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SHORT COMMUNICATIONS

DYTHEMIS CANNACRIOIDES CALVERT, A LIBELLULID WITH UNUSUAL OVIPOSITING BEHAVIOUR (ANISOPTERA)

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The microhabitat and reproductive behaviour of the non-sexually dimorphic *D. cannacrioides* are described. An outstanding feature is the unusual method by which ovipositing females attach egg-filaments to floating roots of a liana. Use of the term "epiphytic" (sensu MATHAVAN & PANDIAN, 1977, *Hydrobiologia* 54: 257-272) instead of "exophytic" to describe such oviposition is recommended.

INTRODUCTION

The cosmopolitan Libellulidae constitutes the dominant group of Anisoptera and behaviourally is one of the best known families of Odonata. Adults occupy a wide range of freshwater habitats, from temporary ponds and permanent lakes to streams and rivers. Some species have specialized mechanisms of habitat selection which have permitted them to colonize particular microhabitats such as the spray zone near cataracts, as in *Zygonyx,* or the water contained in broken bamboo or fallen trees, as in *Hadrothemis camarensis* (Kirby) (CORBET, 1963, 1983).

Within this large and diverse family the predominant method of oviposition consists of dipping the abdomen on to the water surface and thereby washing off the eggs. A few species deposit eggs on the surface of aquatic and non-aquatic plants and on objects which float on the water surface: for example, females of *Perithemis tenera* (Say) and *Plathemis lydia* (Drury) deposit egg masses on floating objects (JACOBS, 1955). Females of some species of *Micrathyria* and *Tetrathemis* alight on the substrate and attach their eggs there (PAULSON, 1969; McCRAE & CORBET, 1982).

Some species which attach eggs directly to a substrate are inhabitants of lotic waters: for example, *Brachythemis lacustris* (Kirby) oviposits on stems of plants a few centimetres above or below the water surface (CORBET, 1963; MILLER, 1982) This behaviour may prevent eggs from being washed downstream (MILLER, 1982) Another libellulid, *Malgassophlebia aequatoris* Legrand lays eggs under leaves which overhang the water, as do some amphibians (LEGRAND, 1979).

In tropical America, the number of libellulids which inhabit lotic waters is relatively small compared with species occupying lentic waters. *Brechmorhoga, Libellula (Belonia)* and *Macrothemis* are important components of the odonate fauna of the streams and rivers of Mexico and Central and South America. In Mexico, the genus *Dythemis* has two species which are truly inhabitants of swiftly flowing waters. *D. maya* Calvert is found at streams and rivers at the bottom of canyons; and *D. cannacrioides* Calvert inhabits some tropical streams and rivers of southern Mexico. On March 23, 1983 during a collecting trip, I incidentally observed a female of *D. cannacrioides* ovipositing on a floating root of a plant at Rio Izapa (Mpio. de Izapa) in Chiapas State, Mexico.

During 1984, I observed in detail the reproductive behaviour and microhabitat of *D. cannacrioides* in southern Veracruz, Mexico. A conspicuous feature of its oviposition behaviour is the unusual method employed by the females which attach masses of egg-filaments to the surface of floating roots of some non-aquatic plants. This observation apparently represents the first record of deposition of egg-filaments within the Libellulidae.

D. cannacrioides is a non-sexually dimorphic species: males and females both have a reddish-brown body and luteous face. My collections represent the first specified locality for this species in Mexico, although it is listed from Mexico by PAULSON (1982) who gave no locality. Specimens of *D. cannacrioides* from Los Tuxtlas are unusually large (♂ $\bar{X}$ = 36.2 mm abdomen and 44.2 mm hind wing; N = 6) in comparison with specimens collected by the author in Chiapas (♂ $\bar{X}$ = 29.8 mm abdomen and 34.8 mm hind wing; N = 3) and with the size's range given by CALVERT (1906) for specimens from Central and South America (♂ range = 27.5-33 mm abdomen and 31.5-38 mm hind wing).

HABITAT AND HABITS

Observations were made at Rio La Palma (18°30'N and 95°00'W) located at 26 km N of Catemaco during May 25-27 and June 23-24 1984. The river was swiftly flowing. Several overhanging roots of the liana *Cissus gossypifolia* Standley (Vitaceae) were constantly aerated at the water surface by the rapid water current (Fig. 1). My observations were conducted at the shallowest part of the river which contained two suspended root masses defended by a male. I selected that territory for continuous observation because it apparently was the most attractive to females (the greatest number of eggs were present in the roots of that territory). I also recorded the general behaviour of other upstream males whenever possible.

