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OVIPOSITION BEHAVIOUR OF *TETRATHEMIS POLLENI* (SELYS): A POSSIBLE ADAPTATION TO LIFE IN TURBID POOLS (ANISOPTERA: LIBELLULIDAE)

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A settled female of *T. polleni* places a mass of eggs, up to 2 m above the prevailing water level, on the surface of upright sticks or dead sedge stems. The eggs, several hundred to a mass, adhere to the stem and hatch there, without falling into the water. Females of exophytic Odonata seldom attach eggs directly to a substrate, and very rarely when settled. Such behaviour may enable *T. polleni* to oviposit successfully in turbid, astatic, standing waters immediately after the onset of the rains and thus to prey intensively on larvae of the mosquito, *Anopheles gambiae* Giles. In its oviposition behaviour, the African *T. polleni* closely resembles other species of *Tetrathemis* in Africa and India, except that it selects dry bark or dead stems instead of green foliage as oviposition substrates.

INTRODUCTION

Representatives of the archaic libellulid subfamily Tetratheminae occur in tropical and subtropical Africa, Madagascar and Asia (cf. PINHEY, 1951; 1962). In the few instances when oviposition has been witnessed, the female has placed the eggs directly on to a surface, above the prevailing water level. To do this is exceptional among those Odonata which (like all Libellulidae) are exophytic, i.e. which lack an ovipositor able to penetrate an oviposition substrate.

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Two species of Tetratheminae have been seen to oviposit while in hovering flight, both doing so in forest. *Notiothemis robertsi* Fraser placed its eggs on a stone projecting above the surface of a pool (CORBET, 1962, p. 16); and *Malgassophlebia aequatoris* Legrand placed its eggs on the underside of a leaf overhanging the water of a permanent stream (LEGRAND, 1979). This kind of ovipostion has no explicit place in EDA's existing classification of oviposition types (1964), but falls close to his categories (d) or (e): "flying-oviposition" into mud or sand, and into water, respectively.

Other Tetratheminae, comprising species of *Tetrathemis*, have been seen to lay while the female is settled on the oviposition substrate. Either or both of two Indian species of *Tetrathemis* (but perhaps only *T. platyptera* Sélys) were reported by FRASER (1936, p. 250) to lay eggs on objects overhanging the water. FRASER writes (1952, p. 262): "In the tropics I have watched species [of *Tetrathemis*] .... alight on the surface of a leaf, often some feet above the level of a pond, and then proceed to exude a mass of eggs which stuck fast to the leaf, where they were left to hatch. On other occasions I have observed them depositing the egg-masses on the surface of moss covering piles projecting from water...." Among African species of *Tetrathemis*, oviposition has been reported previously only for *T. bifida* Fraser which placed its eggs at the edge of a small rain pond, well above water level, directly onto an herbaceous plant on which the female was resting (PINHEY, 1961, pp. 119, 121). Noting that the vulvar scale of *T. polleni* differs from that of other species of *Tetrathemis*, PINHEY (1961) surmised that *T. polleni* would be found to oviposit in the manner that is customary for libellulids — ejecting the eggs onto the water surface while in flight.

Here we present what we believe to be the first observations of oviposition of *T. polleni*. They do not confirm Pinhey's supposition, but on the contrary show *T. polleni* to resemble closely other members of this genus in its oviposition behaviour, thus lying close to categories (a) and (b) of EDA (1964) (i.e. "sitting oviposition" into plant tissue and into mud or moss, respectively) with the important qualification that, because the oviposition is exophytic, eggs are placed on, and not into, the substrate. And because the eggs are laid well above the water surface, such oviposition behaviour conforms with category (δ) of INOUE & SHIMIZU (1976).

