

SHORT COMMUNICATIONS

**REPRODUCTIVE BEHAVIOUR OF
NOTIOTHEMIS ROBERTSI FRASER
(ANISOPTERA: LIBELLULIDAE)**

V. CLAUSNITZER

Kirchweg 5, D-35043 Marburg, Germany

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Mating and oviposition behaviour of this tropical dragonfly was studied at small rain forest pools in West Kenya. Males were present at the oviposition site between 10:00-16:00 h local time. Females visited the pools infrequently. Copulations lasted a mean of 174 s and occurred rarely. Mating and oviposition of one female were spatially and temporally separated. The females deposited eggs unguarded well above the water. During oviposition the female hovered in front of the substrate, keeping the legs attached either the whole time or only during the dip.

INTRODUCTION

In territorial dragonflies most often the males wait in more or less distinct territories for the females at the oviposition sites. The distribution of the females, which are often a scarce resource for the males, is determined by the oviposition site. The causal link is from resource over female dispersion to male dispersion (DAVIES, 1991). EMLEN et al. (1977) define this in their classification of mating systems as "resource defence polygyny".

CONRAD & PRITCHARD (1992) have classified different odonate mating systems. The reproductive behaviour of *Notiothemis robertsi* is described and compared with this classification. Like other behavioural patterns of the Tetratheminae described so far (LEGRAND, 1979; LEMPERS, 1988; McCRAE & CORBET, 1982) it contains some extraordinary libellulid features.

Notiothemis robertsi is an inconspicuous dragonfly, which inhabits rain forest pools in tropical Africa. The males are territorial for comparatively long periods during their lives (CLAUSNITZER, 1996). A brief presentation of oviposition behaviour is given by LEMPERS (1988).

LOCALITY AND METHODS

The study sites were seven small man made pools (1-7) in the Kakamega Forest/West Kenya (00°08'-00°24'N, 34°20'-34°33'E; 1500-1700 m a.s.l.). This forest is the last remaining high-land rain forest of Kenya and contains several species belonging to the faunal region of West Africa. The pools were made by gold diggers along the Lugusida River and were situated next to each other, covering about 65 m². The average diameter of a pool was 2 m (min: 1 m; max: 3.5 m) and the depth varied between 0.05-0.90 m. Most of the time the pools were fully shaded. Submerse vegetation consisted of Characeae only.

N. robertsi was observed at the study sites between 2 December 1994 and 2 February 1995 on 56 days. The animals visited the pools every day between 10:00-16:00 h local time. In cloudy weather and in the late afternoon they disappeared into the tree canopies. Only territorial males spent most of the time at the pools; females and non-territorial males came infrequently from the tree tops (CLAUSNITZER, 1996). Eighty-nine males and 19 females were marked individually with a permanent pen (EDDING 780/silver).

For recognition and observation I used a short-focus binocular (8 × 30). Mating and oviposition behaviour were filmed with a video camera (Panasonic, NV-G1E). Duration of oviposition was timed and the dips counted; some clutches were collected.

RESULTS

Females of *Notiothemis robertsi* visited the territories very infrequently and sometimes a territorial male left the pool in the late afternoon without getting the sight of a female. Females came between 10:00 - 16:00 h from the tree canopies with a small increasing frequency around noon. They stayed only for a short time at the pools, either for copulation or egg laying. For the latter the presence of a male was not important. Sometimes a female patrolled for a few seconds at a pond without a present male and left it without oviposition.

Copulations were observed between 11:00 and 16:00 h (Fig. 1). No courtship behaviour preceded mating. The territorial male grasped the female in flight and the tandem was formed. They settled for a short time (maximum: 15 s) in a sunny spot and formed the wheel position in a short flight before settling again. The copulation lasted for a mean of 174 s (s.d.= 109 s; min.= 22 s.; max.= 522 s; n= 18).

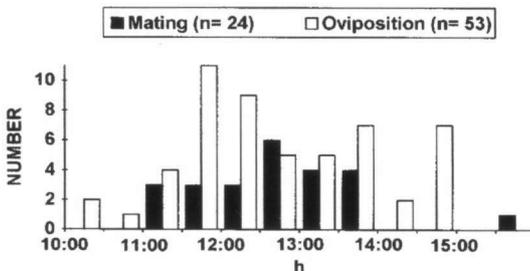


Fig. 1: Distribution of mating and oviposition activities *Notiothemis robertsi* in the course of the day.

After copulation the male flew immediately back into his territory. The female rested for some minutes before leaving for the tree canopies.

