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BEHAVIOUR OF *PERITHEMIS MOOMA* KIRBY AT THE OVIPOSITION SITE (ANISOPTERA: LIBELLULIDAE)*

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The reproductive behaviour of the neotropical *P. mooma* has been studied at a farm pond in southern Brazil. Males, ready for reproduction, arrive in the course of the forenoon at the water in search of a suitable oviposition substrate, such as a floating mat of algae or emergent root-felt of water plants. The site is selected visually and then examined thoroughly by repeated touches with the tips of the hind legs. If the substrate is found appropriate it will become the center of a vigorously defended territory. Sexual behaviour follows a well-defined sequence of male-female interactions including courtship display, copulation and postcopulatory activities. In addition to the main pathway, a number of alternative steps exist. Thus, besides the main situation leading to copulation, 3 precopulatory behavioural elements may occur. The mean duration of copulation is 15 ± 6 s. Oviposition is performed attended and may last up to 170 s if undisturbed.

INTRODUCTION

Perithemis is one of the few anisopteran genera with a clearly developed courtship behaviour, comparable to that in the zygopteran *Calopteryx* (e.g. HEYMER, 1973; WAAGE, 1988) and in the Chlorocyphidae (ROBERTSON, 1982). In the framework of her classical study on territoriality and sexual selection in dragonflies, JACOBS (1955) described the reproductive behaviour of *P. tenera*. The same species was the subject of a film by RUPPELL et al. (1989). The other members of the genus, however, have not been studied so far. The aim of the present study was to obtain additional information on the behaviour of *Perithemis* at the oviposition site and to compare *P. mooma* with *P. tenera*. The

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work also served as a basis for an investigation of the problem of dragonfly species-specific recognition of the oviposition substrate (WILDERMUTH, 1991).

LOCALITY, MATERIAL AND METHODS

The study site was a man-made farm pond near Guaiba, S of Porto Alegre, Rio Grande do Sul, Brazil (30°06'S, 51°18'W), ca 200 m in diameter, bordered by a dam on its eastern side and surrounded by pasture and woodland. The water was bare of vegetation except for small scattered patches of *Eichhornia azurea*, *Ludwigia* sp., *Typha* sp. and *Nymphoides indica* (Fig. 1). The observations lasted from November 1990 until January 1991 and were made by eye or with the aid of binoculars (Nikon Travelite II, 7x20) which allowed a short working distance up to 2.8 m. Additionally, the behaviour was filmed with a video camera (Panasonic F 10) equipped with strobe effect shutter (shutter speed 1/1000 s, 50 video signals per second). The wind velocity was measured with an aerometer.

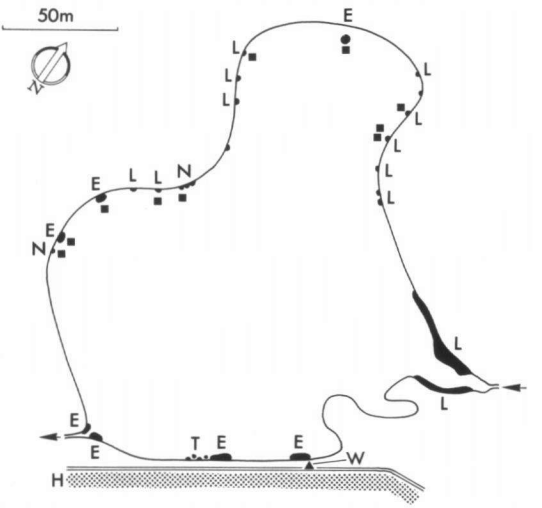

Fig. 1. Situation at the study site (farm pond) on 29 November 1990, 10.00 h Brazilian Summer Time. 10 males of *P. mooma* have established their territories (squares). — [H = hedge along dam; — W = shrub serving as "waiting room" for adults of both sexes. — E, L, N, T = patches of water plants (E = *Eichhornia*, L = *Ludwigia*, N = *Nymphoides*, T = *Typha*).

