

**OVIPOSITION OF *COENAGRIOCNEMIS REUNIENSIS* (FRASER)
IN VOLCANIC ROCK AS AN ADAPTATION TO
AN EXTREME RUNNING WATER HABITAT
(ZYGOPTERA: COENAGRIONIDAE)**

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Received August 8, 2000 / Revised and Accepted September 1, 2000

The sp. inhabits streams and rivers in the mountain forests of the Indian Ocean of La Réunion. Because of heavy seasonal rainfalls and steep inclines, there are drastic changes of water level. As a consequence, no water plants, roots or wet driftwood at all are available for oviposition. The sp. seems to be well adapted to this habitat: females oviposit into wet soft and porous lava stones. The closely related *C. insularis* and *C. rufipes* inhabit streams and rivers on Mauritius, where there are less extreme conditions. Both spp. deposit eggs in plant tissue.

INTRODUCTION

Zygoptera have a well developed ovipositor and place their cylindrical eggs in or among living or dead plant tissue (TILLYARD, 1917; CORBET, 1980). Oviposition in plants may give a better protection to the eggs against predation, drift or drought. On the other hand, Zygoptera need this kind of substrate for useful reproduction and this may provide problems in torrential mountain streams where aquatic macrophyte plants are rare.

In running waters most zygopteran species behave opportunistically in the choice of plants (MARTENS, 1996). Many species use wet driftwood for oviposition (e.g. ROBERTSON, 1982; ORR, 1996). At ephemeral lentic waters, plants also may be rare, and some Zygoptera are able to colonise these waters by laying their eggs in mud or wet soil. This has been reported in *Lestes tenuatus*, *Leptobasis vacillans* (D. Paulson in CORBET, 1999) and *Indolestes peregrinus* (INOUE, 1988, cited after CORBET, 1999). Also, this is known from some Anisoptera with endophytic

ovipositors, e.g. *Anax ephippiger* (MILLER, 1983), *Gynacantha vesiculata* (GAMBLES, 1960), *G. nervosa* (DUNKLE, 1976) and *Aeshna affinis* (KLEIN, 1932; UTZERI & RAFFI, 1983). But is there a chance for oviposition when the habitat contains neither plant material nor mud? This question arose during a field trip to La Réunion, where I found a zygopteran species at running waters without any living or dead plant material.

Coenagrioncnemis reuniensis (Fraser) is endemic to La Réunion. It is a large zygopteran species which is known from some mountain forest localities only (FRASER, 1957). It belongs to a genus which is restricted to the Mascarenan archipelago (PINHEY, 1962). The other species, *C. insularis* (Selys) and *C. rufipes* (Rambur), are endemic to Mauritius (FRASER, 1949; PINHEY, 1976). For the specific status of a third Mauritian form, *C. ramburi* Fraser, confirmation is needed (FRASER, 1950; PINHEY, 1962). Until now almost nothing is known about the biology of the genus.

METHODS

During a field trip to La Réunion in March and April 1996, twenty-seven localities in different parts of the island were visited in order to get data on the odonate fauna. *Coenagrioncnemis reuniensis* was recorded at 6 localities (Tab. I). Most observations on the behaviour were made on 4-IV and 6-VI-1996 at the Rivière de Marsouins in the Forêt de Bébour near the bridge of the Route Forêtstiere (21°06'03"S, 55°34'23"E; alt. 1310 m). The water was marked by strongly varying water levels. During the observations, with the exception of some pools, the river was only 1 to 2 m wide in a 25 to 40 m wide rocky river bed. The river bed was built of volcanic material of different consistencies. There were neither roots of trees in contact with water, nor vegetation such as algae layer to provide oviposition substrate. Wet driftwood was extremely rare. There were no superficially slime covering rocks. Rocks and differences in incline caused

Table I

Localities with records of *Coenagrioncnemis reuniensis* – [Names and data on altitude were taken from local tourist maps, 1:25 000, nos. 4402 RT and 4403 RT of the I.G.N.-Paris, 1992]

Locality on La Réunion	Altitude	Date
Rivière de Ste-Suzanne at the destroyed bridge SSW Bagatelle (20°57'45"S, 55°34'12"E)	730 m	7 to 9-IV-1996
Bras des Lianes, above Cascade du Chien (21°00'52"S, 55°37'02"E)	660 m	7-IV-1996
Rivière des Marsouins in the Forêt de Bébour, near the forest path (21°06'02"S, 55°34'06"E)	1330 m	4-IV-1996
Rivière des Marsouins in the Forêt de Bébour, near the Route Forêtstiere (21°06'03"S, 55°34'23"E)	1310 m	4 and 6-IV-1996
Bras Chansons in the Forêt de Bébour (21°06'27"S, 55°34'25"E)	1325 m	6-IV-1996
Bras Cabot in the Forêt de Bébour (21°06'59"S, 55°34'31"E)	1325 m	4-IV-1996

a great variety of currents ranging from still water zones to small rapids. The data referring to oviposition behaviour were gathered at a 80 m long section. Observations were assisted by a video camera (Sony Handycam CCD-V90E).

