Odonatologica 15 (1): 51-60 *January 28, 1986*

BEHAVIORAL ECOLOGY OF THE TROPICAL DAMSELFLY *HETAERINA MACROPUS* SELYS (ZYGOPTERA: CALOPTERYGIDAE)

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Received September 4, 1982 / Revised and Accepted May 31, 1985

Individual male and female *H. macropus* moved only short distances from day to day along a stream near Cali, Colombia. The distributions of the two sexes along the stream were different and teneral males had a more nearly male than female distribution. Mature males tended to perch lower than either females or teneral males; and mature males which perched low were more active in presumably sex-related activities such as chasing and circle flights than those which perched relatively high. Both males and females, especially newly emerged individuals, spent time away from the immediate vicinity of the stream. There was a relatively high rate of individual turnover along the creek during the day even though total numbers remained relatively constant. Mating and oviposition behavior were somewhat variable, but conformed to the general pattern for the genus.

INTRODUCTION

Hetaerina macropus is a common species widely distributed along swift streams in Central America and northern South America (WILLIAMSON, 1923). Virtually nothing is known of its behavior and ecology. This report describes several aspects of its biology, including activities of breeding and non-breeding males, and movements along and to and from water, and compares it with the temperate species *H. americana* (Fabr.) and *H. titia* (Dru.)

SITE AND METHODS

The study was conducted along a small creek near Cali, Colombia (el. 1000 m) in a zone termed "dry tropical forest" by ESPINAL & MONTENEGRO (1963). The stream fit WILLIAMSON's (1923) description of an ideal site for *Hetaerina* almost perfectly. It was 1-2 m wide, in a

shallow depression lined with secondary trees and bushes; 5-10 m back from the stream on both sides were more or less open, brushy pastures.

Damselflies were marked with small patches of model airplane dope on the base of the wing and on the thorax, and a code involving two colors and seven sites permitted individual recognition. Each animal was marked with the same pattern on both sides of its body to reduce error due to lost marks. "Recapture" consisted in approaching an individual carefully, reading its marks, and then moving on, usually leaving it undisturbed. Surveys were made along a 118 m stretch of stream, and the exact site of each "recapture" was determined with reference to markers placed every 4-5 m. Heights of perches were estimated in feet and inches and then converted to metric units because my estimates in the former units are more precise. Each survey took between one and two hours. Teneral males were distinguished from older males by their lack of white pruinosity near the bases of the undersides of their hind wings; young females were distinguished (probably less reliably) by their brighter body colors and unstained, more yellowish wings.

Although this species usually rests on prominent perches, appreciable numbers of damselflies were probably missed during the surveys. It is also possible that, because of their brighter colors and greater activity, males were slightly easier to find than females and were thus overestimated. The intensity and technique of searching were the same during each survey, however, so the counts can be reasonably compared with each other. The surveys and most of the other observations described below were done in March, 1975; counts made before and after this period at a nearby site (Eberhard, unpubl.) indicated that the population of *H. macropus* was declining during this period.

All statistical tests were 2-tailed chi-squares unless otherwise noted.

RESULTS

MALE AND FEMALE PERCHING SITES

As shown in Table I, mature males tended to perch closer to the ground than did either females or teneral males (in both cases, $p < 0.01$). The difference between females and teneral males is not significant. Males also chose especially high perches (> 2.13 m) significantly less often than did females ($p < 0.01$). These differences are probably associated with male breeding activity. When disturbed, males resting close to ground level often flew a short distance to alight on a plant. 0.62-1.22 m above the water, then later returned to the original perch; the number of males perched at < 0.62 m in Table I (25%) may thus somewhat underestimate the fraction actually resting this low.

