A UNIQUE EGG-STRAND IN *PROCORDULIA GRAYI* (SELYS) (ANISOPTERA: CORDULIIDAE)

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Received and Accepted September 15, 1980

The New Zealand endemic corduliid *P. grayi* has been found to produce an egg-strand, the first record of this behaviour in a southern hemisphere dragonfly. The egg-strand is produced into running water by the dragonfly at rest, and differs significantly in structure from that reported in the few northern hemisphere spp. which have egg-strands.

INTRODUCTION

The deposition of eggs united in gelatinous strings is of rare occurrence in the Odonata. Until recently, such oviposition behaviour had been reported only in northern hemisphere Corduliidae: in the Nearctic genera formerly known as *Epicordulia* and *Tetragoneuria* (NEEDHAM, 1901; WILLIAM-SON, 1905; WALKER, 1953; KORMONDY, 1959) and in Palearctic *Epitheca* (HEYMONS, 1896; WESENBERG-LUND, 1913; ROBERT, 1958; SONEHARA, 1967). WALKER (1966) attached taxonomic significance to this distinctive oviposition habit and deemed *Epicordulia* and *Tetragoneuria* to be congeneric with *Epitheca*. In all, egg-strings have been recorded in five *Epitheca* species: *E. bimaculata* Charp., *E. canis* (McL.), *E. cynosura* (Say), *E. marginata* Sel. and *E. spinigera* (Sel.). TILLYARD (1917) asserted that *Sympetrum* species also produce egg-strings but this has not been substantiated. Nor does the production of an egg-string appear to be more widespread in the Corduliidae as KENNEDY (1950) suggested.

A number of gomphid species may produce ova in egg-masses which lack the linear organisation of an egg-string (ROBERT, 1958; EDA, 1973; ISHIDA & HAMADA, 1973; OBANA, 1974), and INOUE & SHIMIZU (1976) discovered that the gomphid *Davidius moiwanus taruii* Asahina & Inoue may produce ova in a single file, the eggs united end-to-end, in what they termed a "moniliform egg-string". They proposed the term "egg-strand" for the structure produced by *Epitheca* spp. wherein there are at least several eggs in each cross section of the strand. The egg-strand in *Epitheca* merely comprises a uniform gelatinous matrix within which the eggs are equally spaced but without a common orientation (KORMONDY, 1959), although the egg-strands which GERARD (1880) described — presumably of *Epitheca* spp. though he could not identify them — had their broad ends inclined outward from the strand and pointing towards its free end. SONEHARA (1967) also found that the eggs in *E. bimaculata sibirica* were orientated radially to the long axis of the egg-strand immediately after oviposition but became parallel to the axis after 24 hours.

The corduliid *Procordulia grayi* (Sel.) is endemic to New Zealand. It normally oviposits in lakes and ponds over weed beds in water 1.2 m to 4.6 m deep by dipping the two terminal segments into the water whilst in flight and releasing its ova singly or in groups of four (ARMSTRONG, 1958). *P. grayi* has also been found to produce an egg-strand but the structure of the eggstrand differs significantly from that reported in other species, as does the manner of its production.

THE EGG-STRAND IN PROCORDULIA GRAYI

On 19 November 1979, a female *P. grayi* was seen alighting on an upright stem in a clump of *Cotula coronopifolia* L. growing in the water at the edge of Gollans Stream (41°,19'S, 174°,54'E), near Wellington. After a few moments, she flitted to another flowering stem further out in the stream but where the depth of water was still only 180 mm. She backed down into the water until several terminal segments of the abdomen were immersed and then commenced the emission of a strand of ova. As the egg-strand lengthened, the female continued to inch further down the stem, at the same time raising the abdomen so that the strand was maintained at the same depth in the water but moved across the current. As a consequence of this movement, the trailing end of the egg-strand snagged on a downstream stem in the *C. coronipifolia* clump. The female continued backing down the stem and raising her abdomen until the abdomen formed an acute angle with the water surface. Oviposition proceeded gradually for an estimated period of five minutes and at its conclusion the female flew immediately.

Trailing in the water, the egg-strand had a total length of 110 mm, 30 mm on one side of the plant stem and 80 mm on the other. The strand, which was collected intact, was found to contain 966 eggs of which 6 (0.62%) had failed to darken in colour by the next day and were presumed infertile.