Two smaller stones of approximately 5 cm diameter were taken directly after a female palpated them intensively for longer than 2 minutes with the ovipositor. After two days stored in water these stones were placed in 70% ethanol. Later their surface was scraped off, keeping them continuously in alcohol. In ethanol the dust and the crumbs were examined under a dissecting binocular.

Comparative observations on the other *Coenagriocnemis* spp. were made during three field trips on Mauritius in March and April 1997, 1998, and 1999, respectively. However, in more than 60h of observation of *Coenagriocnemis* adults in the field, only single data on reproductive behaviour could be recorded.

RESULTS

Coenagriocnemis reuniensis was recorded from swift-flowing rivers and streams in the mountain forests of La Réunion (Tab. I). These stretches were marked by drastic changes of water level. During the reproductive period these waters were small pools in broad rocky beds and long fast flowing stretches without any vegetation. At some permanent pools in the outlying areas of the main drainage with *Juncus* at the border, no adults were observed.

REPRODUCTIVE BEHAVIOUR

Individuals only appeared at water in sunshine. Males settled on stones and rocks at the water, holding their abdomen horizontally near to the ground, mostly at a distance of more than 5 m from each other. With short attacks they drove flying conspecific males away.

Females were grasped in flight. The male landed on her thorax and forced her to land. Just after copulation while hanging at a rock, duration 15.06 minutes ($n = 1$), both partners separated and females started with oviposition unguarded and unaffected by their mates. They settled just above water level and palpated the submerged parts of rocks or stones intensively with their ovipositor. From 56 cases observed 69.6% lasted up to 30 s (minimum = 1 s), 12.5% longer than one minute (maximum = 4 min 24 s). Sometimes, they held their abdomen straight (duration: 2 s to 1 min 18 s, median = 36 s, $n = 8$), or began with cleaning of the ovipositor. They changed sites with brief flights (median = 2 s, maximum = 14 s; $n = 45$). In two cases a female landed at a log and touched the wet surface, for 57 s and 13 s respectively but without making incisions. Two different female colour forms were observed showing reproductive behaviour. One had the tip of the abdomen and the lateral side of the thorax with blue like the males. The other form is marked in those places with greyish brown to olive green.

Two smaller stones of approximately 5 cm diameter were taken directly after a female palpated them intensively for longer than 2 minutes. But no eggs were

found there, neither fixed in the pores nor attached to the surface. There was no detectable film of algae on these or other stones in the surroundings.

The ovipositor shows no distinctive features. The carina shows fine teeth and has a moderate sclerotisation.

COMPARATIVE NOTES ON *COENAGRIOCNEMIS RUFIPES* AND *C. INSULARIS*

The Mauritian *Coenagriocnemis* spp. also inhabit rocky lotic waters. But compared with *C. reuniensis* their habitats do not have dynamic and extreme floodings, because the island of Mauritius rises to a far lower altitude (827 m) than La Réunion (3069 m).

C. insularis was recorded at forest streams and at one wide rocky river within a forested gorge (Tab. II). Except for single individuals at one locality, it was never recorded at waters in cultivated areas. *C. rufipes* inhabited a wider range of waters (Tab. II) and was the most abundant zygopteran at rocky rivers. At rivers and streams within sugar cane fields and without gallery forest – which were the majority of Mauritian waters – it was also missing.

At shady forest streams, males of *C. insularis* perched in leaves high above the water, preferentially in sun spots. Only in sunshine did individuals come down to

Table II

Localities with records of *Coenagriocnemis insularis* and *C. rufipes* – [x: presence; – s: record of single individuals only. – Names of the localities follow the map „Ile Maurice, Carte générale à 1:100 000, édition 3“ of the I.G.N.-Paris, 1990]

Locality on Mauritius	Date	<i>insularis</i>	<i>rufipes</i>
Stream into the S edge of the reservoir ‚La Nicolière‘ (20°09'40"S, 57°36'44"E), alt. 250 m	5 to 10-IV-1997, 30-III to 17-IV-1998, 30-III-1999	x	x
Moka river at Moka (20°13'07"S, 57°29'37"E), alt. 320 m	13-IV-1998	-	s
Grande Rivière Sud-Est W Beau Champ (20°16'30"S, 57°44'53"E), alt. 20 m	27-III-1997	s	x
Grande Rivière Sud-Est E Olivia (20°17'46"S, 57°44'47"E), alt. 90 m	11-IV-1998, 4-IV-1999	-	s
Black River (Rivière Noire) in the Black River Gorge (20°23'33"S, 57°25'16"E), alt. 100-150 m	14/15-IV-1998, 7 to 15-IV-1999	x	x
Rivière du Poste W Grand Bassin (20°24'32"S, 57°28'29"E), alt. 645 m	12-IV-1999	-	s
Rivière des Anguilles W Bois Cheri (20°24'55"S, 57°30'14"E), alt. 505 m	16-IV-1999	-	x
Ruisseau Marron, stream W Bois Cheri (20°25'08"S, 57°30'10"E), alt. 515 m	16/17-IV-1999	x	x
Rivière Canal, near the road Baie du Cap -Chamarel (20°27'13"S, 57°23'08"E), alt. 210 m	13-IV-1999	-	x

the water, males to a level of 1.5 m above the ground. They approached each other, but did not drive off rivals completely. Male *C. rufipes* were sitting lower, near to the water. Male *C. insularis* perched in leaves, male *C. rufipes* also on stones.