Table I
Perch heights of adult males, teneral males, and females (% of animals observed; N =253, 30, and 268 respectively)

Sex and age	Numbers of individuals at estimated height above stream level (cm)							
	<15	16-61	62-91	92-122	123-152	153-183	184-213	> 214
Mature male	22	8	6	26	23	10	5	0
Teneral male	0	7	3	17	40	10	17	7
Female	0	1	4	12	26	18	16	22

CORRELATION BETWEEN A MALE'S PERCH AND HIS BEHAVIOR

Although the density of males in some parts of the stream was often quite high, many males seemed to be engaged in feeding, and it appeared that those resting nearer the ground were more aggressive. To test these impressions, the activities of marked males perched very high (1-2 m) and very low (≤ 15 cm) were recorded during alternate 15 minutes intervals on several days. When the male being observed flew away during the observation period, I attempted to complete the interval with another male, but this was not always possible. The activities observed, which are summarized in Table II, were these:

— Circle flight. — Two or more males flew in a more or less circular pattern, usually one to two feet above the water, with a peculiar bobbing type of flight. From less than one to several circles 1-4 m in diameter were described, sometimes with the participants moving slowly up or downstream several meters. Sometimes the flight ended with one male chasing another for a short distance. Typically each male returned to his original perch after the flight.

— Chase. — A male flew quickly after a passing *H. macropus* male or other odonate. Often, when chasing a conspecific, the chasing male pursued until the other landed on a plant on the bank several feet above the water; then leaving him there, the pursuer returned to his original perch.

— Predation. — The male flew out to catch a passing insect and returned directly to his perch. Since I was only seldom able to see the small insects caught, it was often difficult to be sure a given flight was predatory. In general, short straight flights, less than 1.5 m, which were directed toward no obvious object and from which the damselfly returned to his perch immediately afterward were classified as predatory. In a few cases the male was observed feeding after such a flight. In one case the male captured and fed on an insect from the surface of the water, but otherwise all predatory flights were strictly aerial.

— Flights of undetermined type.

— Clean wings. — The damselfly rubbed his abdomen up and down one or more times between his wings and then, sometimes after a pause, bent his abdomen forward and cleaned it with his legs.

— Wing warning. — A perched individual partially spread his wings, flashing the bright red color on their upper surfaces, and raised his abdomen at the approach of another male or female.

— Clean eyes. — With the head tilted to one side, a front leg wiped once or several times over one eye.

— Leave. — The male disappeared from sight for more than 30 seconds; occasionally individuals returned after absences of a minute or more.

The results of 160 minutes of observation of low resting males and 176 minutes of high males (Tab. II) show clear differences. Lower males were only somewhat

Table II

Activities of males at high (1-2 m) and low (< 15 cm) perches during 160 minutes of observation of low-resting males and 176 minutes of high-resting males (% of activities observed; total numbers of activities 114 and 100 respectively)

Position	Circle flight	Chase	Chase?	Predation	Predation?	?	Clean wings	Wing warning	Leave	Clean eye
Low-resting	12	20	10	15	8	25	6	0	3	1
High-resting	0	6	2	39	16	8	5	5	15	4

more active (average of 0.662 vs 0.534 flights/minute; $p > 0.1$); they chased and made circle flights more often and made predatory flights and left less often ($p < 0.01$ in all cases).

MATING

Five copulations were observed. In the three cases in which I was certain of the location of the male's perch prior to his seizing the female, he had been resting low, less than 15 cm above the stream. In one case the female landed on the stone the male was on, and in the other two she flew nearby. In all three the male seized her in flight and they immediately flew in tandem either to the site where the male had been resting or to a plant near the edge of the stream. They copulated as soon as they landed. In two cases the male first curled his abdomen forward so that the top of the female's head came close to his secondary genitalia, then straightened it and the female brought the tip of her abdomen forward to copulate. This was presumably sperm translocation, by which the male charged his secondary genitalia with sperm (BICK & BICK, 1965, 1972). In at least one other copulation however this preliminary movement did not occur.

All five copulations were brief, lasting one to two minutes, and the female appeared to be flexing the tip of her abdomen against the male the entire time. When copulation ended, the female straightened her abdomen and the pair immediately flew off upstream in tandem. In three cases they disappeared from sight flying rapidly and low over the water's surface 3-6 m upstream from the copulation site. Other males flew near these tandem pairs, but were not persistent in bothering them. Indeed, one of the two pairs which I succeeded in following landed within two feet of a male which only briefly bothered them before returning to his perch on a stone in the stream.

