Odonatologica 3 (3): 167-177 *September 1, 1974*

THE REPRODUCTIVE BEHAVIOUR OF *COPERA MARGINIPES* (RAMBUR) AND *C. VITTATA ACUTIMARGO* (KRUGER) (ZYGOPTERA: *PLATYCNEMIDIDAE*)

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Received January 11, 1974/Accepted April 9, 1974

The reproductive behaviour of *Copera marginipes* (Rambur) and *C. vittata acutimargo* (Kruger) was examined in the field. The male establishes a circular territory about a base perch. In *C. marginipes* this perch is defended by the abdomen-raising display. The territory is established by the patrolling, chase and elaborate confrontation-flash displays. The function of the territory, the increasing complexity of these displays, and the bivalency of the flash display, are discussed. Mating occurs outside the territory, and copulation is of long duration. Oviposition is endophytic, in tandem and outside the territory; it occurs at the water's surface.

INTRODUCTION

Previous studies on platycnemidid reproduction consist of brief notes on *Copera marginipes* (FRASER, 1934; MULLER, 1937), detailed analyses on *Platycnemis pennipes* and *P. dealbata* (BUCHHOLTZ, 1956) and *P. latipes* and *P. acutipennis* (HEYMER, 1966, 1967), and brief observations on *P. foliacea* (ASAHINA & EDA, 1956; OBANA, 1968). In view of the poor literature on *Copera*, an investigation on the reproductive behaviour of *Copera marginipes* (Rambur) and *C. vittata acutimargo* (Kruger) was undertaken.

Taxonomic determinations, made from FRASER (1934) and LIEFTINCK (1940), were verified by Dr. M.A. Lieftinck (formerly of the Rijksmuseum van Natuurlijke Historie, Leiden).

All observations were made in the field near Kuala Lumpur, Malaysia using methods described earlier (FURTADO, 1972). On 33 days 500 *marginipes* were observed at four lowland and hill-country streams (Sungei-sungei Chongkok, Ampang and Klang, Selangor and Sungei Tanglir, Pahang), and on four days 80

acutimargo at two hill-country ponds (ponded Sungei Kongsi Lapan, Selangor and Sungei Wang Tangga, Perlis). The population density was 2-24 *marginipes* and 2-50 *acutimargo* per 100 m. of edge. Certain morphological features are relevant in behaviour. Both species are heterochromatic with the males more brightly coloured and possessing creamy white terminal abdominal segments, and with *marginipes* slightly larger than *acutimargo*. The meso- and metathoracic tibiae of both species are dilated being more pronounced in *marginipes*. The male legs are bright orange in *marginipes* and carnelian red in *acutimargo*.

RESULTS

Both *marginipes* and *acutimargo* show the flapping and hovering flight patterns as in coenagrionids (FURTADO, 1972).

Adults rest on a perch with their wings folded over the dorsum, usually facing the shore, and with their body in a horizontal posture. The male alone occupies a base perch (resembling the "settling base" of CORBET, 1962) which consists of a herb, grass or reed leaf, or a twig, and which is located usually in the shade, at pool regions of streams and bays of ponds in *marginipes* and forest pools in *acutimargo*, and at a height of about 30 cm and 100 cm above the water surface in *marginipes* and *acutimargo* respectively. This perch is located over the shore within 100 cm of the shoreline in *marginipes*, and over water within 100 cm as well as over the shore within 60 cm of the shoreline in *acutimargo*. Base perches are located 45-60 cm apart in both species (Fig. 1) with the male resting continuously for as long as 15 minutes on it in *marginipes* and considerably longer in *acutimargo*.

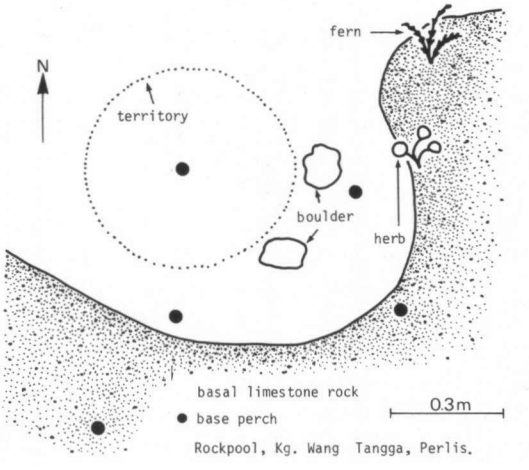

Fig. 1. *Copera vittata acutimargo*: diagrammatic representation of the distribution of base perches at a forest pool (Kampong Wang Tangga, Kaki Bukit, Perlis).