In May, a solitary male was present at the reproductive site perching on a vertical liana. Judging by his bright coloration and still glistening wings I assumed that such a male was one of the earliest males to arrive at the reproductive site after completing the maturation period. No eggs were found at this time of the year in any root systems of *C. gossypifolia* and the two ovipositions seen occurred on the overhanging roots of an unidentified plant. In June, twelve available root systems were shared by four territorial males which used the roots as vertical perches and as vantage points for territorial defence. Males defended those parts of the submerged roots which were in contact with the water's surface where females oviposited. Some roots contained an enormous number of eggs (one had approximately 100,000).

Fig. 1. View of Río La Palma, showing several overhanging liana of *Cissus gossypifolia*. (Drawn from a photograph).

OBSERVATIONS

BEHAVIOUR OF SOLITARY MALES

Aggressive interactions between conspecific males consisted of a high-speed pursuit flight by the resident toward the intruder during which both followed the course of the river. Most prolonged interactions occurred when a female was ovipositing. Territorial males were aggressive toward other dragonflies and even toward hummingbirds passing their perches. They chased away *Brechmorhoga* sp., *Hetaerina titia* (Drury), *Phyllocycla volsella* Calvert and *Phyllogomphoides* sp.

Males exhibited basking positions at their perch sites (in the manner that is usual for most Libellulidae) and also adopted postures for decreasing the incidence of solar radiation, pointing the abdomen toward the sun

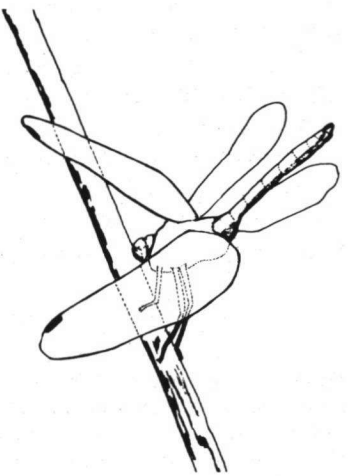

Fig. 2. *D. cannacrioides*, male on a vertical perch assuming a "semi-obelisk" posture. (Drawn from a photograph).

and shading the thorax with the wings. This position is similar to the "obelisk" position found in other libellulids, but with their abdomens not completely vertical (due to the use of vertical perches) in comparison with other libellulids which perch on horizontal substrates (Fig. 2).

COPULATION

Durations of four copulations (i.e. the wheel position) were 8.8, 6.3, 4.6 and 5.2 minutes respectively ($\overline{X} = 6.2$ min). The event commenced in flight but after a few seconds the pair settled on vegetation 8-10 m above the oviposition site. Copulations occurred between 1000-1200 h Local Time (Solar noon occurred at 1204 h June 23-24, 1984).

Three copulations by males which defended upriver territories were witnessed. These pairs in flight closely approached one of the oviposition sites which was guarded by the resident male which I was observing continuously. After examining the oviposition site each pair flew away to a neighbouring tree and continued copulation. At the termination of copula, the wheel position was broken and both sexes remained hovering face to face within a few centimetres of the copulation site. After a few seconds the female perched at the spot where copulation had occurred and the male descended to the oviposition site and engaged in long and violent interaction with the resident male. During this time the female descended to oviposit. Aggressive behaviour initiated by the intruder seemed to allow the female to oviposit without interference from the resident male.

OVIPOSITION

Although oviposition was witnessed on several occasions, I saw only four instances when the process could be observed in its entirety. After copulation, females remained at their perches for some seconds before descending to oviposit. During this interval they prepared large masses of eggs in a manner similar to that reported for *Gomphus postocularis* Selys (EDA, 1973); however I never observed the vibratory wing movements reported by Eda for this species.

In the four complete ovipositions witnessed females oviposited alone and

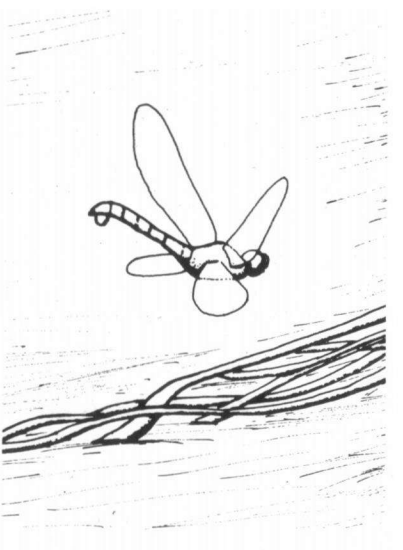

Fig. 3. *D. cannacrioides*, female with a large egg-mass approaching an oviposition site. (Drawn from a photograph).