The egg-strand comprised a central gelatinous core 0.3 mm to 0.5 mm thick, of surprising strength, from which the ova radiated discretely in whorls, for the most part in groups of four. Each egg was united to the core by 0.6 mm to 1 mm petiole-like prolongations of the gelatinous membrane covering the egg. The apical pedicel was oriented outwards from the strand (Fig. 1) which would facilitate hatching. If necessary, the term "vorticellate egg-strand" will distinguish the *P. grayi* structure from the "composite egg-strand" in *Epitheca* spp.

About half the egg-strand was placed in a water-filled petri dish for further observation but a daily examination was not possible. Kept at room temperature fluctuating up to 18°C, all of the fertile eggs hatched within seventeen days. ARMSTRONG (1958) found that hatching took 25 to 33 days in *P. grayi*.

DISCUSSION

As DEWSBURY (1978) has pointed out, one must always be cautious in the degree of reliance placed on essentially anecdotal information but the behaviour witnessed here in *P. grayi* appears to be too ritualistic to be merely aberrant. ARMSTRONG (1958) found that ovipositing *P. grayi* females are wary and difficult to approach. It was fortunate on this occasion that I was standing motionless in the water when the female landed close to me and I was able to approach within 1.5 m to view the whole procedure. Dragonflies at rest can be remarkably cryptic and the black and yellow abdominal colours of *P. grayi* blend in well amongst the yellow flowers of *C. coronopifolia*. Female *P. grayi* had been seen flying slowly about similar low streamside vegetation on other occasions but I had placed no significance upon it. In the circumstances, it is not surprising that this particular behaviour has not been reported previously.

The eggs in *Epitheca* are extruded in flight and held in place by the vulvar lamina for a time while they "mature" (WILLIAMSON, 1905). The vulvar lamina is small in *P. grayi* and would be ill-suited to this task. *Epitheca* females oviposit in flight by dipping the abdomen into still water and scraping the egg-strand off on any suitable underwater structure (KOR-MONDY, 1959). ARMSTRONG (1958) observed that when *P. grayi* oviposits directly into water the ova, emitted singly or in groups of four, separate and fall singly to the bottom; on the other hand, he found that ova passed into the air while the insect was flying remained together as an adherent mass. In collecting eggs from females of *P. grayi* into vials I have had several females express their eggs very rapidly under water in a mass which did not separate in the water column. It is conceivable that such a mass could be drawn out into a strand if it were dragged through the water.

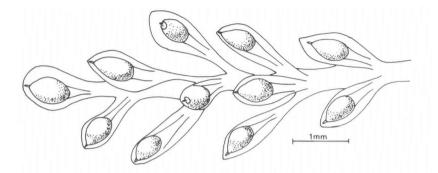


Fig. 1. Terminal section of the egg-strand of Procordulia grayi.

The possibility cannot be excluded that *P. grayi* may produce an egg-strand in flight as do *Epitheca* spp.

In some *Epitheca* species dense aggregations of egg-strands can occur leading to delayed development and high mortality in the innermost eggs in the clump (KORMONDY, 1959). Otherwise, as with *P. grayi*, the ova are placed at shallow depths where optimum conditions for development in terms of light, temperature and dissolved oxygen occur (CORBET, 1962). No aggregation of egg-strands in *P. grayi* has been observed; a careful search of the *C. coronopifolia* clump in which oviposition was observed, and of others close at hand, revealed no other egg-strands. KORMONDY (1959) found that there was little aggregation of egg-strands in *E. canis* which deposits its eggs along the edges of fairly slow streams and pondlike impoundments in streams as well as in lakes. *E. cynosura* may also oviposit in the mouth of slow streams (WALKER & CORBET, 1975).

