Odonatologica 27(2): 259-265 *June 1, 1998*

ON THE BIOLOGY OF THE DAMSELFLY *EUPHAEA AMEEKA* VAN TOL & NORMA-RASHID IN BORNEO (ZYGOPTERA: EUPHAEIDAE)*

D. J. THOMPSON
Population Biology Research Group, School of Biological Sciences (Nicholson Building), University of Liverpool, P. O. Box 147, Liverpool, L69 3BX, United Kingdom

Received November 18, 1996 / Reviewed and Accepted February 5, 1997

The habitat and the territorial and reproductive behaviours of this recently discovered Bornean euphaeid damselfly are described. It breeds in narrow shady streams in lowland forest in northern Borneo. Territories are defended vigorously against conspecific males. Some fights take the form of head to head contests during which the combatants can fly high into the forest canopy. Males show considerable site tenacity and return day after day to the same small section of stream. Females climb underwater down protruding branches to oviposit into decaying twigs or leaves. Males remain perched above the oviposition site during the early part of the oviposition bout, but increasingly towards the end, return regularly to their preferred territorial perches.

INTRODUCTION

Euphaea ameeka Van Tol & Norma-Rashid is the most recent of the eight euphaeid species (6 *Euphaea*, 2 *Dysphaea*) described from Borneo (VAN TOL & NORMA-RASHID, 1995). It most closely resembles *E. impar* Selys, but the hind wing of *ameeka* is hyaline, whereas the distal one-third or two-fifths of the hind wing of *impar* is opaque brown. Nothing has been published about the biology of the species other than that the holotype specimen was collected from a stream under a closed canopy.

It follows that nothing has so far been published about the behaviour or reproductive biology of the species, or indeed, of any other species of *Euphaea*. Detailed descriptions of the reproductive biology of any euphaeid species are scarce.

* This paper is dedicated to the memory of Peter M i l l e r, an inspirational colleague who I know would have enjoyed watching *Euphaea ameeka* in a Bornean rain forest.

The aim of the present work is to describe in more detail the habitat, behaviour and reproductive biology of *E. ameeka*.

METHODS

All of the results reported below and all of the behavioural observations were made on marked individuals. A unique number was marked on the left forewing in waterproof permanent ink (Edding 780), a technique repeatedly shown to be harmless to damselflies (BANKS & THOMPSON, 1985a, 1985b; THOMPSON, 1990). The forewing lengths of most individuals were measured on capture using dial callipers (to 0.05 mm). Animals were watched using close-focussing binoculars which made it possible to read the number on the wing. Observations were made by several observers (typically six) along a 60 m length of the stream and formed part of a project on the odonates of Brunei. The detailed study was made daily between 14 September and 27 September 1992 and then less frequently (because of increased stream flow and depth – see below) up to 12 October 1992. Data were collected on *Euphaea ameeka* and *Vestalis amabilis* (reported elsewhere). A total of thirteen animals was marked, eleven males and two females. An unknown but very small number of males remained unmarked. These were males that visited the stream but which were not able to establish a territory. At most two unmarked females were also seen.

The stream was watched from around 0830 (before the onset of odonate activity) to when the daily rains started, usually around 1500 (when odonate activity had typically ceased in any case). In terms of the prevailing seasonal weather conditions, the study period corresponded with the onset of the rainy season.

STUDY SITE AND HABITAT

The study was made in Brunei. The study site was in the forests around the upper Belait river (Ulu Belait) in the Sungai Ingai Conservation Area within the Labi Hills Forest Reserve. The area in the vicinity of the Sungai Topi/Sungai Ingai in Ulu Belait is the only locality in Brunei where four of Brunei's six forest types (alluvial (empran), heath (kerangas), peat swamp (hutan payah) and mixed dipterocarp (meranti) forests) occur very close to one another in a more or less undisturbed condition. The principal study site was a stream which runs into the Ingai river, where it crosses the trail that follows the river, on the eastern side (4°9'21"N, 114°42'56"E).