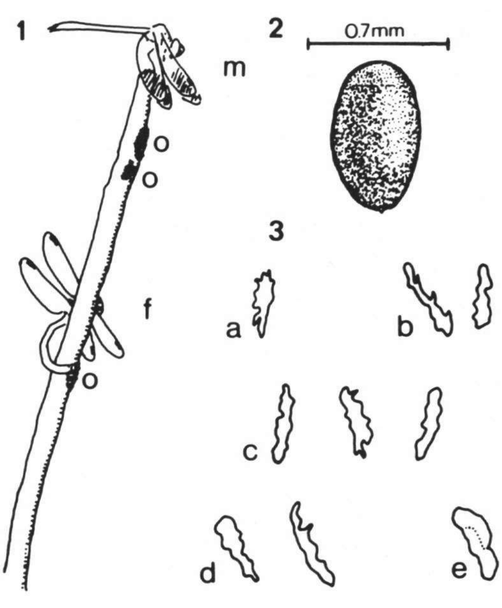
OBSERVATIONS

The observations were made by A.W.R. McC. 1½ km from the town of Rabai, Kenya (39°34'E, 3°55'S) at Simakeni Dam, a shallow, exposed, rain-fed pond made some 26 years before by constructing a bund across a shallow valley. The maximum depth of water in the dam is about 130 cm, and the dam occasionally dries up completely, having done so in March 1977 and March 1980. The water is always turbid, preventing establishment of any rooted, submerged vegetation. In the terminology of HARTLAND-ROWE (1972), Simakeni Dam would be classed as "perennially astatic" — drying out occasionally but not on a regular seasonal or annual basis. It is polymictic, the water mixing every night and occasionally also on windy days, especially when the water level is high and reaches the grassy, marginal (terrestrial) vegetation. From properties of small, turbid pools studied in hot, sunny climates in the Andes (HUTCHINSON & LÖFFLER, 1956) and in Arizona (FOSTER, 1973), we would expect (as indeed we have repeatedly found) abrupt thermal stratification to develop by day in Simakeni Dam. This pond is unequivocally eutrophic, especially when water levels are low and turbidity is high: algal blooms sometimes occur, and the macrofauna of the anoxic benthic layer consists almost exclusively of chironomid larvae.

When the following observations on oviposition behaviour were made, visible water occupied an area of about 25 x 40 m (maximum depth about 1 m); dead sedge stems of *Cyperus exaltatus* Retz., about 1 m high, stood around about half of the water's edge; and 6 closely grouped sticks rising 1-2 m above the water level stood near the middle of the pond. There was negligible floating vegetation.

The male adults of *Tetrathemis polleni* (Sélys) were identified by P.S.C. from photographs, sketches and descriptions of flight behaviour provided by A.W.R. McC. The female adults were assigned to *T. polleni* on the basis of their association with males, and because in gross appearance (i.e. size, shape and abdominal colour pattern) they conformed with a published description of the female of this species (PINHEY, 1951). No adults were captured. We may note here that one of us (P.S.C.) has reared adults of *T. polleni* from larvae obtained in June 1954 from two small, turbid, standing waters in Buyende District, Uganda (33°5'E, 1°15'N and 33°9'E, 1°12'N).

On November 2, 1979 mature adult males of *T. polleni* were competing for the tops of the sticks as perches; a male would return to a perch after disturbance, and would toleate another perched male up to about 30 cm away. One such male was perched on the top of a stick. About 15 cm below him, a female clung with her abdomen twisted and arched beneath her (Fig. 1) as she placed eggs on the surface of the stick, about 120 cm above the water. As they were laid, the eggs were pale yellowish,



Figs. 1-3. *Tetrathemis polleni*: (1) A female (f) ovipositing on an emergent stick while a male (m) perches above her; egg masses (o) are shown; Simakeni Dam, November 1979; — (2) A laid egg; the scale represents 0.7 mm; — (3) Egg masses containing approximately (a) 200, (b) 350, (c) 400, (d) 500 and (e) 780 eggs, the last one (e) apparently consisting of 2 masses in apposition.

and in a discrete mass. Dead sedge stems around the edges of the pond had several similar yellow masses and also many that were light brown — the colour of egg masses a day or so after they have been laid. Males were perching on most of these sedge stems also. On stems or sticks which were slightly inclined to the vertical, egg masses were laid on the 'under' surface, i.e. the one closer to the water; nevertheless egg masses could receive direct sunlight at certain times of day. Perhaps the severity of such insolation is mitigated by the female's choice of a nearly vertical surface and also of the surface's solar aspect: of 10 egg masses examined in November 1980 for aspect, none was on the western (warmest) side of stem, although on other occasions egg masses were found on the western side. In one such case the temperature was recorded next to an egg mass on a virtually vertical surface on one of the sticks. On a day in March 1981 that was cloudless from about 1 hour before Solar Noon, a thermistor probe (a short type with a green nylon bead head inside a clear nylon cover), fastened against the stick surface next to the egg mass, recorded a maximum of 51.5°C in almost windless conditions about 2 hours after Solar Noon — a time when the shaded air temperature, measured on an adjacent stick with an identical probe placed inside an inverted thermosflask refill, was 33°C and falling. On that day, insolated surface temperatures by the egg mass were 48°C or higher for each of the five measurements made at quarter-hour intervals during the period 1342-1442 hrs Solar Time. Eggs next to the probe subsequently hatched normally. Clearly the eggs must have a high thermal tolerance.

The stimulus for oviposition appears to be rain: most egg masses appeared on stems immediately after the first few heavy falls of the rainy season.

