial disputes are defined as lasting less than one minute. The mean duration was 16.9 s (UCL = 20.0, LCL = 13.8 s). (N = 29). Data are for disputes observed on 2 August. — (b) The frequency distribution of duration of "long" territorial disputes. "Long" disputes were defined as those exceeding one minute in duration. The mean duration was 5.3 minutes (UCL = 7.5, LCL = 3.7 minutes). (N = 27). Data for all "long" disputes observed during the nine-day observation period.

was favoured by the territorial resident. When other males approached the pool, the resident male flew from his perch and chased the intruder. At the end of a dispute the winner returned to the favoured perch site. Most disputes consisted of one, but sometimes two, brief flights away from the pool, with the winner resuming patrolling or perching immediately and the loser leaving the area of the pool. The duration of 29 such disputes observed on 2 August — a typical day — was 16.9 s (Upper 95% confidence limit (UCL) = 20.0, Lower 95% confidence limit (LCL) = 13.8 s). The frequency distribution of contest duration is shown in Figure 1a. We term these disputes "short" disputes. Fights of this type were observed only when there was a territorial resident at a pool: short disputes did not occur when no male occupied the pool and several males arrived simultaneously at the pond. The resident won 92 of the 103 short disputes observed but the status of the individual winning the remaining 11 disputes was unknown. Thus at least 89% (and possibly 100%) of "short"

disputes were won by the resident. The number of "short" disputes occurring during each half-hour period throughout the day (data for all nine days combined) is shown in Figure 2. Also shown in Figure 2 is the number of matings observed in each hour throughout the day. In both cases there are two peaks of activity, one at about 1100 h and a second at about 1300 h. Resident males are thus involved in more "short" disputes at times when our data show that females are more common at the pools.

Some disputes consisted of more than two short flights away from the pool. In addition to chases away from the pool individuals often circled the pool. Occasionally two individuals crashed into each other. Disputes of this kind always lasted for more than one minute, so we term them "long" disputes. Twenty seven long disputes were observed (Fig. 1b), 17 of which occurred when there was an unmistakable resident at the pool and five when there was no unmistakable resident prior to the dispute. The status of individuals involved in the remaining five disputes was not known. One dispute exceeded 60 min (but not more than 90 min); if this dispute is assumed to have lasted 60 min the mean of log-transformed dispute duration is 5.3 min (UCL = 7.5, LCL = 3.7).

(A log transformation was applied to normalize the highly skewed distribution). The resident won 10 of the 17 disputes for which an unmistakable resident existed before the dispute and the intruder won seven. This result is in marked contrast to the outcome of "short" disputes which the intruder never won. The mean of log-transformed dispute durations for resident-won contests was 4.0 min (UCL = 11.00, LCL = 1.5 min) and for intruder-won contests was 6.3 min (UCL = 13.0, LCL = 2.9 min): these means do not differ significantly ($t = 1.016$, $df = 1$, $0.4 > P > 0.2$). The diel distribution of the onset of "long" territorial disputes is also included in Figure 2: as with matings and "short" territorial interactions there are peaks of onset of

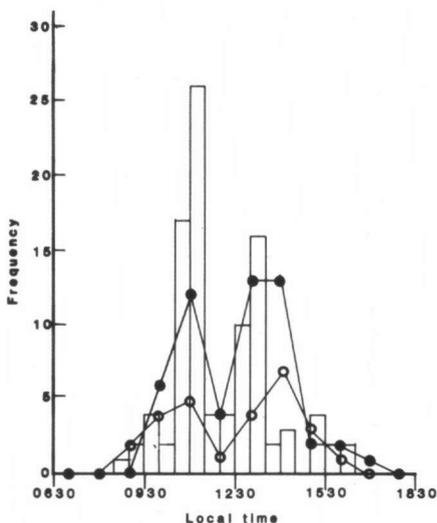


Fig. 2. The diel distribution of activities of male *Orthemis ferruginea*. The histogram shows the number of "short" territorial disputes during each half-hour observation period. Closed circles show the number of "long" territorial disputes commencing in each one hour period. Open circles show the number of matings per hour. Data for all nine days observations combined.

"long" disputes at 1100 and 1400 h.

NON-TERRITORIAL MALES

The behaviour of some males differed from that of territorial residents. Such males were involved in few territorial disputes with residents; rather, they perched three to five m from the pool and remained there, making very few patrol flights. Territorial disputes with residents occurred only if the territory holder flew close to the perched male. On occasion, non-territorial males were seen to mate with females before resident males did so. Some individuals were observed to behave both as non-territorial males and as territorial residents at different times. For example, non-territorial males early in the day were occasionally seen as territorial residents later in the day. Similarly, individuals observed as non-territorial males when young were observed as territorial residents when older. In the early part of the study some of these individuals may have been overlooked: when the locations of perches which non-territorial males tended to occupy were identified, non-territorial males were usually observed to be present at each pool. The mating success of non-territorial males is dealt with in the following section.

COPULATORY BEHAVIOUR

As soon as a female arrived at a pond she was either mated by a male, or she began to lay eggs. In the latter case a maximum of 20 abdominal dips (see later) was observed before a male mated with the female. The pattern of female arrival at the pond is likely to be an important factor determining male mating strategies. Altogether 53 females arrived at the pools during the period of observations. The following numbers of females arrived on each successive day of the study: 8, 1, 6, 2, 0, 17, 1, 11, and 7. This distribution differs significantly from the expected number of 5.9 per day ($G = 45.2$, $df = 8$, $P \ll 0.001$).