Copulations were observed for territorial males exclusively. Only 2.4% (n= 1691) of their flights were sexual flights (flight towards females). Out of these flights 58.5% (n= 41) led to copula-

Table I

Distribution of mating and oviposition of female *Notiothemis robertsi* on the pools (1-7= pool numbers). The matings do not deviate significantly from a continuous distribution ($\chi^2= 8.3$; d.f.= 6; $0.3 > p > 0.2$), while the oviposition distribution is significantly discontinuous ($\chi^2=30.2$; d.f.= 6; $p < 0.001$)

| Pool | Mating (%) (n= 24) | Oviposition (%) (n= 53) |
|------|-----------------------|----------------------------|
| 1 | 2 (8,3) | 15 (28,3) |
| 2 | 7 (29,3) | 7 (13,2) |
| 3 | 2 (8,3) | 4 (7,5) |
| 4 | 5 (20,8) | 12 (22,6) |
| 5 | 5 (20,8) | 14 (26,5) |
| 6 | 1 (4,2) | - (0) |
| 7 | 2 (8,3) | 1 (1,9) |

In the other cases the tandem was released after a few seconds, because the female refused or belonged to another species (*Notiothemis jonesi* Ris, *Tetrathemis corduliformis* Longfield). In 13 cases observed a male approached an ovipositing female and grasped her in 8 cases. From these only 25% led to copulation. In the other cases the females refused the male.

Mating and oviposition of a female were spatially and temporally separated (Fig. 1; Tab. I). After mating the females disappeared into the tree-canopies and were never observed ovipositing on the same day. Out of 19 marked females 21,1% were observed at least a second time at one of the pools. Neither location loyalty nor high dispersal tendency could be demonstrated with the data.

While mating did not deviate significantly from a continuous distribution on the pools, oviposition showed a significant discontinuous distribution (Tab. I).

Females deposited eggs on structures 1 - 2 cm above water level. These were stones, dead wood or small sticks, which rose above the water. They selected places while dipping 5-7 times without releasing eggs. When they found a place they hovered before it, depositing the eggs on the substrate. Oviposition took place with the legs attached the whole time to the substrate (Fig. 2 A) or with the legs contacting the substrate only when the abdomen reached the substrate for placing some eggs (Fig. 2 B). No matter how the legs were used the ovipositing female hovered all the time.

The dip frequency was 55.25 per minute ($n= 35$; s.d.=9.33). Number of dips and duration of oviposition was correlated, the

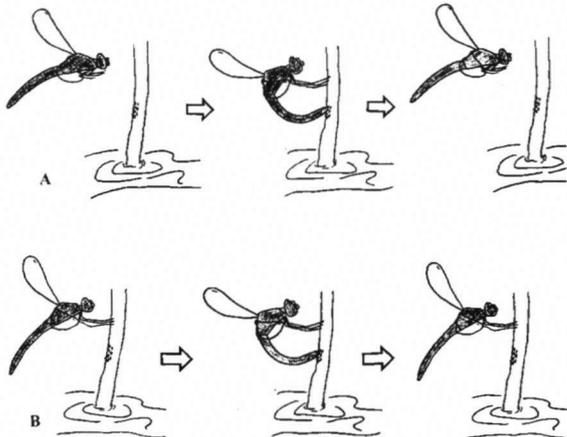


Fig. 2: During oviposition the female of *Notiothemis robertsi* moved the wings all the time; legs were used in two ways: either attached to the substrate only when the eggs were placed (A), or kept in contact with the substrate during the whole process (B).

number of dips per minute decreased over the time (Fig. 3). Mean egg-number per dip was 5 ± 0.8 s.d. ($n = 3$) (Tab. II). The eggs were all placed next to each other in one single layer (Fig. 4).

DISCUSSION

Males of *Notiothemis robertsi* are territorial for an extraordinarily long period (average: 14 d; max: 43 d; $n = 31$) (CLAUSNITZER, 1996). This is associated and may be explained with the scarcity of females. Females of *N. robertsi* visit water for oviposition and mating only. Females lay also eggs without the presence of a male. Some females leave ponds lacking males without showing oviposition. These females come with a mating motivation as discussed by JACOBS (1955) and MOORE (1964). I cannot exclude that mating does also occur in the tree tops. Ovipositing females are rarely "forced" to copulation by a male, as it has been described for other dragonflies by JACOBS (1955) and SAGAKAMI et al. (1974). Females of *N. robertsi* can avert the wheel position actively, which has been described for other species before (WAAGE, 1984). The cautious male behaviour prevents them from making unsuccessfull mating attempts. Males of *Brachythemis lacustris* Kirby perform courtship behaviour to distinguish between receptive and non-receptive females (MILLER, 1991). In this way they save time and energy and ovipositing females are not disturbed. I interpret the careful approach of male *N. robertsi* towards a possible mate in the same way.