Territorial behaviour

The male establishes a base perch which he maintains by an aggressive and formal abdomen-raising display ("threat display" of FURTADO, 1966) resembling the "threat posture" of MOORE (1960) and the "obelisk posture" of Lieftinck (in CORBET, 1962). This display, initiated when any sudden movement occurs near the perched resident, consists of the resident raising his entire abdomen and exhibiting posteriorly his posterior colours as in coenagrionids (FURTADO, 1972), and terminates when the interference ceases. This display (12 observations) lasts for up to 2 seconds in *marginipes*, and is performed towards moving libellulid dragonflies and conspecific males besides other extraneous movements; it has not been observed in *acutimargo*.

The perch forms the centre of a circular territory maintained by a non-aggressive patrolling display, and defended against intruding conspecific males by the chase and/or the elaborate confrontation-flash aggressive and formal display(s) (Figs. 2 and 3). The territory overlaps up to 50% with each of the adjacent

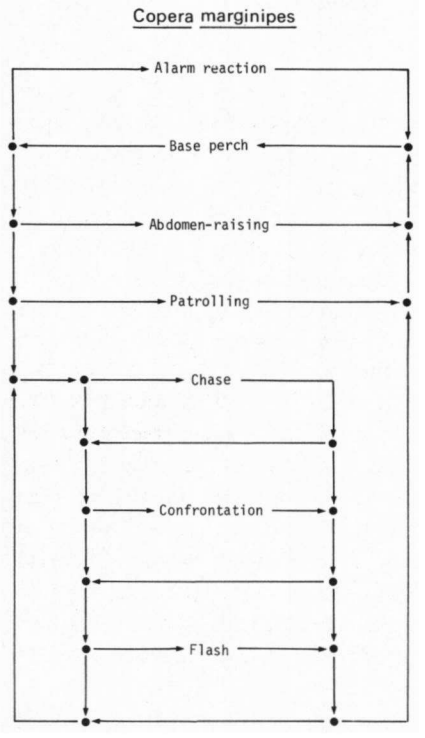

Fig. 2. *Copera marginipes*: Schematic representation of male territorial and non-territorial displays.

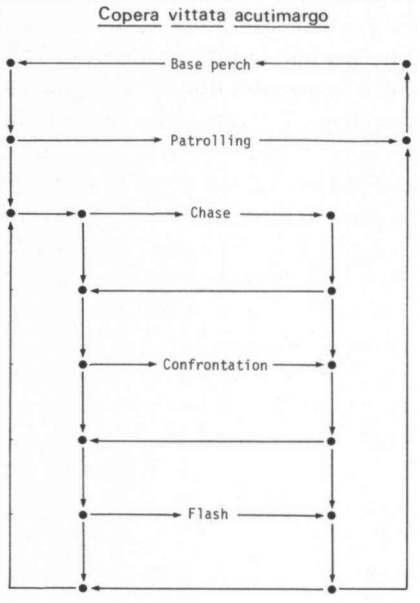

Fig. 3. *Copera vittata acutimargo*: Schematic representation of male territorial displays.

territories, and measures 45-120 cm in diameter in *marginipes* and 50-60 cm in *acutimargo*. The patrolling display ("territorial patrol" of FURTADO, 1966) resembles the "fluttering flight" of LIEFTINCK (1934, 1955), the "inspection flight" of ZAHNER (1960), and the "flight no reason" and "patrol flight" of BICK & BICK (1965, 1971), and occurs irregularly. In performing it the resident leaves his perch, flies to the edge of his territory on one side of his perch, and hovers for a few moments before returning. The patrolling display (six observations in each species) occurs occasionally and lasts a few seconds. In *marginipes* the male hovers frequently between forward flights.

The chase display resembling the "flight toward" of BICK & BICK (1965) is simple, and is initiated when an intruder enters the resident's territory and approaches his perch. In this display, the resident leaves his perch and pursues the intruder to the boundary of his territory as in coenagrionids (FURTADO, 1972), and returns when the intruder withdraws. The chase display lasts several seconds in *marginipes* (six observations) and 1-2 seconds in *acutimargo* (several observations). In *marginipes* it is performed also towards intruding males of *Trithemis aurora* (Burmeister) and *Orthetrum chrysis* (Selys). In *acutimargo* it sometimes involves a pursuit well beyond the territorial boundary over a distance of up to 1 m from the base perch.