RESULTS

TERRITORIAL BEHAVIOUR

After emergence young adults spent their maturation period on the pasture surrounding the pond. Individuals ready for reproduction appeared on calm and sunny days on bushes along the dam, from 09.00 h onwards. An isolated conspicuous shrub, about 2 m high and close to the water, served as a waiting room for males and females, of which up to 10 were found perched rather close to each other, without showing any sexual interactions. The shrub was occupied permanently all day, almost until sunset (ca 20.00 h).

The first males arrived at the water around 09.30 h. They flew slowly along the bank and examined emergent root-felts of water plants, logs, stones and other matter as possible oviposition sites by repeated short dips, touching the substrate quickly with the hind leg tarsi. The procedure could last several minutes and was

often interrupted by patrolling flights ranging up to 10 m and including hovering near or above the substrate. The individuals finally perched on leaves or stems, extending 5-25 cm above the water surface (Fig. 2). During calm spells their body axis was mostly directed towards the open water (Fig. 3), however, during windy spells they headed against the air flow and were able to withstand wind velocities up to 4 m/s. In gusts exceeding 6 m/s they were blown off, but returned afterwards to their perches. Obelisk postures similar to those described by HARDY (1966) for *P. tenera* could be seen only during windless periods at extremely intense radiation.

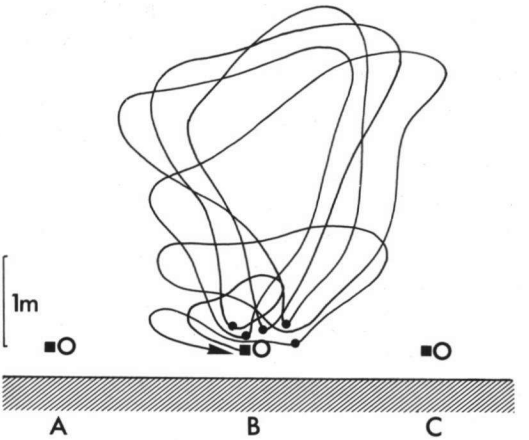

Fig. 2. Three experimental oviposition sites (A, B, C) with substrate (circle) and perch (square). The line indicates an exemplified patrol flight including points of hovering (dots).

At stretches of the pond margin lacking vegetation I could easily attract males by setting up experimental oviposition sites. These consisted of emergent patches of *Eichhornia* rootlets, with a leaf or stick as a perch. At these places males established territories in the same manner as they did at natural sites. Neighbouring males tolerated each other if their oviposition places were not closer than 3 m apart. In one of about 20

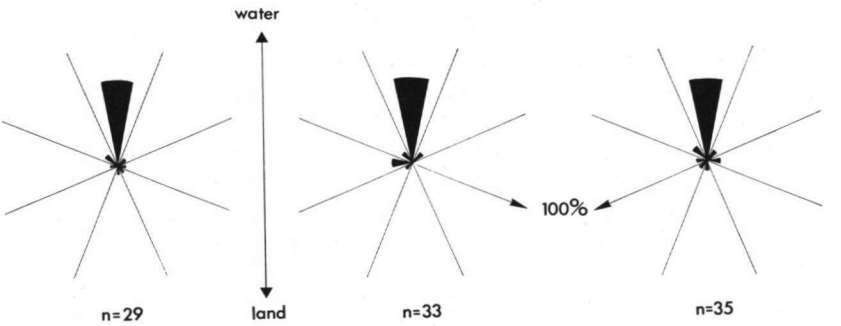

Fig. 3. Direction of body axis of three territorial males on experimental perches after patrol flights or aggressive interactions with conspecifics. The circle is divided into 45° sectors. Single values within one sector are summarized, thus resulting in 8 group values. These are expressed in percentage, indicated by black sectors. — [n = number of single values].

experimental cases two neighbours set up territories with their centers only 1.8 m apart. If the proprietor of a territory was experimentally driven off from this perch, he would soon return to it, even when chased off 10 times in succession. If he was not allowed to perch at the same site, he settled somewhere in the neighbourhood and returned later. Removal of the oviposition material caused the male to search for it where it had been before for several minutes until he finally left. The same occurred in both sexes when the substrate was removed during copulation. However, the female tended to leave the site rather soon after she had discovered the absence of an oviposition substrate, whereas the male stayed longer and repeatedly tried to lead his partner back into the territory.