The stream was situated in alluvial forest and had a highly variable water level. During the course of the study period, it was typically 15 cm deep, though following a period of particularly heavy rain the depth rose to 5 m over 48 h. There was a closed canopy over most of the study site, though this was broken in places where the trees had fallen most recently. The odonates most often seen at the site were *Vestalis amabilis* Lieftinck, *Libellago aurantiaca* Selys, *L. hyalina* (Selys), *L. l. lineata* (Burmeister), *Sundacypha* sp. nov., *Rhinagrion borneense* (Selys) and *Archibasis viola* Lieftinck. *Euphaea ameeka* was also seen, though less frequently, on narrow streams in tropical heath forest. The odonates most associated with it in this habitat were *Devadatta p. podolestoides* Laidlaw, *Prosopticta feronia* Lieftinck, *Prodasineura dorsalis* (Selys), *Coeliccia macrostigma* Laidlaw and *Amphicnemis erminea* Lieftinck. A.G. Orr (pers. comm.) has also recorded *Euphaea ameeka* in Brunei from streams bordered with the rheophytic palm *Pinanga tenella* in mixed dipterocarp forest. Thus the habitat of this species can best be described as narrow

shady streams in lowland forest in northern Borneo.

No data are available on seasonality in *E. ameeka*. Mature adults were present in the study area throughout the study period and one individual (female) was seen to complete emergence from the study site. She emerged shortly before midday on 17 September.

TERRITORIALITY AND FIGHTING BEHAVIOUR

The study length of stream was surveyed, mapped and divided into 5m by 5m grid cells. All records of *Euphaea ameeka* taken referred to particular grid cells and sometimes to prominent features within particular cells (partially-submerged branches etc.). Males invariably perch low against the water on protruding rocks or on fallen twigs or branches. Unlike most damselflies they often rest with their wings partially open, particularly when in sunlight. Males of *E. ameeka* are territorial and will fight for ownership of territories. We attempted to record all fights between males in the study area and note the duration of the fight, the identities of the combatants and whether the winner was the resident or the intruder. Before going on to discuss the fighting behaviour it is worth noting some problems in obtaining and intepreting the data. It was not easy to record all of the fights in their entirety despite the high ratio of observers to fights on the site. Fights in which unmarked damselflies were involved are generally under recorded because unmarked males that lost fights tended to disappear from the study area and could not then be caught. Marked males that lost fights tended to return to a perch within the study area and could be identified. Thus fights between two marked (and therefore well-established males) are over recorded compared with the total number of fights that occurred. The final problem and that which prevents detailed analysis of the fighting behaviour is that many of the fights occurred between the same individuals and even on the same day, and since the total number of individuals in the study area was small, there is a clear problem of pseudoreplication.

Figure 1 shows the distribution of fights throughout the day. There is a small peak in fights in the morning when animals first arrive at the study site, then a relatively quiet pe-

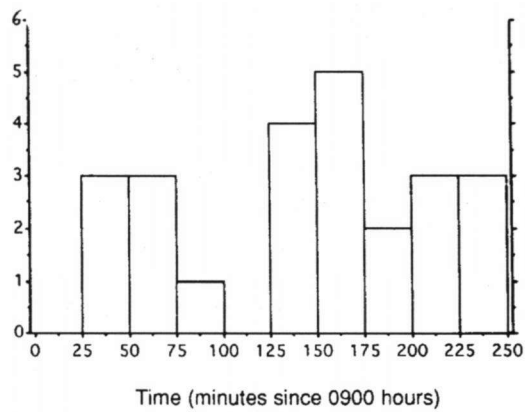

Fig. 1. Distribution of fight times during the day. Those in the early part of the day were of significantly shorter duration than those around midday (see text).

riod in which there are few fights followed by a lengthier period of around two and a half hours in which most fights occur. There is a significant difference between the lengths of fights early in the morning and those distributed around midday; those in the morning are shorter ($\underline{t} = 2.05$; $\underline{P} < 0.05$). The likely explanation is that early morning fights establish territory ownership when there are no females present and there are no immediate rewards, and thus the resource of a territory is not so valuable. It is, however, of some value to have a territory early in the day because ownership of a territory is likely to convey an advantage in subsequent more important fights for territories around principal female arrival times.