In *N. robertsi* mating and oviposition is spatially and temporally separated; hence no mate guarding behaviour has developed. Dragonflies with such infrequent occurrence of females should be expected to perform a very distinctive mate guarding (SHERMAN, 1983; MILLER, 1983). The absence of such behaviour for *N. robertsi* may have two reasons: (1) oviposition behaviour hampers males attempting to grasp the female thus male-male sperm competition is low (if it exists at all), and (2) females with fertilised eggs are important for the dispersal and colonisation of new potential breeding places. The latter reduces also predation

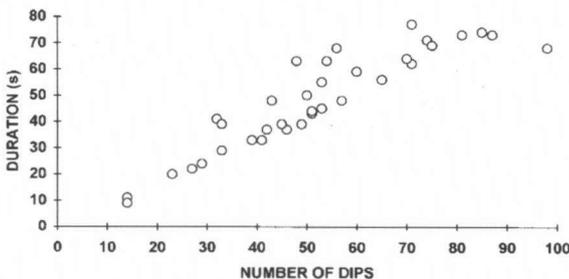


Fig. 3: Relation between duration of egg deposition and number of dips in *Notiothemis robertsi* ($n = 35$).

and interspecific as intraspecific larval competition, which can be considerable in small rain forest habitats (FINCKE, 1992a, 1992b; HASSAN, 1976). Reproduction over the whole year and a long territorial phase enable such low competition.

The mating behaviour of *N. robertsi* does not fit

Table II

Number of eggs and dips and duration of total oviposition in comparison of three clutches of *Notiothemis robertsi*

| ♀ | Duration (min.) | Dips | No of eggs | Eggs / Dip | Egg/min. | Dips/min. |
|---|-----------------|------|------------|------------|----------|-----------|
| 1 | 0.29 | 24 | 134 | 5,6 | 335,0 | 49,7 |
| 2 | 1,10 | 64 | 312 | 4,9 | 267,4 | 54,9 |
| 3 | 1.21 | 71 | 335 | 4,6 | 248,2 | 52,6 |

into the classification of odonate mating systems by CONRAD & PRITCHARD (1992). They might be placed between “encounter-limited” and “resource-control”. The frequency of male-female encounters (“very rare”) and the lack of mate guarding behaviour are appropriate characteristics for “encounter-limited”. These characteristics are opposite in “resource-control” – very frequent male-female encounters, guarded oviposition only. Matching characteristics for “resource-control” are the defended territories (no territories in “encounter-limited”) and short duration of copulation (>5 min. in “encounter-limited”). This incompatibility reflects the small data basis of rain forest dragonflies, which is available so far. I regard life-span and reproduction throughout the year for important factors influencing the mating behaviour.

N. robertsi does not spent much time and energy in copulation. This may explain the lack of feeding behaviour at the ponds. Similar behaviours have been recorded for *Eothemis zygoptera* Ris, *Tetrathemis bifida* Fraser and *T. godiardi* Lacroix (LEMPERT, 1988). The low energy expenditure of a territorial male increases the length of the territorial time and therefore the reproductive success. This corresponds to MAY’S (1984) studies showing that perchers with a long life span spend less energy in daily activities and short time reproduction behaviour.

The oviposition behaviour of *N. robertsi* is epiphytic after definitions given by MILLER & MILLER (1985) and SORIANO (1987). Before oviposition females fly about 10 cm above the water, probably searching potential sites for oviposition. The females examine potential structures with the abdomen by dipping without releasing



Fig. 4: Egg clutch of *Notiothemis robertsi* on a piece of wood 2 cm above the water level; egg size: 0,8 mm.

eggs. By this they can respond to the micro-structures and moisture of the place. Older egg clutches may be detected, which can stimulate the female to place her eggs next to it and prevents the positioning of egg-clutches in several layers. A similar behaviour has been described for *Perithemis mooma* Kirby, which use the hindlegs for examination of potential breeding sites (WILDERMUTH, 1992).

During oviposition the legs function to allow accurate placing of the eggs. I have not observed the same female using legs in both ways shown in Figure 2. It would be interesting if this behaviour is individually specific. Keeping the legs on the substrate may save energy during the whole egg depositing process. Hovering free in the air makes possible a quick escape. Similar ovipositing behaviour is shown by species which deposit their eggs epiphytically. *Malgassophlebia bispina* Fraser places the eggs with the help of the legs at every dip (LEMPERT, 1988), while *M. aequatoris* Legrand does not use the legs at all (LEGRAND, 1979). The number of eggs laid per dip seems to decrease over the whole oviposition (Tab. II; Fig. 3), while the number of dips remains stable. This may be the result of the decreasing number of mature eggs in the ovaries.

All Tetratheminae place their eggs above the water, either while settled as *Tetrathemis* or while hovering like described for *N. robertsi*. This might be an adaptation to ponds with very fine sediment and a low concentration of dissolved oxygen (due to deep or shady water bodies without submerged plants). In this way the embryonic development might be more successful than being exposed to the substrate of muddy ponds (LEMPERT, 1988; McCRAE & CORBET, 1982). Additionally this form of egg laying does not need any plants and enables a rapid colonisation of new ponds.

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