The pattern of female arrival during the period in which males were present at the encounter site was examined by calculating a frequency distribution of periods that males waited at the pond for females to arrive, assuming a random pattern of female arrival. This was compared with the observed distribution. We first define "waiting time" to be the period between matings for males (or between male arrival at the pool and first mating, or between mating and the male leaving the pool). The observed frequency distribution of waiting times can be compared with a distribution of waiting times expected from a random pattern of female arrival at the pool. We determined the random distribution by simulation. For each day of the study the time of male arrival at the pool and male departure from the pool was obtained from field records. Random times for the females to arrive were then selected (in time units of one minute) and the duration of each waiting

time calculated. The number of females to arrive was the same as the observed number of females at the pool. This was repeated 500 times for each day of the study. Figure 3 shows the observed and expected distributions of waiting times. Observed and random distributions differ significantly (Kolmogorov-Smirnov test: $D = 0.179$, $n = 61$, $0.05 > P > 0.02$). Short and long waiting times occur much more frequently than expected and thus the temporal distribution of female arrival is clumped.

Fifty-three matings were observed, 11 by males of unknown status. Of the remaining 42 matings 35 were by a territorial resident and 7 (17%) by non-territorial males. Ignoring the males of unknown status, non-territorial males obtained a significantly lower number of matings ($G = 20.2$, $df = 1$, $P \ll 0.001$) than territorial residents.

The mean duration of the wheel position, which took place in flight, was 11.7 s ($n = 29$, $UCL = 13.4$, $LCL = 10.0$ s; range 5-30 s). There was no difference in duration of the wheel position during matings by non-territorial and territorial males respectively.

POST-COPULATORY BEHAVIOUR

Pairs separated within a few seconds of completion of the wheel position and females immediately commenced egg-laying by scooping small drops of water, each presumably containing one or more eggs, with the expanded tergites of the seventh and eighth abdominal segments. These drops of water landed either on the pool sides just above the water level, or occasionally on vegetation just above the water surface. Between 50 and 300 dips of the abdomen were observed during egg-laying, which lasted for no more than three minutes.

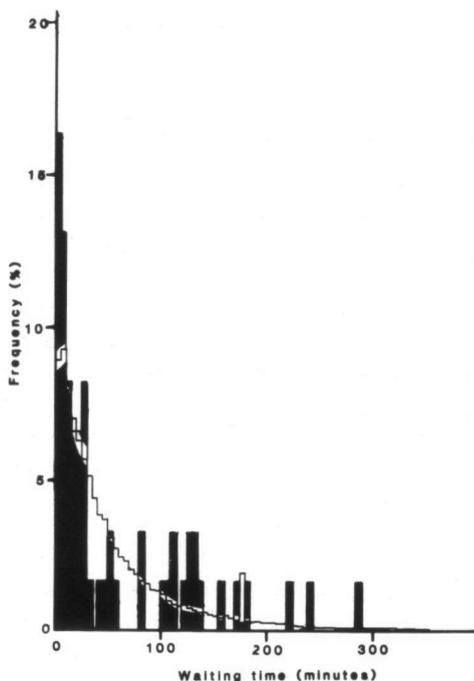


Fig. 3. Observed and expected times between matings. The solid histogram shows the observed distribution of waiting times for females. The open histogram shows the results of a simulated random pattern of female arrival at the pool. Observed and expected frequencies differ significantly (Kolmogorov-Smirnov test: $D = 0.179$, $n = 61$, $0.05 > P > 0.02$). Data for all nine days observations combined.

During egg-laying, males non-contact guarded females, by hovering about 10 cm away from the female and chasing off conspecific and other males if they interfered with egg-laying females. Males also chased after females if they left the pool area and escorted them back to the pool, especially within the first two minutes of the commencement of egg-laying. On five occasions (out of 53) a female was mated by a second male while being guarded. On two of these occasions a non-territorial male was the first to mate with the female. Males were twice seen to mate with a second female while guarding. On both of these occasions the male then guarded both females until they finished laying eggs.

DISCUSSION

Territorial disputes between *Orthemis ferruginea* males could be divided into two categories on the basis of duration. Short disputes lasted for less than 35 s and occurred only when there was a resident at the pool prior to the dispute. Long disputes not only occurred when there was a resident at the pool, but also when two individuals arrived more or less simultaneously at an unoccupied pool. In the former case 41% of disputes resulted in a change of ownership of the pool. Long disputes often included physical contact between individuals.

Two suggested advantages of non-contact guarding over contact guarding are: first, that non-contact guarding allows males to mate with other females while guarding; and second, that it allows males to defend territories while guarding (see SHERMAN, 1983; WAAGE, 1984). One suggested disadvantage is that it increases the probability that a female will be remated by another male before she has finished egg-laying. SHERMAN (1983) found the first advantage to be of little importance for *Pachydiplax longipennis* (Burm.) because there was a low probability of two females arriving close together in time. However, high male density at encounter sites made the second factor important. ALCOCK (1982) showed that mating opportunities for the calopterygid *Hetaerina vulnerata* Sel. were relatively rare and so it was unlikely that non-contact guarding increased the chances of a male mating while guarding. In contrast *Calopteryx maculata* (P. de Beauv.) males do mate with other females while guarding (ALCOCK 1979; WAAGE 1979). This study showed that male *Orthemis ferruginea* mated with females while guarding on about 5% of occasions. A comparison of the temporal pattern of female arrival with that of a random model showed female arrival to be clumped in time and this may be important in increasing the probability of males mating while guarding.

Finally, we observed that non-territorial males in this species obtained 17% of matings near water. We do not know if males expelled from territories were able to obtain matings away from water but because all females which arrived at the pools were mated by a resident or non-territorial male the payoff for such a strategy may be small.

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