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OVIPOSITION HIGH ABOVE WATER IN *MICRATHYRIA DICTYNNA* RIS (ANISOPTERA: LIBELLULIDAE)

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A ♀ was observed to attach eggs onto the underside of a leaf hanging more than 2 m above the water level of a small rainforest stream in Costa Rica. It was found that the eggs usually remain in this position until the larvae hatch. This type of oviposition, the first recorded in a member of the subfamily Brachydiplactinae, is similar to that of some Old World Tetratheminae and it is suggested to be a case of convergence due to similar environmental conditions. Its adaptive significance is discussed briefly.

INTRODUCTION

Regarding the behavioural ecology of the subfamily Brachydiplactinae sensu FRASER (1957), the only species studied so far are *Nannophya pygmaea* Rambur (TSUBAKI & ONO, 1986) and *Eleuthemis buettikoferi* Ris (LEMPERT, 1988) from the Old World, as well as six species of the neotropical genus *Micrathyria*: *M. aequalis* (Hagen), *M. atra* (Martin), *M. hageni* Kirby, *M. mengeri* Ris, *M. ocellata* Martin and *M. schumanni* Calvert (NEEDHAM, 1943; PAULSON, 1969; DUNKLE, 1995). According to PAULSON (1969) the genus *Micrathyria* shows a great inter- and intraspecific variability of oviposition behaviour. In detail he distinguished seven different types including 'dropping eggs from above', 'tapping the water', 'tapping exposed leaves' as well as 'egg-laying while settled' on mud or floating leaves (see also NEEDHAM, 1943). Some of these methods are quite unusual among the Libellulidae, which mostly oviposit by washing their eggs off in flight, by tapping the water surface or floating vegetation (CORBET, 1962). However, since Paulson´s work little was added to our knowledge about the behavioural plasticity in the genus. The aim of this paper is therefore to describe a mode of oviposition hitherto unpublished for *Micrathyria* or other neotropical Odonata.

STUDY SITE

The observation was made on December 12, 1996, at a small rainforest stream north of the trailmark "SUA 350" in La Selva Biological Station (OTS), 2.5 km S Puerto Viejo de Sarapiquí, Province Heredia, Costa Rica (10° 26′ N, 83° 59′ W, 40-45 m alt. at SUA 350). The stream was 1-2 m wide, with a maximal depth of about 50 cm and a negligable current velocity. It was located within dense primary forest. There was no vegetation in the stream or along the water's edge. However, many palms and ferns stood nearby and overhung the water. As possible predators for aquatic insects many small fishes were recorded inhabiting the stream.

The average annual precipitation at La Selva is 3,962 mm with a period of least precipitation from February to April. The average monthly air temperature is 25.8 °C with a diurnal range of 6 - 12 °C and a less than 3 °C average monthly change (all data from SANFORD et. al., 1994).

The ovipositing female was collected and later identified from photographs and a description by Dr S.W. Dunkle.

OVIPOSITION BEHAVIOUR

At 10:20 (CST) a female *Micrathyria dictynna* visited the stream. She flew between 0.5 and 3 m above the water through the vegetation searching for a suitable oviposition site. I saw her hovering in front of the tip of several palm leaves. In each case she made one dipping movement to the underside of the leaf without laying eggs, then changed to a new site.

After some minutes of searching the female began to deposit eggs in flight on the underside of a palm leaf near its tip, about 2.3 m above the middle of the stream. The way she was doing so is illustrated in Figure 1. The female hovered in front of the tip of the leaf and extruded a clearly visible mass of eggs, lasting about 5 s. Then she bent the abdomen down and tapped the underside of the leaf to attach the eggs. Following this she again hovered, extruded eggs and attached them to the same site. Altogether she repeated this process 4 times before I caught her. In hand she extruded more eggs and I noted that the eggs had a rather liquid glutinous layer.

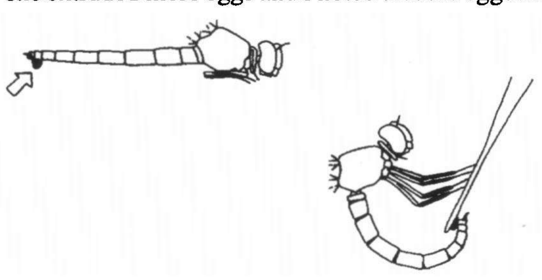

Fig. 1: Process of oviposition in *Micrathyria dictynna*: the female extruded eggs while hovering in front of a leaf, followed by attaching the eggs to the underside of the leaf while in flight, probably using the second and third pair of legs for a slight contact with the substrate (according to J. Lempert, pers. comm.).

Although I couldn't see the position of the legs at the moment the female was depositing her eggs due to an unfavourable angle of view and the rapidity of movement, it is likely that she used the second and third pair for a slight contact with the substrate, as shown in the figure.

Before and after oviposition no *Micrathyria* male was recorded along the stream section. But on the next day two

Fig. 2: Egg mass of *Micrathyria dictynna*, hanging about 2 m above the middle of a small rainforest stream on the underside of a palm leaf, containing eggs of different developmental stages.

males probably of the same species were observed perching on leaves above the water, but no further female appeared.