Both pairs which I followed landed where there was vegetation growing both above and below the surface. The male quickly released the female and she crawled down into this vegetation, completely submerging herself. In one case the male then returned to his original perch about 2 m away, and in the other he engaged in an intense circle flight with a nearby male, and one of the two (neither was marked) then perched nearby. In one case when a tandem pair was lost from sight the male, which was marked, returned alone to his original perch within one minute after leaving.

OVIPOSITION

Oviposition by two females was seen. Both were completely submerged, and each appeared to probe in various directions with her abdomen and insert her ovipositor into small living stems and roots that had been washed clean. In one case the entire oviposition sequence lasted 38 minutes, with the female walking

slowly along the bottom and on twigs in a small area in shallow (2-5 cm) flowing water from which she partially emerged several times. Her wings and thorax had silvery sheens, indicating that they were covered with air. When the female finally emerged completely, she rested for about one minute, then flew off.

SITE PREFERENCES AND MOVEMENTS TO, FROM, AND ALONG THE STREAM

On March 8 and 9, 63 males and 60 females were marked along a 71 m stretch of the stream. On each of the next eight days, the same stretch plus an ecologically similar 47 m on the downstream side were inspected between 11: 00 and 13: 00. The sex, location (to the nearest m), height of the perch above the ground, and mark or lack of mark were recorded for each individual seen.

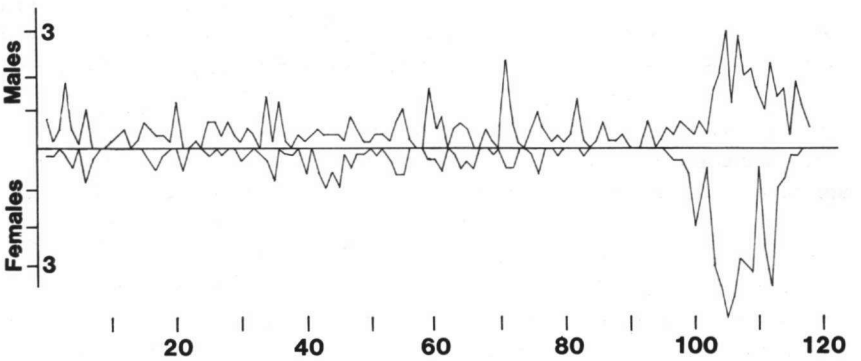
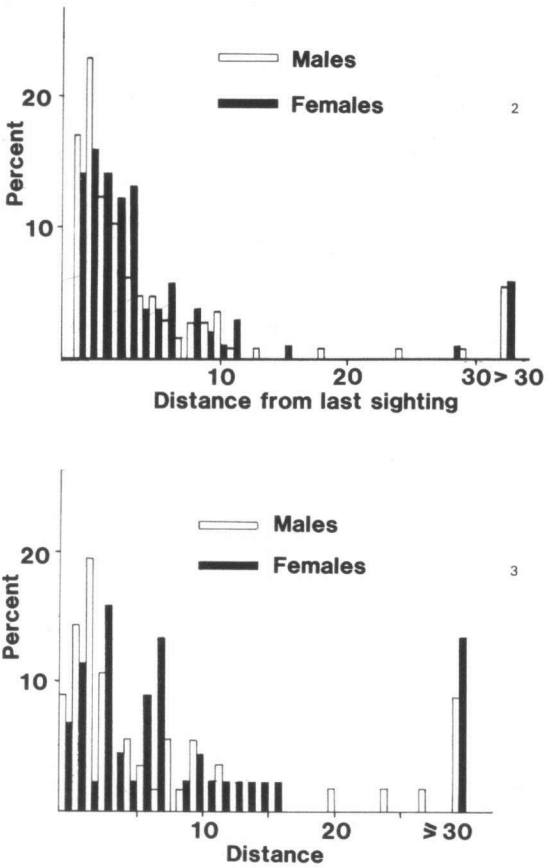


Fig. 1. Distribution of male and female *Hetaerina macropus* along a 118 meter stretch of stream. Each point represents the average number of individuals seen per inspection in a meter segment of the stream.

