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OVIPOSITION BY EGG-THROWING IN A ZYGOPTERAN, *MECISTOGASTER JOCASTE* HAGEN, 1869 (PSEUDOSTIGMATIDAE)

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M. jocaste was observed laying eggs in a water-containing tree-hole in a forest of Bolivia. The insect hovered above the hole and making jerky movements with the curved abdomen, threw individual eggs at the water surface in the direction of the shaded area underneath the roof of the hole. The abdomen did not touch the water and the eggs, after drifting horizontally for a short distance, remained floating. The increased efficiency brought about by the possibility of throwing eggs into tree-holes from the outside was probably the most important selective factor involved in the appearance of this unique type of oviposition. A new interpretation for the long abdomen of pseudostigmatids is proposed based on its mechanical advantages for throwing eggs.

INTRODUCTION

The forest damselfly family Pseudostigmatidae contains the largest known members of the order Odonata (TILLYARD, 1917). The larvae of the species *Mecistogaster modestus* breed in the water accumulated in the leaves of epiphytic bromeliads (CALVERT, 1911) and larvae of *Microstigma* have been recently found in the water accumulated in the pods of Brazil nut pods (*Bertholletia*) fallen on the forest floor (SANTOS, 1981). In spite of its remarkable morphological and biological characteristics, the reproductive behaviour of Pseudostigmatidae is poorly known, the only data available on the subject being the recent observations of YOUNG (1980, 1981) on mating and oviposition in *Megaloprepus coerulatus.* The long abdomen of the females of *Mecistogaster* has been regarded as an adaptation for penetrating deeply into leaf axils of bromeliads during oviposition (CALVERT, 1911), but the actual oviposition of *Mecistogaster* has never been reported.

We describe now the oviposition of *Mecistogaster jocaste*, based on observations made by one of the authors (A.M.) in a forest of Bolivia.

OBSERVATIONS

The observations were made in a forest at the place called Tacú, Pallilo, Provincia of Ichilo, Buenavista, Dep. of Santa Cruz, Bolivia. At the borders of an enlarged "trail", on the forest floor, there was a partially rotten fallen log about 80 cm diameter and 5-6 meters of length. On the upper part of this log, near one of its extremities there was a coarsely rectangular hole of about 35 x 150 cm which communicated with a larger cavity inside the log. This cavity contained about 80 liters of water of a brownish coloration due to the presence of large amounts of dissolved organic matter. Since the water did not fill completely the cavity there was a space about 10 cm left between the roof of the cavity and the water surface (Fig. 1).

At about 10 a.m. one of the authors (A.M.) stood motionless by this log peering at the water surface in an attempt to detect mosquito larvae and pupae. All of a sudden, a large flying damselfly appeared and remained hovering in the air close to his eyes. The damselfly then curved its abdomen (Fig. 1) and started a series of jerky abdominal movements that resulted in eggs being scattered individually on the water surface without the abdomen coming into contact with the water. It could be clearly observed that the eggs were not simply dropped into the water as they struck the water surface obliquely and drifted horizontally for a short distance on the surface. For a short time the insect hovered above the hole trying to throw the eggs toward the shaded area, on the water surface situated underneath the roof of the hole. The yellow eggs remained floating on the water surface and, when the hole was stirred, more floating eggs drifted out of the dark area under the roof. It could not be observed whether these eggs would eventually sink. During about two hours the same kind of behaviour was observed at the same site in four females, three of which were netted. The female always oviposited unattended by the male. No attempt was made to retrieve odonate larvae from the water, which contained a fairly rich population of mosquito larvae and pupae (*Orthopodomya, Haemagogus*) as well as their predators, the larvae of *Toxorhynchites*.

The taxonomic study of the three females and one male collected in the same area revealed the species to be *Mecistogaster jocaste* Hagen, 1869.