The elaborate confrontation-flash display ("ritualised display" of FURTADO, 1966) is complex consisting of the alternate and repetitive performance of the

confrontation and flash display and is initiated when an intruder enters the resident's territory and approaches his perch. It consists of the resident leaving his perch, flying towards the intruder and facing him. It begins with a confrontation display initiated by the resident and it terminates usually when the intruder withdraws after a flash display, whereupon the resident returns to his perch. The elaborate display in *marginipes* (several observations) lasts several seconds, and is performed when the intruder persists in the territory after the resident's abdomen raising or chase displays. In *acutimargo* (three observations) this display lasts 2-3 seconds and involves the males moving over a horizontal area of a square metre and rising up to a level of a metre above the water. The confrontation display which resembles the "dual flight" of JACOBS (1955), the "threat display" of JOHNSON (1962) and the "frontal threat" of PAJUNEN (1966), consists of the males hovering facing each other for several seconds up to 10 cm apart. In *marginipes* the males are 3-6 cm apart whereas in *acutimargo* they are 5-10 cm apart. This display is succeeded by the flash display when one male (initially the resident) lunges forward. The flash display consists of one male lunging forward and displaying anteriorly his tibial colours, while the other simultaneously retreats backward. In *marginipes* the advancing male lunges 10-15 cm while the retreating male withdraws 20-30 cm; whereas in *acutimargo* both the advancing and retreating males move over a distance of 15 cm. This display lasts a few moments and is performed alternately by the males, although interspersed with the confrontation display which is initiated when the retreating male hovers to face the advancing one.

When sudden extraneous movements occur in his vicinity, the perched resident performs the alarm reaction (cf. CORBET, 1962) moving suddenly and rapidly backwards over 10-15 cm, and hovering for several seconds before returning. In *marginipes* this display lasts up to 3 minutes (20 observations), and in three observations was followed by the patrolling display.

Mating behaviour

Courtship behaviour and the formation of the tandem position were not observed. The male and female fly in tandem to a copulation site which is a grass or shrub leaf in a position similar to the base perch. The male settles on this site with the female suspended vertically below him. He then initiates precopulation rhythms by alternately arching and relaxing his entire abdomen at the slow rate of one cycle every 2-3 seconds, during which his wings are folded (Fig. 4). These bends are shallow and dorsad, and the female responds by alternately and rhythmically flexing and relaxing her abdomen with her rhythm lagging behind his. After a period of slow rhythms, the rate is gradually increased to one cycle every 1-2 seconds. During these fast rhythms, the male's abdomen is acutely arched and his wings are flicked and flapped, while the female's abdomen is also flexed

acutely and ventrally. After a period of these fast rhythms, the male initiates very slow rhythms with a pause varying from a few seconds to a few minutes between each movement. These very slow rhythms consist of the male arching his abdomen acutely and dorsally, holding the arched pose for several seconds while simultaneously flapping his wings, and then relaxing his abdomen. The female responds to the arching by bending her abdomen acutely, so that her ovipositor touches her legs, and then pushing her ovipositor forward between her legs and below the male's abdomen to his accessory genitalia. In doing so, the female rotates her entire body downward and forward using the male's grip on her thorax as a pivot. She locates the male's accessory genitalia with her ovi-

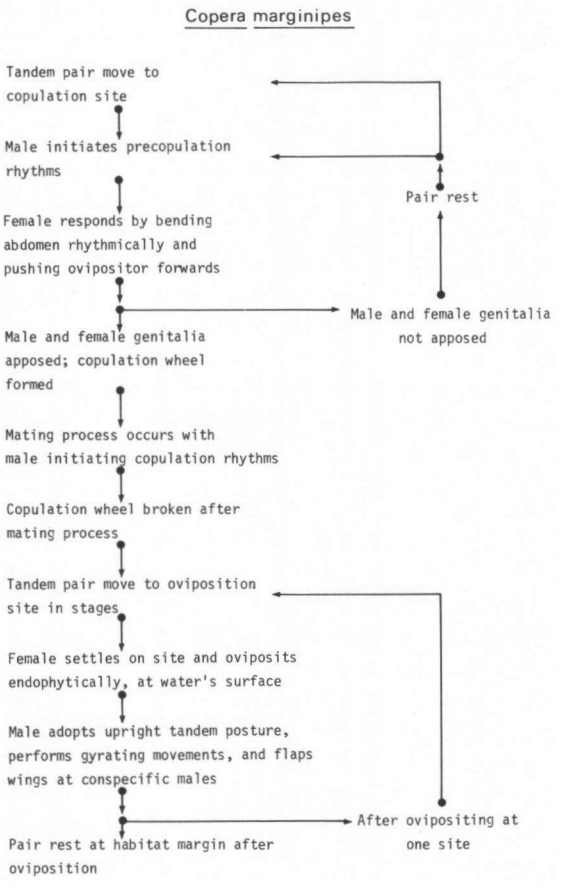

Fig. 4. *Copera marginipes*: Schematic representation of mating and oviposition behaviour.

