

ON THE BIOLOGY OF THE DAMSELFLY *VESTALIS AMABILIS* LIEFTINCK (ODONATA: CALOPTERYGIDAE) IN BORNEO

David J. Thompson

Population Biology Research Group, School of Biological Sciences,
Nicholson Building, University of Liverpool,
P. O. Box 147, Liverpool L69 3BX, U.K.

Received 27 October 1999, revised 28 February 2000; accepted 01 March 2000.

Key words: Borneo; Odonata; reproductive behaviour; territory; *Vestalis amabilis*.

Abstract

The habitat, territorial and reproductive behaviour of the Bornean calopterygid damselfly *Vestalis amabilis* are described. Males are territorial and will remain at the same site defending a territory for up to three weeks. Territories take the form of sun flecks whose physical location changes slowly throughout the day as the sun moves across the sky. There is a considerable amount of fighting between males, ranging from simple, short chases to more extensive escalated contests. Longer contests are thought to be brought about due to confusion over residency as the physical location of the territory changes. Courtship is brief and simple, copulation duration is around 2 minutes and females oviposit alone while being non-contact guarded by the male. Oviposition takes place in dead leaves, usually over about 30 minutes during which time the pair is harassed by other males. Matings are infrequent and females prospect either the territories or the territory owners before accepting courting males, resulting in more copulations later in the day.

Introduction

Vestalis amabilis Lieftinck was first described in Lieftinck's (1965) review of the so-called *Vestalis amoena* Sélys group. Until Lieftinck's paper the "Vestalis complex" of the Calopterygidae was divided into three genera, *Vestalis* Sélys (1853), *Vestinus* Kennedy (1920) and *Vestalaria* May (1935). Lieftinck, who was more familiar with the group than either Kennedy or May, found that some of the characters, which defined *Vestinus*, were almost as unstable as those separating the three existing vestaline genera. In view of this he found little justification in retaining generic or sub-generic groupings within the basic genus *Vestalis*. Within the taxon *Vestalis amoena* (which formerly occurred within the *Vestinus* group) he redescribed the type species *V. amoena* (the most widely distributed) and defined six new species, *amethystina* (from Malaya and Sumatra), *amaryllis*, *amabilis*, *amnicola*, *atropa* and *anacolosa* (all from Borneo).

Lieftinck pointed out that these species are superficially very similar. They are all more or less the same size, with wings that are uniformly tinted with a purplish

iridescence, and the sexes are similar. All were described as shade-loving jungle insects that breed in small streams and brooks.

The aim of the present paper is to describe some aspects of the biology of one member of this complex, *Vestalis amabilis*, with particular reference to its territorial and reproductive behaviour, and to draw comparisons with other calopterygids.

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 paya) 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, which was between 3 and 5 m wide, 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 rivers and streams of alluvial forests are characterised by the many fallen trees that cross their courses. The force of the water in periods of flood meant that there were more gaps in the canopy around the streams of the forest than elsewhere. The odonates most often seen at the site were *Euphaea ameeke* van Tol & Norma-Rashid, *Libellago aurantiaca* Séllys, *L. hyalina* (Séllys), *L. l. lineata* (Burmeister), *Sundacypha* sp. nov., *Rhinagrion borneense* (Séllys) and *Archibasis viola* Lieftinck. *Vestalis amabilis* 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, *Prososticta feronia* Lieftinck, *Prodasineura dorsalis* (Séllys), *Coeliccia macrostigma* Laidlaw, *Amphicnemis erminea* Lieftinck and *Euphaea ameeke*. A.G. Orr (pers. comm.) has recorded this species from twelve other locations in Brunei. As well as the streams in alluvial and heath forest recorded in the present study he has also recorded it in small, sluggish streams in mixed dipterocarp forest. Thus the habitat of this species can best be described as narrow shady streams in lowland forest in northern Borneo.

Methods

The section of stream, which formed the study site, was mapped and divided into 22 sections in order to aid recording. The centre of the site was the place where a path, which ran more or less parallel with the Sungai Ingai, crossed the study stream.