Males in search of oviposition sites were highly selective. In the morning, when the male density at the water was low, they refused substrates where there was little or no emergent vegetation in the vicinity. On the other hand, they were firmly attracted by dense patches of *Eichhornia* and *Ludwigia* vegetation with the oviposition substrate partly hidden in the foliage. Such localities were also preferred by females. According to a spot-check count around 10.00 h on a cloudless and calm day, 10 males had established their territories at the pond (Fig. 1). Towards midday the number increased and peaked around 13.00 h with approximately 60 male individuals and then decreased during the course of the afternoon. The last males left their territories only half an hour before sunset.

When arriving at an occupied territory, a male intruder would immediately start an examination of the oviposition substrate. He was then instantly followed by the owner of the territory. After a period of common examination manoeuvres they made wild roundabout flights over the water. In the beginning these were short-ranged, but in due course they became longer and led over the free water surface, far beyond the boundary of the territory. In between, the competitors often returned shortly to the egg-laying site. These dual flights could last up to one hour, and in such "dances" above the oviposition substrate up to 5 males might have been involved. Mutual aggressive frontal display was only rarely observed. In these the contestants then hovered for 1-2 s ca 0.5 m above the water surface, facing each other, with their abdomens slightly raised.

SEXUAL BEHAVIOUR

Most females appeared at the water between 11.00 h and 16.00 h. The course of events after the arrival of a female at a male territory is schematically summarized in Figure 4 and will therefore only briefly be commented on here. The whole sequence of undisturbed sexual events comprising courtship, copulation and oviposition was followed 46 times. The most frequently observed sequence of behavioural elements will be designated as main-pathway. Besides this, a number of alternative steps were recorded and quite often the chain of events ceased at an early stage if the female did not respond to the courtship of her partner and left the