positor, and the copulation wheel is formed by the apposition of the two sets of genitalia.

In *marginipes*, one pair was unable to form the copulation wheel even after two attempts at the site. The pair then moved to a new site within 30 cm of the previous one, where the wheel position was formed within 10 minutes after an initial rest of two minutes.

Copulation occurs at the copulation site immediately after formation of the copulation wheel. During copulation the pair exhibits distinct rhythms in which the male alternately flexes his posterior abdomen, and depresses his second abdominal segment ventrally. These rhythms initially occur at the rate of one cycle every second, but they soon increase to two cycles every second, and then gradually decrease towards the end of copulation. The wheel position is broken after copulation and the pair then rests in tandem at the site. In *marginipes* (five observations) copulation lasts at least 40 minutes with initial rhythms lasting 5 minutes; and the pair rest for 1-3 seconds after copulation.

Oviposition behaviour

After mating the male and female fly in tandem to an oviposition site which is a rotting leaf, twig, rootlet or stem of an aquatic herb or grass, situated in the surface waters at a biotope similar to that near the base perch (Figs. 4 and 5). The female initiates this flight with the male accompanying her. This flight may occur in stages, alternating with the female resting on a perch and the male adopting an upright tandem posture. In *marginipes* the pair rests for up to 10 minutes in between movements to the oviposition site. The female settles on the oviposition site and holds her abdomen horizontally; she may then raise her

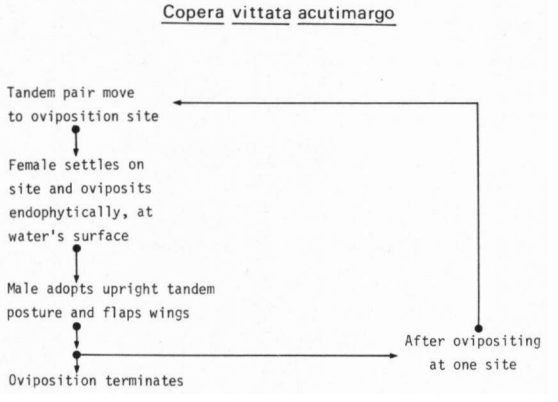

Fig. 5. *Copera vittata acutimargo*: Schematic representation of oviposition behaviour.

abdomen irregularly through 5-20°. Meanwhile, the male adopts the upright tandem posture with his body vertical standing on the tip of his abdomen (his anal appendages still interlocked with the female's thorax). In assuming this posture, the male usually folds his wings in *marginipes* and vibrates his wings continuously in the outstretched position in *acutimargo*. Also in *marginipes*, but not in *acutimargo*, the male revolves his body by successive jerks sidewards, backwards, sidewards and forwards using his anal grip on the female's thorax as a pivot, at a rate of a cycle every 2 seconds, encompassing an angle of 5-20° at the pivot. In *marginipes* the male occasionally flaps and vibrates his wings laterally in the outstretched position. These vibrations are continuous when the pair is in an open and well-lighted area, or occur when a conspecific male or an odonate flies, or any extraneous movement persists, near the pair.

The female then arches her abdomen acutely dorsad so that her ovipositor contacts the site immediately behind her legs. She oviposits endophytically, and moves the abdomen gradually posteriorward with each successive incision so that the arch of her abdomen becomes shallower. She oviposits continuously or discontinuously at one site, and at several sites close together. In both species, oviposition is at the water's surface with only her posterior abdomen, ovipositor and tarsi immersed. During oviposition the male performs the upright tandem posture. In *marginipes* (35 observations) oviposition is discontinuous at one site and is composed of ovipositioning acts of 1-2 minutes duration alternating with rests of 30-60 seconds duration. It lasts 2-5 minutes at one site; and oviposition occurs at least at four sites within an area of 1,500 cm^2 with a total duration of 15-90 minutes. In *acutimargo* (2 observations) oviposition is continuous and lasts for several seconds at one site, before the female initiates movements to a new site within 30 cm of the previous one, and total oviposition lasts 3 minutes. After oviposition, the pair flies to a marginal perch on which the male and/or the female settle(s). In *marginipes*, the female occasionally ceases to oviposit after 5-10 seconds presumably because the site is unsuitable; she then resumes her resting position with abdomen horizontal, and initiates movement to another site.