GENERAL DISCUSSION

The possibility that a flying odonate could drop its eggs on the water surface without touching it was first reported by GARDNER (1950) in the

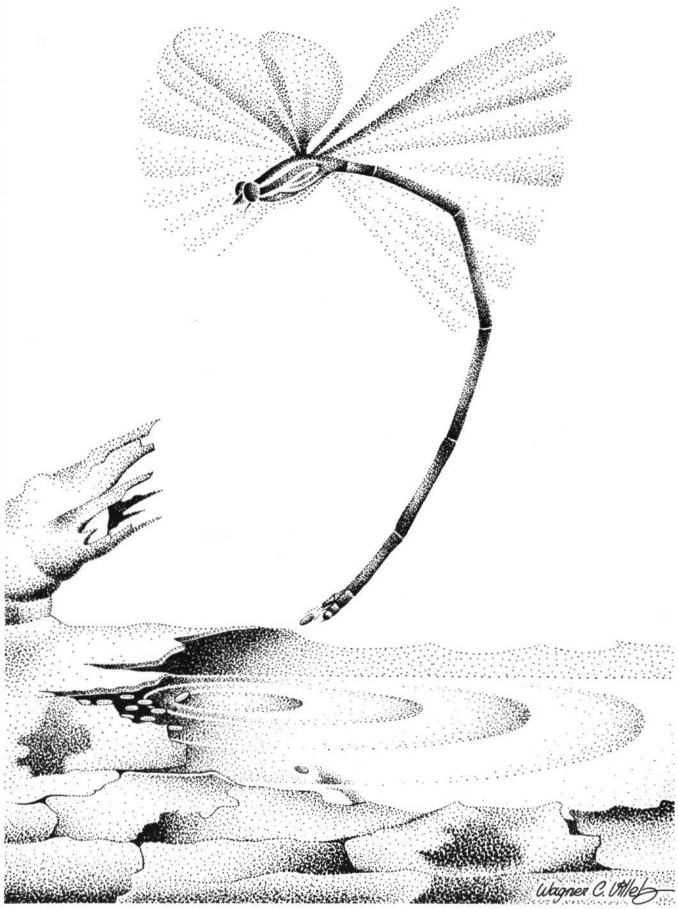

Fig. 1. Artistic view of a female *Mecistogaster jocaste* throwing eggs on the water contained in a tree-hole. Since the drawing was not based on a photograph, the position of the insect should be regarded only as approximately correct. The proportions of the insect to the fallen trunk and its hole were purposely modified.

anisopteran *Sympetrum sanguineum.* Although denied by FRASER (1952), thus raising a controversy (LONGFIELD, 1953), the fact has been confirmed and is now regarded as part of the normal oviposition behaviour in several species of *Sympetrum* (EDA, 1962, 1965), some species of the gomphid genus *Davidius* (INOUE & SHIMIZU, 1976) and some species of the libellulid genus *Micrathyria* (PAULSON, 1969). Oviposition of this type has been denominated non-contact flying oviposition according to the classification of EDA (1960). The finding of this rare type of oviposition in *M. jocaste* is quite unexpected as it departs considerably from the usual endophytic pattern observed in the Zygoptera.