deposited the egg-mass in flight only once touching with her abdomen the surface of the root (Fig. 3). The deposition of the egg-mass was almost instantaneous and afterwards the female rapidly flew away to the vegetation (almost to the spot where copulation had occurred) and prepared a second mass of eggs. This process was repeated three times in 3 of the females I observed. I saw only one female descend and deposit a fourth egg-mass. Three females descended to oviposit at the spot which was previously examined during copulation and one oviposited at a previously unexamined site. In all cases after oviposition was completed, the female rapidly touched the water several times with the tip of her abdomen and left the site.

Although in the four cases described above females descended to oviposit alone, I occasionally saw two incomplete ovipositions in which a male hovered close to and above an ovipositing female. These observations suggest that at least under certain circumstances males can guard their females against the sexual attacks of conspecific males.

Some of the roots were collected and preserved in 70% ethanol for further observation in the laboratory.

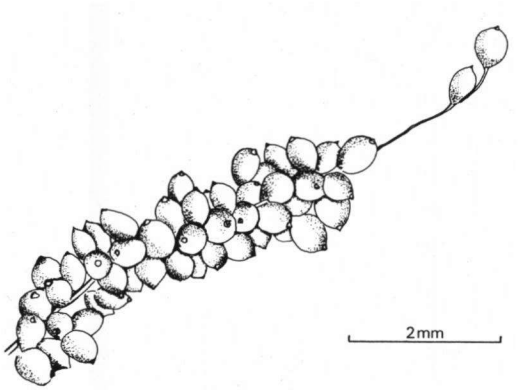

Fig. 4. *D. cannacrioides:* terminal section of an egg--strand. (Drawn from a photograph).

THE EGG STRAND OF *D. CANNACRIOIDES*

When I observed the roots under the microscope I first concluded (due to the enormous number of eggs deposited by several females) that the eggs did not have a definite orientation and were contained in a complex fibrous matrix. However, at sites where egg density was less I discovered the filamentous nature of the matrix. The strand consisted of a central filament formed by numerous individual coiled fibres to which the eggs were attached individually or in clusters of 4-5 eggs. The apical pedicel of the eggs was orientated toward the outside part of the strand. The filament was sticky and the eggs were held to the root by their entanglement (Fig. 4).

DISCUSSION

The deposition of eggs in filaments is a method which was thought to be restricted to the Corduliidae (WINSTANLEY, 1981). INOUE & SHIMIZU

(1976) also reported that the gomphid *Davidius moiwanus taruii* Asahina & Inoue produced eggs sustained by a single filament. They proposed for the latter species the term "moniliform egg string". *D. cannacrioides* is the first libellulid reported to produce eggs in filaments. TILLYARD (1917) reported that some species of *Sympetrum* also produce filaments but this has not been confirmed.

The fibrous egg-strand of *D. cannacrioides* differs from those reported for the corduliids *Epitheca* and *Procordulia* which have the eggs included in a gelatinous matrix (NEEDHAM, 1901; WINSTANLEY, 1981). Also the strand of *D. cannacrioides* is more compact than those of the latter two genera which produce linear egg-strands. The fibrous egg mass of *D. cannacrioides* is probably more resistant to water current than a gelatinous one would be. The oviposition of *D. cannacrioides* also differs from the pattern I have observed for other *Dythemis* e.g. *D. maya* Calvert, *D. multipunctata* Kirby, *D. nigrescens* Calvert and *D. sterilis* Hagen. Females of these four species oviposit in the manner that is normal for most Libellulidae (i.e. dipping the abdomen in the water) (Gonzalez, unpubl. obs.).

EDA (1960) proposed six categories for odonate oviposition behaviour:

Type I : Sitting oviposition into the plant tissue
Type II : Sitting oviposition into mud or mosses
Type III: Sitting oviposition into water
Type IV: Flying oviposition into mud or sand
Type V : Flying: oviposition into water
Type VI: Non-contact flying oviposition

He also proposed two further possibilities: Type VII: Flying oviposition into plant tissues and Type VIII: Non-contact sitting oviposition (EDA, 1964).

Although the oviposition method of *D. cannacrioides* has no specific place in the above classification, it could be a modification of the Type VII, with the important qualification that because of the lack of an ovipositor the eggs are placed on the surface of the plant and not within it.

INOUE & SHIMIZU (1976) also proposed 10 different categories based on the mechanism by which eggs are released but I am not able to accommodate the observed oviposition of *D. cannacrioides* in their classification.