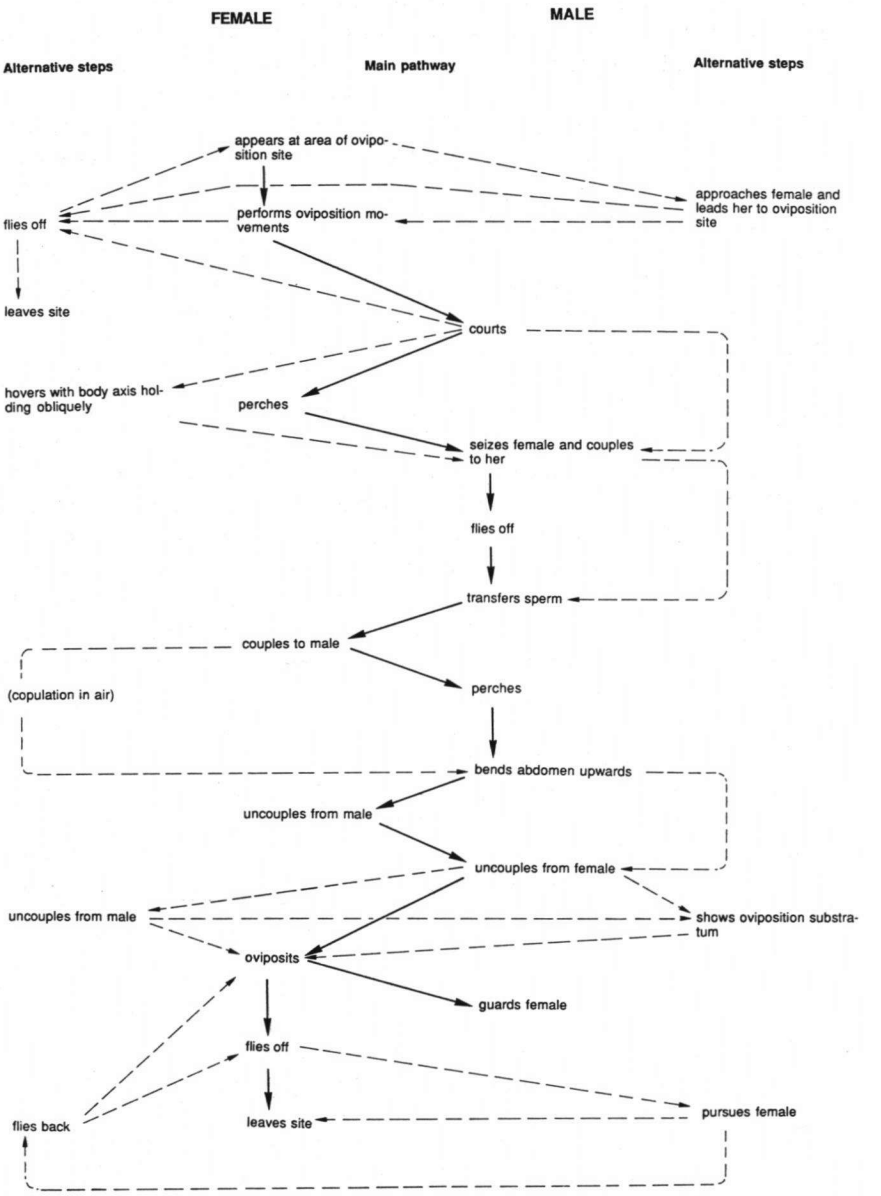

Fig. 4. Sequence of male-female interactions during courtship, copulation and oviposition in *P. mooma*. The uninterrupted main pathway is indicated by bold-faced arrows.

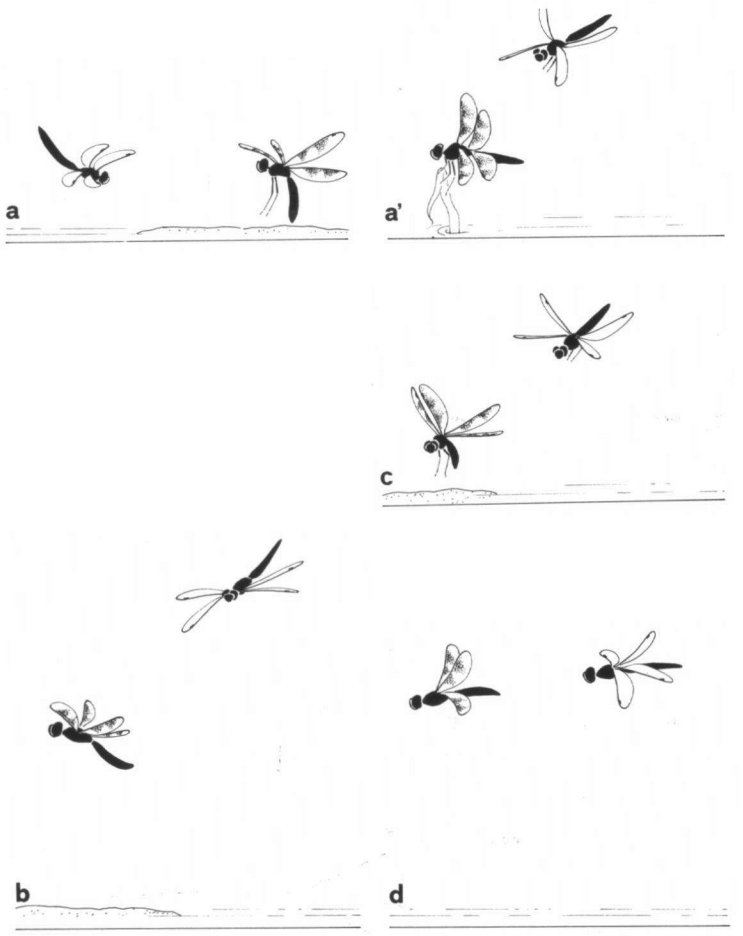

Fig. 5. Four different precopulatory situations in *P. mooma:* (a, a') normal event: male courts in front of female who makes oviposition movements; subsequently she perches and will be seized by her partner — (b) female hovers above substratum thus inviting male to copulate — (c) female does not respond to the courtship of the male and continues ovipositing; he might then catch her in the air and thus initiate copulation — (d) male pursues female trying to escape; if he succeeds to catch her copulation may result — [b, c and d are exceptional events].

side. The sexual activities of a pair could also be disturbed by other males.