In all instances in which non-contact flying-oviposition has been reported in Odonata the eggs are simply dropped from the air, and the flicking movement of the abdomen observed in some species has been interpreted as a mechanism for releasing the eggs from the vulva (INOUE & SHIMIZU, 1976). In *M. jocaste,* however, non-contact flying oviposition is more elaborated. The jerky movement made by the curved abdomen (Fig. 1) allows individual eggs to be actively thrown from the abdomen to strike the water surface obliquely. Thus, it is possible to distinguish two types of non-contact flying oviposition in Odonata, by egg-dropping (*Davidius, Sympetrum, Micrathyria*) and by egg-throwing (*Mecistogaster*). The ability of *M. jocaste* to throw eggs by jerky movements of the abdomen while hovering indicates that this animal has a very sophisticated control of wing movements. This is consistent with the observations that *Mecistogaster* are able to pluck a small spider from the web while fluttering in front of it (BEEBE & BEEBE, 1910; N.D. Santos, pers. comm.), a behaviour also observed in *Megaloprepus* (CALVERT, 1923; YOUNG, 1981). The egg-throwing oviposition of *M. jocaste* probably allows the species to throw eggs into tree-holes which sometimes have narrow apertures and seldomly offer large open water surfaces as in the case of our observations. Even in this case, however, it could be observed that, instead of laying the eggs on the open surface of water, the females threw them at the water toward the dark space underneath the roof of the hole. This fact indicates that the females of *M. jocaste* prefer to throw their eggs on water situated in dark narrow spaces and crevices rather than in illuminated open spaces. It is possible that darkness provided the main cue for such a behaviour. The increased efficiency of oviposition brought about by the possibility of throwing eggs into tree-holes from the outside was probably the most important selective factor involved in the appearance of the unique type of oviposition now reported in *M. jocaste.* Species with contact-flying or contact -sitting oviposition would have to penetrate into such holes for laying their eggs, and the hazards of such a penetration could be enormous. It is even possible that eggs might be thrown into dry tree-holes and hatching postponed until the hole is filled with water. A similar phenomenon occurs in certain species of *Sympetrum* (CORBET, 1962) which drop their eggs in grassy dry depressions in the ground.

The observation that the eggs of *M. jocaste* thrown by the female at the water surface remain floating is apparently unique in Odonata. The phenomenon might be correlated with the necessity of protecting the eggs against the unfavourable physical conditions for egg-development that presumably exist on the bottom of a water-containing tree-hole. It would be very interesting to verify whether other Odonata whose eggs are laid in tree--holes also lay floating eggs or use any special device to maintain their eggs close to the water surface.

In dragonflies the method of oviposition has been closely correlated with the morphology of the female ovipositor (TILLYARD, 1917). In the groups with endophytic oviposition (Zygoptera, Aeshnidae and Petaluridae) the ovipositor is well developed and provided with a terebra for making incisions in plant tissues, while in the groups with exophytic oviposition the ovipositor is reduced or absent.

We studied under the stereomicroscope the last abdominal segments of the three females of *M. jocaste* collected in Bolivia. The ovipositors are of the usual zygopterous type, similar to those of several other pseudostigmatids that we could examine. Indeed, on morphological grounds, one could never guess that the oviposition of *M. jocaste* would be exophytic. This fact could have two explanations: either the exophytic oviposition of *M. jocaste* developed so recently that there was no time for the ovipositor to modify, or the species is able to perform both exophytic and endophytic oviposition. The latter alternative would be in agreement with the fact that the oviposition behaviour in Odonata may be very plastic (CORBET, 1980) and a single species may utilize more than one type of oviposition (PAULSON, 1969), although there is no example of a species that utilizes the two extremes, namely endophytic and exophytic oviposition.

YOUNG (1980, 1981) observed the oviposition behaviour of two females of *Megaloprepus coerulatus* in a small 6-8 cm deep pool of crystal-clear rainwater gathered in a depression of a recently fallen tree. The females alighted on the bark above the water line at the side of the pool and began probing crevices in the bark just under the water with the tips of their abdomens. Even though it was not clear whether eggs were actually deposited, the females performed typical oviposition movements of the endophytic type. It would be very interesting to know whether in other oviposition habitats *Megaloprepus coerulatus* might use oviposition by egg--throwing as now described for *Mecistogaster jocaste.*

The ecological characteristics of water-filled tree-holes as a habitat for several aquatic organisms have been discussed by KITCHING (1971). The water-filled tree-hole used by *M. jocaste* for oviposition fits well into

Kitching's category of rot-holes. It contains a rich population of larvae and pupae of mosquitos, potential preys for a damselfly larva. Even though no attempt was made to retrieve larvae of *M. jocaste* from the hole, there is little doubt that they actually live there. This fact, Young's observation in *Megaloprepus*, Calvert's classic report about the presence of larvae of *Mecistogaster modestus* in tank bromeliads and the recent discovery of larvae of *Microstigma* in the water accumulated in pods of Brazil nut pods (SANTOS, 1981), strongly indicate that the larvae of pseudostigmatids regularly occupy the water contained in or upon plants (phytotelmata). This ecological characteristic of the family may help to explain its success in colonizing the tropical forest.