In fact territory owners won significantly more fights than intruders. Of the 29 fights for which data on winners and losers are available, 23 were won by residents. Of the 6 won by intruders, 4 (2 pairs) were actually instances of defeat by the original resident followed by subsequent victory a short time later (as an intruder). There is clearly a good case for disregarding these fights as intruder wins in which case the long-term takeover of territories occurred on just two occasions.

Later in the day it is more important to secure a territory during the time period when females visit the study site (between 1117 and 1437 h; n = 4). The resource becomes much more valuable and fights become more intense. Two basic types of fight were observed. The first simply involved one male chasing another. This type of fight was commonest and took less time the second type of fight. It was, nevertheless, an intense form of fighting, much more prolonged than the fights between, for example, coenagrionids of the same size. The second type of fight involved the two males facing one another and flying higher and higher in a head to head position. It was unclear whether they actually butted one another. Very often both males would disappear out of site into the canopy. These fights lasted longer than the chasing kind of fight and occurred only around midday, not during the early morning peak of fighting activity.

SITE TENACITY

Table I

First and last dates on which individuals that appeared at the study site for five or more days were seen, and the % of those days that they were present at the site. Between 25 and 27/IX the stream rose by 15 m, bringing a premature end to the detailed study. – Number 9 was also seen on 2/X when the stream level had dropped to its pervious level

Code no.	First date seen	Last date seen	% days present
5	17/9	25/9	87.5
6	19/9	25/9	85.7
7	19/9	25/9	100
8	19/9	24/9	67
9	21/9	25/9*	80
10	21/9	25/9	100

Table I shows the relationship between the percentage of days that the individual was present and the minimum length of the adult life for those individuals that were present in the study area for a span of five or more days. It is clear from this table that those males that established themselves in the study area showed considerable site tenacity. Number 8, whose percentage is the lowest of those given in Table I, occupied a position on the edge of the study area and could have been present on the stream close to the site on the days when it did not appear on site.

Table II

The occupancy of sites (5m x 5m grid cells) within the study area by those individuals that spent 5 or more days present

Code no.	Sites occupied as a % of those available
5	28.6
6	38.1
7	23.8
8	19.0
9	19.0
10	28.6

As well as displaying considerably tenacity for the study area those males that were regularly present also displayed tenacity for particular territories. Table II shows the number of available grid squares in which each individual held a territory as a percentage of those that it could have been recorded in over the whole time it visited the study area. Individuals tended to occur over a relatively small part of the study area. Even this table does not tell the whole story in that, for example, number 8 (referred to above) visited about one fifth of the study area but spent over 95% of its time in the two grid cells that represented the northern extremity of the study area. On one day number 7 remained on the same perch for 136 min and most of its total time in the study area was spent within the same grid cell. It was when individuals moved from their "usual" locations that most of the fights referred to above occurred.

REPRODUCTIVE BEHAVIOUR

Only three matings were seen from the onset of copulation (wheel) to the end of oviposition. All three matings were obtained by males that had previously been territory owners at the site. The mean length of copulation was 165 s (range 105--202 s). After copulation the pair fly off in tandem. Once they have selected an oviposition site, they split and the female walks under water along a narrow branch or twig. Oviposition occurs either at the base of these twigs or in dead leaves attached to them in areas of the stream out of the main flow. The male remains perched above the oviposition site for most of the oviposition period but does fly off from time to time, particularly towards the end of the oviposition bout, to his usual territorial perch. Table III shows one particular mating and oviposition sequence that was recorded in detail.

Of the mating systems published for calopterygoids, that of *E. ameeka* most closely resembles the *Hetaerina* type (e.g. *H. vulnerata*, ALCOCK, 1982) rather than the *Calopteryx* type (e.g. *C. maculata*, WAAGE, 1973).