A single egg mass occupied an area of 10-18 x 3-6 mm, and contained about 200-800 eggs (Fig. 3); sometimes many masses were combined so that one stem bore several thousand eggs. Eggs within a mass are orientated irregularly; they are usually only 1 or 2 eggs deep but occasionally 3 eggs deep. Egg-masses were always well above the water surface.

To the naked eye an egg mass appears pale yellow when it is first laid, becoming brownish grey within a few hours. This is due to the darkening of the chorion as it assumes a burnt umber colour and a shiny surface (therefore presumably lacking any plastron structure), normally obscured beneath a semi-opaque outer layer of accessory substance or spumaline (cf. HINTON, 1981). This spumaline layer occasionally fails to cover the free end of the egg but usually covers the egg entirely (Fig. 2); it may also show markings where contiguous eggs have adhered. The end of the egg often attached to the substrate is sometimes slightly flattened and bears a minute acuminate projection, the pedicel. The pedicel is composed entirely of spumaline. Once dry, the spumaline layer is not hygroscopic, i.e. it neither swells up nor is dissolved when wetted.

Dead sedge stems bore empty eggs; so eggs can hatch without falling into the water. But even if the embryo within an egg appeared fully developed, the egg did not necessarily hatch if placed on water. Two simple tests gave information about the physical conditions which allow development and hatching of the eggs.

In the first test (August 1979) a brown egg-mass (attached to a piece of stem) was immersed in water and then placed damp within a wide-mouthed, capped glass jar. Although the eggs appeared ready to hatch (because they contained fully formed embryos) none did so during the next 3 days. However, during the succeeding 10 days almost all the eggs either hatched or collapsed. Prolarvae were found stuck to the side of the jar as if they had sprung vigorously from the eggs. Other eggs, from several masses which had been kept dry and placed in a similar jar, did not hatch during the same observation period.

In the second test (November 1980) egg masses (laid on November 17) were collected on November 18, by which time embryonic development had begun: the ventral plate had formed and invagination into the yolk had just commenced. On the same day the masses on their original dry stick were divided into 3 lots, each being placed inside a closed 250-ml screw-capped jar and then treated in one of 3 ways:

— Lot 1 (dry): in jar over silica gel
— Lot 2 (ambient): in jar with nothing
— Lot 3 (wet): in jar over a layer of cotton wool with distilled water beneath.

On November 28 the eggs were examined.

— In Lot 1, the embryos had completed katatrepsis and were dead; none had hatched.
— In Lot 2, most eggs (and perhaps all that were going to do so) had hatched, the prolarvae being spread around as if they had sprung vigorously from the eggs. All were dead.
— In Lot 3, the eggs were invested with a thin layer of fungus and none had hatched. Embryos had completed katatrepsis but were dead and showed incipient degeneration.

Both tests show that: eggs can hatch without being continuously immersed in water, and without receiving a wetting; prolarvae apparently spring away from the egg shell after eclosion; and eggs are intolerant of dry conditions — at least if these persist throughout embryonic development. The second test shows that eggs are intolerant of saturated conditions — at least if these persist throughout embryonic development. Both tests show that eggs can hatch promptly after being laid and that they can do so spontaneously, an observation confirmed when eggs assumed (by their colour and texture) to have been laid on December 18, 1980, and thereafter kept at 25-29°C under ambient humidities, hatched on December 25 or 26. Eggs developing in nature can be expected to develop even more rapidly than this because they are regularly insolated. That direct development is the usual or only pattern is implied by the finding that eggs cannot tolerate (persistently) very low relative humidities; from this we infer that they are unable to survive a dry season.

DISCUSSION

Only a few species of exophytic Odonata are known to attach their eggs directly to a substrate (cf. CORBET, 1962, p. 20); and if such species place the eggs above the water they usually do so in flight — as happens in *Malgassophlebia aequatoris* (LEGRAND, 1979) and *Micrathyria ocellata* Martin (PAULSON, 1969). In very few exophytic species is the female known to oviposit well above the water while settled. Such behaviour has been recorded so far only for 3 (or perhaps 4) species of *Tetrathemis* and for *Brachythemis lacustris* (Kirby) (CORBET, 1962, p. 20).

The information presented in this paper allows some plausible inferences to be drawn regarding the adaptive correlates of this very unusual kind of oviposition.

Simakeni Dam is always turbid, and consequently cannot support rooted, submerged vegetation. We note that turbid pools are usually small, and that they tend to be rainfed and to lack an outlet. So a lot of fine material is continually washed into such pools but not out of them. Simakeni Dam is probably typical in having much material in colloidal suspension which accumulates from surface run-off. In this respect it contrasts strongly with the much clearer residual pools in a nearby river bed.