The whole subject of Odonata in phytotelmata has been recently reviewed by CORBET (1981) who reported up to 47 species that live there, most of which in the leaf-base of certain plants. In tree-holes, however, only seven species have been observed among which three Zygoptera, viz. the African *Coryphagrion grandis* reported by LOUNIBOS (1980), the Australian *Podopteryx selysi* reported by WATSON & DYCE (1978) and the neotropical *Megaloprepus coerulatus* reported by YOUNG (1980).

A NEW INTERPRETATION OF THE LONG ABDOMEN OF PSEUDOSTIGMATIDAE

The enormous abdomen of pseudostigmatids has long intrigued the odonatologists. According to CALVERT (1911) the excessively long abdomen of the adult *Mecistogaster* and other pseudostigmatids may be a special adaptation to the life of their offspring in water-containing plants. "The space between the leaf of a bromeliad and the leaf next without, decreases downward, and if *Mecistogaster*'s eggs are deposited in the plant tissue in or near the contained water, in accordance with the general habit of the Zygoptera, it would often be necessary for the female to reach far down into crevices possibly too narrow to admit of the entrance of her thorax and wings. The long abdomen with the ovipositor near its hind end would therefore be of distinct advantage". This often quoted interpretation would be quite reasonable if pseudostigmatids only deposited their eggs in the plant tissue of bromeliads "in accordance with the general habit of the Zygoptera".

The finding of a pseudostigmatid that oviposits by egg-throwing and the possibility that the same phenomenon might occur in other species suggest another interpretation. Indeed, by using principles of classic mechanics it is possible to demonstrate that a long abdomen is more efficient than the usual zygopterous abdomen for throwing eggs into special areas of the environment.

The kinetic energy imparted to the egg by the abdomen is used for releasing it from the ovipositor and for setting it in a parabolic path toward the water surface. The most suitable abdomen for egg-throwing is one in which this work is performed with best energetic efficiency for the insect. The kinetic energy of the egg depends on its own mass and on the square of its velocity which depends on the velocity of the ovipositor at the moment of egg ejection. The abdomen moves mainly around an axis situated at the junction between the thorax and the abdomen. Between the initial and final position of the abdomen the ovipositor describes an arc of circle $\overset{\frown}{AB}$ with a linear velocity given by $v = \frac{\Delta \overset{\frown}{AB}}{\Delta t}$. However, $\Delta \overset{\frown}{AB} = \Delta \theta R$, where $\Delta \theta$ is the angle that corresponds to the arc $\overset{\frown}{AB}$ (measured in radians) and R is the radius of the circle that contains $\overset{\frown}{AB}$. Thus we can write that $v = \frac{\Delta \theta R}{\Delta t}$. Since R is proportional to the length of the abdomen this equation demonstrates that the longer the abdomen the higher the velocity of the egg at the moment of ejection.

Since, as stated initially, the kinetic energy of the egg is proportional to the square of its velocity we are led to conclude that long abdomens are mechanically more efficient than short ones for throwing eggs. Therefore the long abdomen of pseudostigmatids might be an adaptation for egg-throwing as well as for penetrating deeply into crevices in order to deposit the eggs in phytotelmata.

These considerations emphasize the need for further observations on the oviposition of pseudostigmatids in order to determine which type of oviposition is prevalent in the family and whether the same species or the same individual can switch from one type to the other in response to environmental requirements. Equally interesting would be finding out the type of oviposition used by the African megapodagrionid *Coryphagrion grandis* to lay its eggs in the tree-holes where the larvae have been found (LOUNIBOS, 1981). The resemblance of this species to pseudostigmatids is so close that FRASER (1955) thinks there can be no doubt that a similar method of oviposition is resorted to. It is therefore tempting to speculate that the unusually long abdomen of *C. grandis* might be an adaptation for throwing eggs in tree-holes as now suggested for *Mecistogaster.*

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