All of the results reported below and all of the behavioural observations were made on marked individuals. A unique number was written on the left forewing in waterproof

permanent ink (Edding 780), a technique repeatedly shown to be harmless to damselflies (Banks & Thompson, 1985a, b; Thompson, 1990, 1998). The forewing lengths of most individuals were measured on capture using dial callipers (to 0.05 mm). Animals were watched using close-focusing binoculars which made it possible to read the number on the wing. Observations were made by several observers (typically six) along an approximately 60m length of the stream and formed part of a project on the odonates of Brunei (see Thompson & van Tol, 1993). The detailed study was made daily between 14 September and 27 September 1992 and then less frequently (because of increased stream flow and depth) up to 12 October 1992. Data were collected on *Vestalis amabilis* and *Euphaea ameeka* (see Thompson, 1998). A total of 98 animals was marked, 43 males and 55 females. 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. Any individuals encountered in the forest within 1 km of the study site were also captured, measured and marked.

The specific observations made were on the location and behaviour of marked individuals, particularly in relation to same sex encounters and reproductive behaviour.

Results

General Observations

From Liefertinck's (1965) description of the *Vestalis amoena* group and from the site description above it would appear that *Vestalis amabilis* is a shade-loving species because it occurs by heavily shaded streams in primary forest. However, that would not be the full story. Almost invariably when individuals were encountered in the forest away from the study site, they would be aggregated in sun flecks created by gaps in the canopy. These may either be basking or feeding stations. Both sexes were found at these sun flecks. At the study site itself most activity was centred around gaps in the canopy created by fallen trees. As the sun moved across the sky so the physical location of the sun flecks would change and the movement of the damselflies would mirror this. Sun flecks were defendable locations whose physical position changed throughout the day. A walk along the stream would always reveal that males could be found only in sun flecks. *Vestalis amabilis* is then a sun-loving species!

Vestalis amabilis is sexually monomorphic for forewing length (mean male length 32.65 mm \pm 1.31 (standard deviation), n = 43; mean female length 32.54 \pm 1.23, n = 47; t = 0.41, P = 0.68).

During the course of the study the deaths of three individuals was noted. One female was eaten by a fish; one of the established territorial males on the study site (no. 12) was taken by a lizard as it rested on one of its familiar perches on a branch over the stream. A third body was seen being carried up a tree trunk by ants, cause of death unknown.

Territoriality and site fidelity

Table 1 shows the distribution of records of those individual males that were recorded on the site greater than ten times. In order to be recorded a male would need to have changed perch. This could be simply relocating to another perch or it could be due to aggressive behaviour towards or from another male, or courtship behaviour towards a female. Of the fourteen individuals that appear in this table, ten were probably present on site at the onset of the study. (Four of these ten were marked on the second day as we concentrated our efforts in marking at the eastern end of the site on the first day). Of these ten, one presumably died between the 17th and 18th of September (no. 7) and another (no. 31) had an unusual distribution of records in that although it lived for at least 12 days as a mature adult, it spent only four of them at the study site; presumably it spent the rest of its time on territory elsewhere along the stream. Figure 1 shows the combined frequency distribution of the records of the remaining eight individuals along the stream. The abscissa represents the stream length as if it were a linear stream with 1 representing the western end and 22 the eastern end. Most activity was concentrated between sections 6 and 11, which was the region beneath by far the two largest gaps in the canopy. Other sun flecks centred at sections 1, 14, 16, 18 and 21. Also marked on Figure 1 are the code numbers of the males for whom 20% or more of their records derive from the marked sections, effectively their centres of activity. This figure, together with Table 1, shows that the males present throughout the major part of the study displayed considerable site fidelity.

Number 8 was restricted to the western end of the site and made infrequent visits to the rest of the site. In fact the centre of its range lay outside the study area. Numbers 9 and 10 provided the most records of all individuals marked. Number 10 was generally found west of 9, and their areas of overlap reflected changes in the exact position on the ground of the two major sun flecks as the sun moved across the sky. Numbers 9, 11 and 30 shared the same modal location, but at different times and 11 was generally found east of 9. Number 30 displayed a bimodal distribution with its easterly mode overlapping with number 34. Number 37 occurred at the eastern end of the site.