Table III
Timetable of mating and oviposition in *Euphaea ameeka*, an example

Time (h min s)	Behaviour	Duration
14 14 45	Male grabbed female and took her into wheel position.	3 min 22s
14 18 07	Pair broke from wheel and flew off in tandem.	1 min 33s
14 19 40	Pair landed at oviposition site on the dry portion of a partially submerged twig.	15s
14 19 55	Pair split and female walked down the twig into the water; male remained on the twig above the water surface.	2 min 20s
14 22 15	Female climbed back up the twig and faced the male.	5s
14 22 20	Female went back down the twig underwater and oviposited. It was not clear if she was ovipositing in the base of the twig or in rotten vegetation attached to it. Male remained perched on twig.	37 min 42s
14 40 27	Male left the twig and returned to perch on territory.	18 min 7s
14 42 00	Male returned to twig above ovipositing female.	1 min 33s
14 49 42	Male left the twig and returned to perch on territory.	7 min 42s
15 03 04	Male returned to twig above ovipositing female.	13 min 22 s
15 05 02	Female climbed out of the water; male and female flew off separately.	1 min 58 s
15 15 (approximately)	Male seen again on familiar perch on territory.	

GENERAL COMMENTS

The *Euphaea impar* group consists of three species, namely *E. impar, E. cora* Ris and *E. ameeka* (VAN TOL & NORMA-RASHID, 1995). A. G. Orr (pers. comm.) has noted that *E. impar* and *E. ameeka* can occur in different parts of the same stream in Brunei, but show habitat segregation in these streams. VAN TOL & NORMA-RASHID (1995) observed no intermediate forms despite the sympatric occurrence of the two species. As they pointed out one might expect that isolation of calopterygoid species would be enforced as much by the pre-mating phase of reproductive behaviour as by some feature of the secondary genitalia. They also give a comparison of the structures of the two species, which are quite similar. What is surprising is that no elaborate courtship was observed in the pre-mating phase of reproductive behaviour. The only semblance of courtship behaviour noted by one observer in the present study was at one point before mating began male and female were perched head for a few seconds on a branch close to the water surface.

On the basis of the forewing measurements of the 11 males and 2 females that were measured, there is no evidence for sexual size dimorphism in *E. ameeka*; males 26.73 mm, females 26.65 mm, $\underline{t} = 0.12$, $\underline{P} = 0.92$.

ACKNOWLEDGEMENTS

I am grateful to Raleigh International for the provision of a travel bursary that enabled me to get to Brunei, and for providing many excellent volunteer field assistants. JAN VAN TOL identified all the Brunei odonate species referred to in this paper and recognized that *E. ameeka* was a new species. In Brunei BERT ORR introduced me first hand to the local odonate fauna.

REFERENCES

ALCOCK, J., 1982. Post-copulatory mate guarding by males of the damselfly Hetaerina vulnerata Selys (Odonata: Calopterygidae). *Anim. Behav.* 30: 99-107.

BANKS, M.J. & D.J. THOMPSON, 1985a. Emergence, longevity and breeding area fidelity in Coenagrion puella (L.). *Odonatologica* 14: 279-286.

BANKS, M.J & D.J. THOMPSON, 1985b. Lifetime mating success in the damselfly Coenagrion puella. *Anim. Behav.* 33: 1175-1183.

THOMPSON, D.J.,1990. On the biology of the damselfly Nososticta kalumburu Watson & Theischinger (Zygoptera: Protoneuridae). *Biol. J. Linn. Soc.* 40: 347-356.

THOMPSON, D.J. & J. VAN TOL, 1993. Damselflies and dragonflies from four forest types in Brunei. *Brunei Mus. J.* 8: 57-72.

VAN TOL, J. & Y. NORMA-RASHID, 1995. The genus Euphaea Rambur in Borneo (Odonata: Euphaeidae). *Tijdschr. Ent.* 138: 131-141.

WAAGE, J.K., 1973. Reproductive behaviour and its relation to territory in Calopteryx maculata (Beauvois) (Odonata: Calopterygidae). *Behaviour* 47: 240-256.