Adults of *T. polleni* appear at the very beginning of the rainy season. Such a prompt arrival implies that it is the adults which survive the dry season and that they do so (in the manner of *Gynacantha* (cf. CORBET, 1962, p. 124)) locally, and in sheltered situations, such as stream gullies and thickets.

At the beginning of the rainy season, when adults of *T. polleni* first arrive at Simakeni Dam, the water level may not yet have risen enough to reach the marginal vegetation of living grasses. Egg masses (and perching males) have only been found on dead stems or on sticks, but never on foliage and only on those stems which lack flowering heads and which are standing in water. By selecting dead or dry stems, *T. polleni* may be ensuring that it inhabits astatic water bodies and also that it can oviposit at the beginning of the rainy season, before the water has extended far enough, or has stood for long enough, to make potentially suitable oviposition sites available at the vegetated margin, such as living, green foliage, or green stems of sufficient thickness, which might be required by (for example) *Palpopleura lucia* (Drury).

Under these conditions, were *T. polleni* to lay its eggs on the water surface they might suffer in either of two ways. If near the pond margin, they might become stranded and extremely hot as a result of the wide fluctuations in water level which characterise the beginning of the rainy season. If laid towards the centre of the pond they would sink to the bottom which (because the water is turbid and without rooted, submerged plants) will be anoxic. Moreover, even if embryonic development could be completed on the bottom, the combinations of very fine sediment and a low concentration of dissolved oxygen would probably prove fatal to the second-instar larva.

Because they are laid well above the prevailing water level, and towards the centre of the pond, eggs of *T. polleni* escape exposure to both these hazards. It seems unlikely that their placement above the water level significantly increases their vulnerability to predation because, so long as the stems remain in water, ants cannot reach them. (If the stems ceased to be in water the hatching prolarvae would presumably die in any case.)

These considerations lead us to suggest that the unusual oviposition behaviour of *T. polleni* is an important element in an adaptive strategy which enables this species to oviposit successfully in turbid, astatic, standing waters at the beginning of the rainy season. We hope that this suggestion may give direction to future studies of the oviposition behaviour of exophytic Anisoptera in habitats of this kind, and to future studies of the habitats occupied by exophytic Anisoptera which place their eggs above the prevailing water level.

The oviposition habits of *Tetrathemis* have so far proved to be unusual among Odonata as well as distinctive within the Tetratheminae. We hope that observations will eventually be made on the oviposition of other species in the subfamily about which at present very little is known (cf. PINHEY, 1961; 1962, p. 222). It will be interesting to discover, for example, whether the presence of a perched male above an ovipositing female constitutes "guarding" behaviour, as exhibited by many other species of libellulids (cf. CORBET, 1962, p. 23) and whether oviposition behaviour shows much intra- and interspecific variation. When such observations are being made, it may be useful to keep in mind the supposition that females which oviposit while settled are more vulnerable to predation (cf. PAULSON, 1969).

If, as our observations suggest, *T. polleni* is specially adapted to colonise turbid, astatic pools at the beginning of the rainy season, we note that on this account it may prey intensively on larvae of the mosquito, *Anopheles gambiae* Giles. In general, Odonata larvae are unlikely to reduce numbers of a prey species significantly, unless the Odonata are closely confined with that species in space and time (CORBET, 1962, p. 65); but we note with interest that such conditions would often be met in turbid, astatic pools. Observations in the Sudan have shown that, from the time that they are 2-3 mm long, larvae of another small libellulid, *Trithemis annulata scortecii* Nielsen, feed in captivity on larvae of *Anopheles gambiae* s.l. (EL AMIN EL RAYAH & SHAMA, 1977, 1978) and that larvae of this dragonfly, when 16-18 mm long, can greatly reduce numbers of *A. gambiae* s.l. larvae in field trials (EL AMIN EL RAYAH, 1975). Likewise we know, from observations made by A.W.R. McC. in May 1981, that a final-instar larva of *Palpopleura lucia* obtained from Simakeni Dam captured pupae of *Anopheles gambiae* s.l. in water only 1-cm deep and did so promptly although the pupae seldom moved, and it was noted that another larva, probably of *P. lucia*, consumed larvae of *A. gambiae* s.l. not only in the light but also in total darkness. Final-instar larvae of *T. polleni*, like those of *P. lucia* are 13-14 mm long (P.S.C., unpublished observations) and one may suppose that in a habitat like Simakeni Dam larvae feed mainly at the pond's edge where the bottom meets marginal vegetation or shallow open edges, and where larvae of *A. gambiae* s.l. congregate. *Tetrathemis polleni* may be exceptional among Odonata in being adapted to occupy small ponds frequented by *Anopheles gambiae* s.l. and to do so under circumstances which allow *T. polleni* to impose significant mortality on the mosquito.

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