Those marked individuals that appeared at the site fewer than ten times were marked at sun flecks in the forest and not seen on site, or were unsuccessful in establishing a territory on site, or established territory towards the premature end of the study brought about by flooding. Following three days in which there were no marked animals at the site, two of the original territory owners returned, nos. 9 and 11, but all of the other sun flecks were occupied by males not previously seen on the site. Curiously, two of the females that appeared in the post flood period were marked on the first day of the study and had not been seen since.

Fighting

Figure 2 shows the distribution of fight durations recorded throughout the study. The modal category is between 10 and 20 s though it is likely that some shorter fights will have been missed, further skewing the shape of the distribution. Most fights were relatively short and involved the territory owner chasing an intruder from the territory

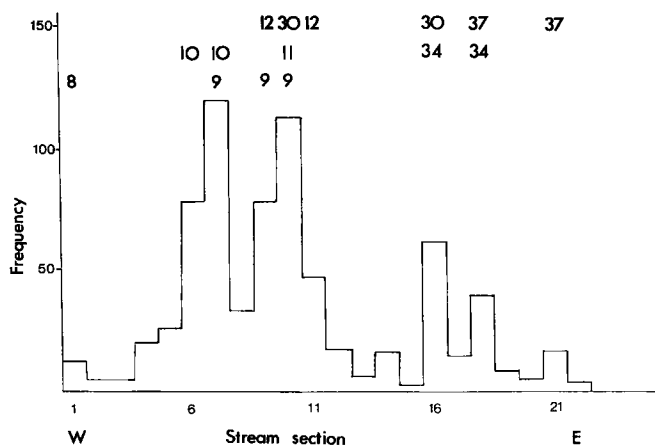


Figure 1. The combined frequency of activities by the eight most recorded males in the study. The abscissa is the length of the study site depicted as if the stream had been linear. Each stream section corresponds to a length of 3 m. Section 1 is at the western end of the site, with section 22 at the eastern end. The numbers above the histogram correspond to the code numbers of the marked males and indicate the centres of activity of those males.

Table 1. Basic statistics on those individual males seen most often at the study site.

Number	Date first marked	Minimum lifetime (days)	Days at site	Records	Matings
7	14/9	4	4	18	0
8	14/9	14	12	31	0
9	14/9	19	17	146	4
10	14/9	18	15	177	2
11	14/9	22	18	112	1
12	14/9	6	6	37	0
30	15/9	13	13	64	0
31	15/9	12	4	15	0
34	15/9	12	12	89	2
37	15/9	12	8	51	0
57	19/9	5	4	15	0
62	21/9	7	5	19	0
65	22/9	3	3	17	0
75	25/9	3	3	18	0

employing normal flight. These fights were essentially jockeying for position among those males that regularly occupied territories on the site. The mean duration of fights is high (34.5 s, S.E. 3.0) because there were a significant number of longer fights. Some involved more intense interactions, with turns and sometimes hovering flight as

both individuals faced one another. In Figure 2, the abscissa is not continuous; two fights lasted for more than 3 min. Both of these long fights took place relatively early in the day (started at 9.36 and 10.15). Both involved number 10. The first lasted for 220 s against no. 32. This animal was not recorded on the site following this lengthy encounter and it may be that it sustained some injury. The longest fight was against no. 9 and lasted 305 s. In this instance 10 was the resident and occupied the preferred site in the centre of the largest sun fleck. In these longer fights, power flying with synchronised wing beats was often observed, and occasionally both animals would engage in spiralling flight that led them up into the canopy and out of sight.