DISCUSSION

The territorial behaviour of *C. marginipes* and *C. acutimargo* is intermale, and uses non-aggressive and aggressive (resembling "reproductive fighting" of TINBERGEN, 1953) displays both of which are formal and not harmful physically. The non-aggressive patrolling display is probably a form of exploratory behaviour regarding the base perch and territory. The aggressive abdomen-raising display (using posterior abdominal colours) of *C. marginipes* defends only the base perch. The aggressive chase and elaborate displays defend both the base perch and territory. The patrolling, abdomen-raising, chase, confrontation, flash and

elaborate displays are increasingly complex. The confrontation, flash and elaborate displays are restricted to conspecific encounters in comparison to the abdomen-raising and chase displays. These displays are somewhat similar to those in coenagrionids (FURTADO, 1972).

The use of leg colours and structures in the flash display in both species is more spectacular in *C. marginipes* because of greater tibial dilation. Although this has been noted previously in some platycnemidids (HEYMER, 1966), it has been reported functionally important in courtship (Eda in CORBET, 1962) and copulation (BUCHHOLTZ, 1956). The flash display may thus have a bivalent function, and complex aggressive displays may be associated with pronounced sexual heterochromatism and dimorphism.

Territoriality thus probably ensures that aggressive and non-aggressive displays primarily disperse males, necessarily fit males, by competition at the habitat. This dispersion probably then ensures the successful meeting of the sexes by the possible occurrence of courtship within the territory, although this was not verified. Territoriality certainly does not ensure successful mating and oviposition since these occur outside the territory. Thus, territoriality is of limited and short-term adaptive value to species survival as in coenagrionids (FURTADO, 1972). Differences in territorial size and behaviour in the two species are due probably to differences in adult size, movement perception (cf. MOORE, 1953, 1960) and ecology.

The alarm reaction of *C. marginipes* is non-territorial and thus differs functionally from the above displays in ensuring the individual's survival. It is probably an overt expression of a tendency to flee, which exists alongside and in conflict with the tendency for aggression in territoriality.

The mating behaviour of *C. marginipes* is generally similar to that of *Platycnemis pennipes* (BUCHHOLTZ, 1956; HEYMER, 1966) and *P. latipes* and *P. acutipennis* (HEYMER, 1966) differing only in details. The long duration of copulation is also similar in these species.

The endophytic oviposition in the two species at the water's surface and at more than one site is similar to that in *P. pennipes* and *P. dealbata* (BUCHHOLTZ, 1956) and *P. latipes* and *P. acutipennis* (HEYMER, 1966), and dissimilar to the underwater oviposition in *P. foliacea* (OBANA, 1968). However, it is of long duration and discontinuous in *C. marginipes* which corresponds to that in *Platycnemis* species, and of short duration and continuous in *C. acutimargo*. The former oviposition behaviour may be due to greater interferences at an open habitat, the latter to less interference at a sheltered forest habitat.

The tandem flight to the oviposition site may be initiated by an attraction to a reflective surface (MULLER, 1937). Although the female initiates oviposition, the male accompaniment probably (1) reduces interferences especially from conspecific males by both his upright tandem posture and wing flapping which somewhat resemble the aggressive territorial displays as in coenagrionids

(FURTADO, 1972), and (2) stimulates the female to initiate and complete a successful oviposition by both his tandem posture and revolving movements. The upright tandem posture thus serves to defend and stimulate the ovipositing female and, though partly aggressive, this display is not territorial. Although the oviposition site is outside the territory, it is identical in structure to the area adjacent to the base perch and to the larval biotope (FURTADO, 1966, 1969).

ACKNOWLEDGEMENTS

This work was performed during the tenure of a tutorship award in Zoology at and with the financial assistance of the University of Malaya. I am indebted to the staff of the School of Biological Sciences for their assistance, particularly to Dr. J.A. BULLOCK for his criticism and to Dr. G.H. BICK (St. Mary's College, Notre Dame) for criticisms and literature.

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