THE OVIPOSITION OF *D. CANNACRIOIDES*: WHY NOT "EXOPHYTIC"

There is a general tendency to classify as "exophytic" all anisopterans which routinely attach their eggs to the surface of plants (e.g. IMMS, 1957; CORBET, 1963, 1980). MATHAVAN & PANDIAN (1977) used the term "epiphytic" to describe the oviposition of *Brachythemis contaminata* (Fab.) which glues the eggs to the substratum. However they did not comment further on the introduction of a new term which I consider justifies discussion here.

In my opinion "epiphytic" dragonflies must be clearly separated from those anisopterans which drop eggs freely into the water or on to bare ground (the true

"exophytic behaviour") for two reasons. First, the choice of a plant or floating object for egg deposition involves a different and more specialized method of habitat selection than is exhibited by those species which only release eggs within water independently of the presence or absence of plants. For example, males of *D. cannacrioides* and *Perithemis* spp. select a suitable object on which the females oviposits (pers. obs.; JACOBS, 1955). Second, the term "exophytic" in its restricted sense means "outside the plant" but it does not indicate any particular site. On the other hand "epiphytic" is more precise meaning "placing on the outside of plants". It is therefore the term of choice to describe the behaviour of *D. cannacrioides* as well as that of other anisopterans which use the surface of plants (or similar substrates) for egg-deposition.

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REFERENCES

CALVERT, P.P., 1906. Neuroptera. *Biologia cent.-am.*, pp. 272-277. Porter & Dulau.

CORBET, P.S., 1963. *A biology of dragonflies.* Quadrangle Books, Chicago.

CORBET, P.S., 1980. Biology of Odonata. *A. Rev. Ent.* 25: 189-217.

CORBET, P.S., 1983. Odonata in Phytotelmata. *In:* J.H. Frank & L.P. Lounibos, [Eds], Phytotelmata: terrestrial plants as hosts for aquatic insect communities, pp. 29-54. Plexus, Marlton, New Jersey.

EDA, S., 1960. Oviposition in Gomphus pryeri Selys, with a note on the oviposition of dragonflies. *Insect. Ecol.* (8)2: 82-88.

EDA, S., 1973. Females of Gomphus postocularis Selys preparing a big egg-mass just before oviposition. *Tombo* 16: 17-18.

IMMS, A.D., 1957. *A general textbook of entomology.* Dutton, New York.

INOUE, K. & N. SHIMIZU, 1976. Moniliform egg-strings laid by Davidius moiwanus taruii Asahina & Inoue, a case of non-contact sitting oviposition (Anisoptera: Gomphidae). *Odonatologica* 5: 265-272.

JACOBS, M.E., 1955. Studies on territorialism and sexual selection in dragonflies. *Ecology* 36(4): 566-586.

LEGRAND, J., 1979. Morphologie, biologie et écologie de Malgassophlebia aequatoris, n. sp., nouveau Tetratheminae du Gabon (Odonata: Libellulidae), *Revue fr. Ent.* (N.S.) 1(1): 3-12.

McCRAE, A.W. & P.S. CORBET, 1982. Oviposition behaviour of Tetrathemis polleni (Selys): a possible adaptation to life in turbid pools (Anisoptera: Libellulidae). *Odonatologica.* 11(1): 23-31.

MATHAVAN, S. & T.J. PANDIAN., 1977. Patterns of emergence, import of egg energy and energy export via emerging dragonfly populations in a tropical pond. *Hydrobiologia* 54(3): 257-272.

MILLER, P.L., 1982. Temporal partitioning and other aspects of reproductive behaviour in

two African libellulid dragonflies. *Ent. mon. Mag.* 118: 177-188.
NEEDHAM, J.G., 1901. Aquatic insects in the Adirondacks. *Bull. N.Y. St. Mus.* 47: 383-612.
PAULSON, D.R., 1969. Oviposition in the tropical dragonfly genus Micrathyria (Odonata; Libellulidae). *Tombo* 12: 12-16.
PAULSON, D.R., 1982. Odonata. *In:* S.H. Hurlbert & A. Villalobos-Figueroa [Eds], Aquatic biota of Mexico, Central America and the West Indies, pp. 249-277. San Diego St. Univ.
TILLYARD, R.J., 1917. *The biology of dragonflies,* Cambridge Univ. Press.
WINSTANLEY, W.J., 1981. A unique egg-strand in Procordulia grayi (Selys) (Anisoptera: Corduliidae). *Odonatologica* 10(1): 57-63.