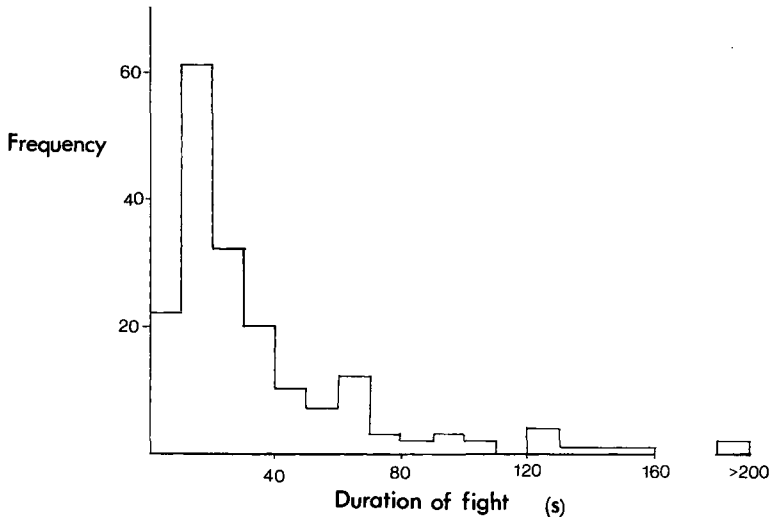


Figure 2. The distribution of fight durations.

Reproductive Behaviour

Female arrival times at the study site are shown in Figure 3. Also shown on this figure are the times at which females either entered or were first seen in the wheel. Females clearly choose to copulate later in the day than the times at which they first prospect either oviposition sites or partners. Those females that arrived at the site early were occasionally courted by males and declined to copulate or simply passed through the site relatively quickly and did not even permit courtship.

Courtship by males consisted of characteristic slow hovering flight in front of perching females, using asynchronous wing beats. The forewings were flapped but the hindwings remained still. Females frequently declined to mate with courting males. Some females that visited the study site did not mate with any of the males present, while others rejected one or more males before eventually copulating with one of the territory owners.

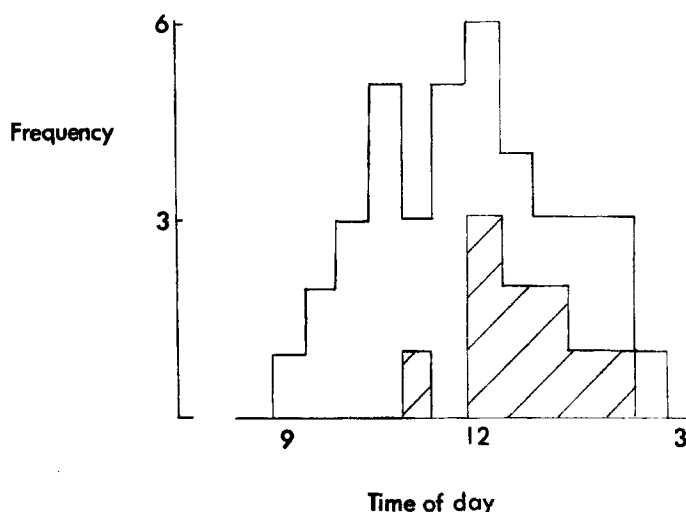


Figure 3. The distribution of female arrival times are depicted in the open histogram. The hatched histogram shows the times at which copulation was first observed. Times were local; the sun was overhead at 12 noon.

Mean copulation duration was 124 s ($n = 6$) with a range from 105 to 165 s. Following copulation the pair flew in tandem to the oviposition site where they separated. The female invariably oviposited in dead leaves in slow running water. She usually perched on the leaf and bent her abdomen underneath it. At the beginning of each oviposition bout the male remained very close to the female, often as close as 1 cm. However, as oviposition continued the distance between the male and female increased, often because the male was forced to chase off intruding males. The females changed location within the study area up to five times during an oviposition bout, with the male non-contacting guarding throughout. The mean length of time from the onset of oviposition to the female leaving the stream was 24.5 min ($n = 6$), with a range from 19 to 34 min. The other notable feature of oviposition bouts was that they attracted much activity from rival males and several of the aggressive interactions noted above occurred when the territory holding male was engaged in guarding an ovipositing female. None of the oviposition bouts that were observed in their entirety were free from harassment by rival males. In copulation no.1 of Table 2 oviposition was curtailed because both the male and female were disturbed by other males. In the oviposition sequence described in Table 3 the male was engaged in seven fights with at least three different individuals. Note, in this instance the female seemed to spend some time prospecting the site, having first appeared the previous day. She was courted by two males, both territory holders, before finally copulating with a third male whose territory occupied the sunniest section of the stream. No females were seen to oviposit alone. Only males holding territories secured any matings. Seven of the nine matings observed were obtained by males holding territories around the two largest sun flecks. The four males that secured matings were those that were involved in the greatest activity on the site (see Table 1).