Courting males hovered in front of the females which performed oviposition movements. Their abdomen was upcurved, the frequency of the wingbeats increased and the amplitude reduced. The courtship flights rarely lasted longer than 10 s. I observed 4 different situations prior to copulation (Fig. 5):

(a) The male courted in front of the female while she made oviposition movements. She then perched and was subsequently seized by her partner (normal event).
(b) The receptive female interrupted her oviposition movements and hovered above the substrate, holding her body axis obliquely; this was a signal of readiness to copulate.
(c) The (non-receptive?) female did not respond to the courtship of the male and continued ovipositing. He might then catch her in the air and thus initiate copulation.
(d) The (non receptive?) female fled from the oviposition site and was pursued by the territory owner, who grasped her in mid-air. This may occur at high male density and was observed only once.

Sperm transfer lasted about 2 s and was performed in flight. The copulation period varied between 9 and 44 s (mean duration 15.25 s ± 5.9 s, n = 36). The pair normally perched after having assumed the wheel-position. Disconnection after copulation was initiated by the male which could be seen lifting up his abdomen.

In one case I observed an attempt at a homosexual mating between territorial neighbours. The tandem flew slowly low over the water, the anterior individual attempting copulation by repeatedly elevating his abdomen. However, they disconnected after a few seconds and both individuals returned to their original territories.

While ovipositing, the female beats her abdominal tip towards the substrate as described for *P. tenera* by MONTGOMERY (1937) and RUPPELL et al. (1989). At each touch-down she stretches out her legs, which come into contact with the ground, thus examining the material. Simultaneously she may measure the distance between her body and the substrate. On the average she makes two striking movements per second. Oviposition lasts up to 170 s, but it is often stopped by disturbing males after a few seconds (mean duration 79.2 ± 50.5 s, n = 19). Oviposition females are guarded by their male partners which first hover for a period over the site and then perch. However, a second male may dash at the female and carry her off.

DISCUSSION

Males of *P. mooma* are strikingly territorial and exhibit conspicuous courtship display. On the whole the sexual behaviour of this species is very similar to that of *P. tenera* as described by JACOBS (1955) and RUPPELL et al. (1989), but there may exist a number of minute differences between the two species. However, on the basis of the material so far published, an exact comparison is not possible, as the different authors applied different methods, and conducted their studies with different objectives , as illustrated by the following example. With reference to copulation JACOBS (1955) reports that "the male catches [the female] as he flies

slowly or perches on the site nearby", whereas RUPPELL et al. (1989) stated that in the same species grasping of the female and tandem formation occur in flight. In *P. mooma* I found that the female normally responds to the courtship of her partner by perching, thus inviting him to copulate. All the other precopulatory behavioural components which I observed were exceptional and probably due to special situations such as high male density or the deficiency of certain behavioural elements in one of the partners. The variability of the behavioural pattern of *Perithemis* in connection with environmental factors would therefore merit a quantitative analysis.

The highly developed sexual behaviour in *Perithemis* is remarkably among Anisoptera, even for libellulids, a family with only a few other known species showing courtship displays, although in a less striking manner (MOORE, 1960; WILLIAMS, 1977). With reference to the complexity and the pathways of the mating behaviour *Perithemis* is comparable to *Calopteryx* among Zygoptera (HEYMER, 1973; WAAGE, 1988), an outstanding duality from the evolutionary point of view, as the similar behavioural patterns have to be considered convergent features.

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