One might suppose that the placement of an egg-strand in the shallow water at the edge of a stream should mitigate the force of the current and, to some extent, reduce the effects of downstream displacement on the species. In Gollans Stream this does not appear to be successful for *P. grayi*. The Gollans Stream catchment has been described more fully elsewhere (WIN-STANLEY, 1980). The stream is about 16 km long, with the upper 7 km of its catchment being in native evergreen forest and the lower stretches flowing through cleared farmland. My work in Gollans Stream has been concentrated in the 1.5 km or so before the stream enters the farmland. Within this zone, *P. grayi* is not uncommon in more open areas in late spring and early summer. *P. smithii* (White) also occurs here but rather later in the season and in greater numbers, sometimes exhibiting swarm-feeding behaviour (CORBET, 1962) such as I have seen elsewhere in this species and in *Hemicordulia australiae* (Rambur). In view of the abundance of adults of *P. grayi* and *P. smithii* within the catchment it is surprising that their larvae do not appear to occur in the upper part of the stream. I have seen both species ovipositing in flight over pools by tapping the tip of the abdomen in the water but in collections of larvae and final-instar exuviae there during two seasons I have found only the obligate lotic species Antipodochlora braueri (Sel.). Progeny of the other species may be more subject to displacement by downstream drift. In the Waitakere River, TOWNS (1978) recovered a larva, subsequently identified as *H. australiae* (R.J. Rowe, pers. comm.), which he thought had drifted from an upstream pool. Otherwise, drift studies in New Zealand have yielded no positive information for the Anisoptera.

Hatching success was in excess of 99% in the *P. grayi* egg-strand examined. Studies on other species with egg-strands have shown a lower hatching success: SONEHARA (1979) found that it varied between 68.8 and 96.7% in 6 egg-strands of *E. b. sibirica* examined; TENNESSEN & MURRAY (1978) in a study of diel periodicity in the hatching of *E. cynosura* ova in strands found that hatching success was high for most strands but low to zero in a few (K.J. Tennessen, pers. comm.).

EDA (1960) proposed the classification of odonate oviposition behaviour into six categories: "a" — sitting oviposition into plant tissue; "b" — sitting oviposition into mud or moss; "c" — sitting oviposition into water; "d" flying oviposition into mud or sand; "e" — flying oviposition into water; and "f" — flying oviposition without contact with the non-aqueous substrate used for oviposition. Two further behavioural possibilities were postulated by EDA (1960): flying oviposition into plant tissue, and sitting oviposition without contact with the substrate on which the eggs were deposited. These categories were styled "g" and "h" respectively by INOUE & SHIMIZU (1976). In terms of this classification, of those species known to have eggstrands, the *Epitheca* spp. fit into group "e", *D. m. taruii* fits into group "h", and *P. grayi* shows types "c" and "e" oviposition.

To permit finer behavioural distinctions than were possible within Eda's broad classification, INOUE & SHIMIZU (1976) proposed further subdivisions of category "e" on the basis of whether eggs were emitted singly or as eggs united in some way, and on the means used to overcome the adhesion between the ova and the abdomen (i.e. surface tension and water friction, or mechanical abrasion). Their three categories were:

- "e" separate eggs, adhesion lowered by immersion, release aided by flicking the abdomen.
- "e-1" egg-mass, adhesion lowered by immersion and friction with the water surface (as in Gomphidae).
- "e-2" egg-strand, adhesion lowered by immersion and severed by abrasion against a solid substrate (as in *Epitheca* spp.).

Sitting oviposition into water ("c") has been reported previously in the gomphine *Lanthus fujiacus*, (TAKETO, 1960) which emits its eggs singly into the water. To accommodate the mode of oviposition witnessed in *P. grayi*

Inoue and Shimizu's category "c" can be sub-divided as follows:

"c" — separate eggs, adhesion lowered by immersion.

"c-1" - egg-strand, adhesion lowered by immersion and severed by water current.

Within this extended classification it is of interest that *P. grayi* demonstrates oviposition behaviour of types "e", "e-1" and "c-1", and possibly "e-2" also.

The production of an egg-strand appears to set *P. grayi* apart from other *Procordulia* spp. but we may yet find that the habit is more widespread within the genus. However, there are features in the larval morphology, particularly the form of the anal pyramid, by which it differs markedly from other described species in the genus, and perhaps further research will lead to a revision of its taxonomic position: *P. grayi* was initially classified in *Epitheca*.

ACKNOWLEDGEMENTS

I am grateful to Dr K.J. TENNESSEN, Alabama, U.S.A., for comments on the hatching ratios in *E. cynosura*. My thanks are also due to Dr B. KIAUTA, University of Utrecht, The Netherlands, for comments on an early manuscript and for suggestions which have since been incorporated. I am grateful to Dr G.W. GIBBS, Victoria University of Wellington New Zealand, for reading the final version.

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