Table 2. Copulation duration and oviposition statistics for the nine matings observed.

Copulation male number (male/female numbers; U = unmarked)	Time of day	Copulation duration (s)	Number of oviposition bouts	Total time in mate-guarded oviposition (min)	Number of fights during oviposition time
1 (9/U)	13.28	-	≥ 2	-	≥1
2 (10/35)	12.13	165	≥1	-	-
3 (9/66)	14.00	106	4	21	7
4 (34/64)	12.15	-	2	19	2
5 (9/51)	11.20	105	-	-	-
6 (34/67)	12.18	120	3	27	2
7 (9/63)	12.45	115	3	34	3
8 (10/U)	13.19	-	5	23	5
9 (11/2)	13.42	134	4	23	3
Mean (± sd)		124.17 (±22.64)		24.5 (± 5.36)	

Discussion

Defence of sun flecks by damselflies has been described several times before (e.g. Hamilton & Montgomerie (1987) for *Argia chelata* Calvert in Costa Rica, Watanabe, Ohsawa & Taguchi (1987) for *Platycnemis echigoana* Asahina in Japan and Conrad & Pritchard (1988) for *Argia vivida* Hagen in Canada). Sun fleck defence is not, of course, confined to odonates (see Davies (1978) for the butterfly *Pararge aegeria*).

Plaisow & Siva-Jothy (1996) working on *Calopteryx splendens xanthostoma* in southern France found that reproductive success of territorial males was far greater than that of non-territorial males (up to one thousand times greater). In the present, more limited, study all of the matings observed involved territorial males and successful sneaking was not observed (e.g. Forsyth & Montgomerie, 1987).

In the studies of Waage (1988a), Marden & Waage (1990) and Plaistow & Siva-Jothy (1996) fights for territories were mostly short, but there were some escalated contests. Waage divided *Calopteryx maculata* fights into three types: unidirectional chases, two-sided contests involving frontal, reversed and lateral threat fights, and escalated contests in which there was intense backward and forward chasing and spiralling contests in which the combatants rose well above the water surface. This description fits the fights observed in the present study very well. Waage's explanation for escalated contests lies in confusion over residency; both males in such contests imagine that they are the territory owner. This is certainly the most likely explanation in the present study. Owing to the changing geographical nature of the territories over the course of

Table 3. A detailed version of one of the mating sequences recorded in Table 2 (no.3). The female (no.66) was first seen the previous day at 1310 when she was feeding in a patch of sunlight about 50 m from the stream. The male was marked eight days earlier and was one of the regular territory holders (no.9).

1256	66 first seen alone moving slowly upstream
1259	male (34) displayed in front of 66 and tried to take in tandem; 66 flies away from stream
1313	66 returns and perches in shade
1328	66 begins to move slowly up and down stream
1353	male (11) chases 66 then begins to court by displaying in front of her; 66 refuses to enter tandem; 11 takes her perch
1400	male (9) courting 66 by flying directly in front of her while she perched
140310	start of tandem
140322	start of copulation
140508	end of copulation; pair separate
140608	66 begins to oviposit in dead leaves in slowly running water; 9 is about 1 cm away from her as she oviposits
140755	9 fights with another male for 5s; returns to close proximity with 66
140940	66 flies to a perch upstream of first oviposition site
141600	66 flies to new perch; 9 has two separate skirmishes with another male (57) and returns to guard 66
141720	66 begins to oviposit in a dead leaf in slow running water; she perches on the leaf with her abdomen curled underneath it
141835	9 has two more short fights with another unidentified male then returns to guard 66
142150	66 stops ovipositing
142230	begins to lay in another leaf in running water
142605	9 and another male (8) begin a protracted fight; 66 had strayed into the territory occupied by 8
142755	66 stops ovipositing and flies to a perch 3m above the last oviposition site
143430	9 returns from an escalated fight with 8 who cannot be seen
1438	66 catches a small fly
1445	9 and 66 perched opposite one another about 3m above the stream
1452	66 flies away from the stream; 9 remains on perch in his territory

the day, as the sun moved overhead, particularly around the largest sun flecks, several males could claim to be a territory owner. Thus, there were perhaps more longer fights observed in the present study due to increased confusion over territory ownership.