At the open rocky river *C. insularis* was restricted to sites with fallen trees lying in the current. They settled on roots and big branches. In contrast, most *C. rufipes* males perched on rocks, but also on floating fruits and on grass or twigs at the shore. The latter interact with conspecifics while presenting their orange legs, with males in face-to-face up-and-down flights at a distance of ca. 10 cm to each other.

In more than 60 h watching adults of the Mauritian *Coenagriocnemis* spp. in the field I saw no copulation and I have only some observations on oviposition behaviour. Females of both species oviposited alone. A female *C. insularis* was observed while depositing eggs in the wet tissue of a brown leaf of a large herbaceous plant lying in the current. One female of *C. rufipes* was seen ovipositing in the green stem of a small herb. During egg deposition the female submerged completely for 6.32 min. Another *C. rufipes* submerged at a twig. A third female was recorded while sitting on a rock in the current for more than 15 minutes and depositing eggs in a reddish moss which covered the rock surface. Three times females were seen while palpating rock surfaces with their ovipositor briefly for some seconds.

DISCUSSION

The behavioural sequence of *Coenagriocnemis reuniensis* females at water does not show any difference in time and movements from the typical ones reported for Zygoptera species which deposit eggs endophytically (cf. MARTENS, 1992, 1993). I failed to find the eggs in the soft rock, but from observation I can exclude oviposition into plant tissue or onto the rock surface.

C. reuniensis is restricted to running waters of the mountain forests of La Réunion. That part of the island is known for one of the highest rainfalls ever recorded in the world (Takamaka mean 7578 mm yr⁻¹; cf. STARMÜHLNER, 1979). The swift-flowing running waters have rocky beds and their valleys form wide, open corridors in the dense mountain rain forest. During the wet season from December to March the rivers carry a lot of water. When cyclones reach the island there is an extreme water-flow. In other periods the rivers become small rivulets. The species avoids the extreme risk of drift and survives the flood period in the adult stage. However, in the period with low water the habitat offer no good conditions for completing zygopteran life cycles as well: for oviposition there is no plant material available. Water plants are completely missing. Roots of trees have only brief contact with the water, when there is an extreme discharge. Wet driftwood is extremely rare.

C. reuniensis has no morphological adaptation to this special situation. The ovipositor shows no marking differences from other Coenagrionidae. The species seems to be adapted only by choosing the soft and porous volcanic material in the riverbed for oviposition. The use of volcanic material for „endophytic“ oviposition

is exceptional and for Zygoptera unknown until now. All members of the genus *Coenagriocnemis* inhabit rocky lotic waters. And there is a clear trend from inhabiting small forest streams (*C. insularis*) and rivers with roots, driftwood and some aquatic and semiaquatic plants (*C. rufipes*) to rivers without any plant material (*C. reuniensis*). Members of the Hawaiian genus *Megalagrion* inhabit similar habitats (MOORE, 1983), and I suppose that there may be a species which uses the same substrates for oviposition as *C. reuniensis* does.

Oviposition is uniformly in Zygoptera (cf. MARTENS, 1999): (1) The eggs are conical in shape and have no adhering jelly coat. Females (2) oviposit while settled and (3) place their eggs in or among living or dead plant tissue. (4) Incisions in the plant tissue mostly contain single eggs. Up to now only single exceptions are known, e.g. the deposition by egg throwing in *Mecistogaster martinez* (MACHADO & MARTINEZ, 1982; as *M. jocaste*), the dropping of eggs without making incisions, in old *Rhipidolestes hiraoui* (ASAHINA, 1994, cited after CORBET, 1999) or occasionally in *Ceriagrion melanurum* (EDA, 1995), the deposition of several hundreds of eggs into a single long slit of a plant in *Phaon iridipennis* (MILLER, 1985; MILLER & MILLER, 1988) or the oviposition in mud or lava material.

ACKNOWLEDGEMENTS

I would like to thank ADELHEID and ARNE MARTENS for their support in the field (sometimes we called it ‚holidays‘, sometimes only I did). I would also like to thank VIOLA CLAUSNITZER, KLAUS REINHARDT, GÖRAN SAHLÉN and FRANK SUHLING for helpful suggestions to the manuscript.

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