Along a 10 m section of the stream around the oviposition site I found 4 more clutches of eggs, all of them located near the tip on the underside of leaves (Fig. 2), hanging between 0.3 and 1.2 m above the water surface. One clutch with fully developed embryos was brought home in a plastic film box, together with some water drops from the stream. After about two hours without examination of the egg mass I recorded some prolarvae crawling around on its surface. When I placed them into water they immediately hatched into the first larval stage.

Two egg masses measured 15 x 9.5 mm and 17 x 9.5 mm, containing approximately 1,100 and 1,400 eggs respectively. Conspicuously they contained eggs of different developmental stages. In general, at the periphery the eggs were mostly well developed, often with clearly visible embryos and of light brown coloration, whereas around the centre they mainly were poorly developed and of milky white coloration. The covering layer of eggs also consisted of poorly developed ones, but in contrast to the central eggs they were dark brown. The alcohol-preserved eggs measured 0.56 mm (range 0.52--0.6 mm; SD=0.02; N=16) x 0.34 mm (range 0.3-0.38 mm; SD=0.02; N=16) and were elliptically shaped.

DISCUSSION

The behaviour of *Micrathyria dictynna* described above probably represents the first recorded case of epiphytic oviposition high above the water in New World Odonata. It resembles in detail the oviposition behaviour described for the African *Malgassophlebia aequatoris* Legrand (LEGRAND, 1979) and *M. bispina* Fraser (LEMPERT, 1988), which belong to the subfamily Tetratheminae (FRASER, 1957). Within this subfamily epiphytic oviposition high (!) above the water is frequently encountered also in the pool breeding species of the Old World genus *Tetrathemis* (CLAUSNITZER, 1995; CLAUSNITZER & LEMPERT, 1998; FRASER, 1952; LEMPERT, 1988; McCRAE & CORBET, 1982), which in contrast to *Malgasso-*

phlebia spp. oviposit while settled.

Micrathyria ocellata was the only species for which PAULSON (1969) mentioned the tapping of exposed leaves (*Typha*) just above the water surface, which could be viewed as an evolutionary stage on the way to oviposition like *M. dictynna.* Similar behaviour combined with gluing eggs to the substrate was also recorded for *Brachythemis lacustris* (Kirby) and *B. leucosticta* (Burm.) (CORBET, 1962; MILLER, 1982), Old World members of the Sympetrinae (FRASER, 1957), as well as for some Tetratheminae (CLAUSNITZER, 1995; LEMPERT, 1988).

Three different suggestions were made to explain the adaptive significance of epiphytic oviposition above the water in libellulid dragonflies of the tropics. It could serve to prevent the eggs from (1) anoxic conditions on the bottom of standing waters (McCRAE & CORBET, 1982), (2) being washed downstream (MILLER, 1982), or (3) predation by fish (MILLER & MILLER, 1985; LEMPERT 1988). However, I suppose that there is no universally valid explanation for the phenomenon and that all these variants apply well for specific cases. This implies that for *M. dictynna* the decisive factors have to be scrutinized criticially.

The conditions in the described stream resembled more or less those of stagnant water. Because of a negligible current velocity there was a thick layer of soft, anoxic bottom deposits. To separate the eggs just from this anoxic condition it should be sufficient to deposit them into shallow water or on a substrate near the water´s edge. So there would be no evident reason to evolve such specialized behaviour like oviposition high above the water. Therefore it seems likely that predation risk by fishes is a more relevant factor for the reproductive strategy of *M. dictynna.* This hypothesis is supported by the occurrence of many small fishes in the stream which were observed to react quickly to all objects dropping onto the water surface. Under this high potential predatory pressure the multi-layered egg masses of *M. dictynna* could be advantageous because of the different developmental stages of the eggs and their different hatching times.

In comparison to other libellulids with egg deposition above the water, *M. dictynna* seems to lay more eggs, as indicated by the two examined clutches. LEMPERT (1988) recorded for the similar sized *Malgassophlebia bispina* an average clutch size of only 417 eggs (range 60-730). In the larger *Tetrathemis polleni,* McCRAE & CORBET (1982) counted between 200 and 780 eggs per mass and they described the eggs to be about 0.7 mm long. It is unlikely that egg masses of *M. dictynna* contained eggs from more than one female because no overlapping clumps could be recognized.

Oviposition in *M. dictynna* was not related to the beginning of the rainy season and therefore egg masses were more likely to suffer from rainless periods during development. Thus the great clutch size could simply be a method to prevent at least part of the eggs from drying up. In this context it would also be of particular interest if there are any differences in the hatching success of eggs positioned experimentally above and in the water at locations where this behaviour occurs.

The described behaviour in *Micrathyria* could be considered to be a case of convergence between Tetratheminae and Brachydiplactinae. It is recorded in this special mode only for tropical rainforest inhabiting *Malgassophlebia* spp. and *Micrathyria dictynna*. Thus it is probably caused by similar environmental conditions in such forests of both the Old and New World.

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