Waage (1988a) analysed three years data on bout durations in terms of Intruders, Neighbours, Sharers and Interlopers. In the present study this was not attempted as many of the fights were between the same individuals and this would have meant that there would have been considerable pseudoreplication. Neither were fights analysed in terms of the size of males for the same reason. In fact the two most successful males in terms of time on territory and number of matings achieved were at opposite ends of the male size distribution.

Mean copulation duration in *Vestalis amabilis* (124s) falls within the range reported by Waage (1988b) for species of *Calopteryx*, which ranged from means of 77s for *C. atrata* to 254s for *C. cornelia*. Other calopterygid copulation durations have fallen within this range too (e.g. 186s for *Hetaerina americana* recorded by Bick & Sulzbach (1966) and 180-240s for *Neurobasis chinensis chinensis* by Kumar & Prasad (1977)). Waage pointed out that these are all short copulations for zygopterans and probably reflect the fact that *Calopteryx* species, at least, tend to be territorial and mate frequently. However, not all calopterygids mate frequently. In the present study just nine copulations were observed along a 60m length of stream in three weeks. Similarly Alcock (1982) found that territorial males of *Hetaerina vulnerata* Selys obtained matings every 3.6 days on average. Similar data have been obtained for *H. macropus* in Trinidad (I.F. Harvey, unpublished).

During oviposition by *Vestalis amabilis*, the males that obtained the copulation prior to oviposition engaged in non-contact guarding. The females were left unattended only when the successful male was involved in disputes with other males. This is in contrast to *Neurobasis chinensis chinensis* in which the females are left totally unattended following copulation (Kumar & Prasad, 1977). The elaborate courtship required by *Neurobasis* males in order to secure copulations probably means that females can be left to oviposit without fear of sperm removal because usurping males would also need to perform lengthy courtships. Courtship in *Vestalis* is not particularly elaborate and females may thus remate if males are not in the vicinity. In the present study, males were frequently attacked while they were guarding ovipositing females, though no successful take-overs were witnessed.

Insufficient data were collected on female behaviour to comment on the patterns of visits to the site. No marked females mated more than once at the study site. Two unmarked females copulated with marked males and evaded capture at the end of oviposition. It is not clear if they subsequently returned to the study site. Several females visited the site on one day only, others made more frequent visits. One female was first captured and marked on 19 September at 10.35. She remained on the site for a further three and a half hours that day, then made two fleeting visits to the site on 22 and 23 September. On 24 September she stayed for two hours but did not copulate with (and was not courted by) any of the territory owners on any of her visits. Thus no obvious pattern in female visits could be determined. It is likely that females wander much more than males and there is some anecdotal evidence to support this view. One female that was marked at a sun fleck about 100m from the study site on 16 September was not seen again until 27 September when she was seen at another sun fleck by other members of the expedition. In this time she had travelled around 2 km including a crossing of the Ingai river.

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, of which Stuart Davison, Russell Spargo, Graham Terry and Henry Tau deserve special mention.

The logistic support provided by Raleigh made it possible to do science in difficult conditions. Jan van Tol identified all the Brunei odonate species referred to in this paper. In Brunei Bert Orr introduced me first hand to the local odonate fauna and provided some unpublished distribution data. Anna Mentzel helped with a preliminary analysis of the data.

References

- Alcock, J., 1982. Post-copulatory mate guarding by males of the damselfly *Hetaerina vulnerata* Sélys (Odonata: Calopterygidae). *Animal Behaviour* 30: 99-107.
- Banks, M.J. & D.J. Thompson, 1985a. Emergence, longevity and breeding area fidelity in *Coenagrion puella*. *Odonatologica* 27: 259-265.
- Banks, M.J. & D.J. Thompson, 1985b. Lifetime mating success in the damselfly *Coenagrion puella*. *Animal Behaviour*. 33: 1175-1183.
- Bick, G.H. & D. Sulzbach, 1966. Reproductive behavior of the damselfly *Hetaerina americana* (Fabricius) (Odonata: Calopterygidae). *Animal Behaviour* 14: 156-158.
- Conrad, K.F. & G. Pritchard, 1988. The reproductive behavior of *Argia vivida* Hagen: an example of a female-control mating system (Zygoptera: Coenagrionidae). *Odonatologica* 17:179-185.
- Davies, N.B., 1978. Territorial defence in the speckled wood butterfly (*Pararge aegeria*): the territory holder always wins. *Animal Behaviour* 26: 138-147.
- Forsyth, A. & R.D. Montgomerie, 1987. Alternative reproductive tactics in the damselfly *Calopteryx maculata*: sneaking by older males. *Behavioural Ecology and Sociobiology* 21: 73-81.
- Hamilton, L.D. & R.D. Montgomerie, 1989. Population demography and sex ratio in a Neotropical damselfly (Odonata: Coenagrionidae) in Costa Rica. *Journal of Tropical Ecology* 5: 159-171.
- Kennedy, C.H., 1920. The phylogeny of the zygopterous dragonflies as based on the evidence of the penes. *Ohio Journal of Science* 21: 24
- Kumar, A. & M. Prasad, 1977. Reproductive behaviour in *Neurobasis chinensis chinensis* (Linnaeus) (Zygoptera: Calopterygidae). *Odonatologica* 6: 163-171.
- Lieftinck, M.A., 1965. The species-group of *Vestalis amoena* Sélys, 1853, in Sundaland (Odonata, Calopterygidae). *Tijdschrift voor Entomologie* 108: 325-364.
- Marden, J. & J.K. Waage, 1990. Escalated damselfly contests are energetic wars of attrition. *Animal Behaviour* 39: 954-959.
- May, E., 1935. Über die Genera *Vestalis* Sélys, *Vestinus* Kennedy und *Vestalaria* n. g. *Senckenbergiana* 17: 207-218.
- Plaistow, S. & M. Siva-Jothy, 1996. Energetic constraints and male mate-securing tactics in the damselfly *Calopteryx splendens xanthostoma* (Charpentier). *Proceedings of the Royal Society (London) Series B* 263: 1233-1238.
- Sélys Longchamps, E. de, 1853. Synopsis des Calopterygines. *Bulletin Academie de Belgique* 20, Annexe: 25-26.
- Thompson, D.J., 1990. On the biology of the damselfly *Nososticta kalumburu* Watson & Theischinger (Zygoptera: Protoneuridae). *Biological Journal of the Linnean Society* 40: 347-356.
- Thompson, D.J., 1998. On the biology of the damselfly *Euphaea ameeke* van Tol & Norma- Rashid in Borneo. *Odonatologica* 14: 279-286.
- Thompson, D.J. & J. van Tol, 1993. Damselflies and dragonflies from four forest types in Brunei. *Brunei*

Museum Journal 8: 57-72.

- Van Tol, J. & Y. Norma-Rashid, 1995. The genus *Euphaea* Rambur in Borneo (Odonata: Euphaeidae). Tijdschrift voor Entomologie 138: 131-141.
- Waage, J.K., 1973. Reproductive behaviour and its relation to territory in *Calopteryx maculata* (Beauvois) (Odonata: Calopterygidae). Behaviour 47:240-256.
- Waage, J.K., 1988a. Confusion over residency and the escalation of damselfly territorial disputes. Animal Behaviour 36: 586-595.
- Waage, J.K., 1988b. Reproductive behavior of the damselfly *Calopteryx dimidiata* Burmeister (Zygoptera: Calopterygidae). Odonatologica 17: 365-378.
- Watanabe, M., N. Ohsawa & M. Taguchi, 1987. Territorial behaviour in *Platynemis echigoana* Asahina at sunflecks in climax deciduous forests (Zygoptera: Platynemididae). Odonatologica 16: 273-280.