Figure 1 shows the differences in the numbers of sightings of males and females (N = 384 and 331 respectively) in each meter of the creek. The area 103-116, a transition between open and shaded creek, accounted for 59% of the female sightings but only 37% of the male sightings ($p < 0.001$). Although the proportion of low-resting to high-resting males was slightly larger in this densely populated area than in other parts of the stream, the difference was not significant ($0.2 > p > 0.1$). Thus neither the total distribution of males nor that of breeding males was identical to the female distribution. Nevertheless, there was a significant correlation between the numbers of males and females at the same points along the stream ($r = 0.734$, $p < 0.01$; cf. also Fig. 1). Low-resting males did not appear to affect the distribution of other males, since when the distances from each low-resting male to the nearest high-resting and the nearest low-resting male were compared to similar distances from high-resting males, there was no significant difference.

The few sightings of teneral males indicate that they had a male rather than a female distribution. They were not as concentrated in the 103-113 stretch of the creek as were females ($p < 0.01$ with respect to females $p \simeq 0.45$ with respect to males).

There was a strong tendency, illustrated by several types of data, for individuals of both sexes to stay in the same limited area of the stream. Figure 2 shows the distances between the sites of successive sightings of marked individuals: 73.5 % of male and female sightings were within 5 m of the previous sighting. There was no tendency for low-resting males to move more or less than high-resting males ($p > 0.4$ comparing moves of < 2 m and > 2 m). The distances between the first and last sightings of individuals (av. elapsed time 4.2 days) were also relatively small (Fig. 3): 61% of the males and 43% of the females were last seen within 5 m of where they were first found. Only 5% of the resightings occurred in the "unmarked" 47 m stretch downstream.



Figs 2-3. *Hetaerina macropus*, distances (in meters) between: (2) sites of successive sightings of male and female; — (3) between first and last sightings of male and female.

Some damselflies may remain for extended periods in the same part of the stream. Some sleeping individuals were found at night on the same plants used as perches during the day. In addition, a small experiment suggested that they do not return to their original home sites when displaced. Eighteen males and eight females were collected on 15 March from an area about 30 to 50 m upstream of the study area, marked, and released at the 47 m marker, about 100

to 120 m from where they were captured. In the next two days, nine resightings of at least seven individuals were made at an average distance of 15 m from the release site; no marked individuals were seen at the original site during the same days.

On the other hand, individuals do sometimes stray from the immediate vicinity of the stream. The rates of recaptures of marked individuals suggest that the damselflies periodically left the stream. The average percentage of marked individuals among all damselflies sighted during a given inspection was 46% (range 40-52%) but the average of the total of 123 marked individuals which were resighted in any given inspection was only 28% (range 20-33%) ($p < 0.01$ Student's t Test). There were no significant differences between the sexes in this respect. Population turnover during the day also suggests that individuals frequently left the stream.

Table III

Numbers of sightings of teneral males and females at the stream (4 counts) and away from it in a grassy yard (6 counts) during the period 29 March to 3 April 1975. The yard and stream are significantly different ($p < 0.01$)

Habitat	Females		Males	
	teneral	older	teneral	older
Yard	49	9	18	7
Stream	8	35	11	84

Both males and females were observed feeding and sleeping in a grassy yard more than 100 m from the nearest stream. Teneral individuals of both sexes were significantly more common in the yard than at the stream (Tab. III, $p < 0.01$ for both sexes). The proportion of females in the yard was higher than that at the stream ($p < 0.01$).

POPULATION TURNOVER DURING THE DAY

On one day (11 March) which was sunny throughout, a 71 m stretch of the stream was inspected every two hours from 09:00 to 17:00. There was an increase in damselflies during the day (the same trend occurred on other days when careful counts were not made). The numbers of individuals observed were 51 (09:00), 96 (11:00), 101 (13:00), 116 (15:00), and 98 (17:00). The 09:00 count is significantly lower than the others ($p < 0.01$).

Even when the population size was relatively constant from one inspection to the next, counts of marked individuals showed that there was substantial individual turnover. For instance, 53 marked individuals were seen at 13:00 and 58 at 15:00, but only 38% of these were present for both counts. This was not due to my

searches being incomplete, since the replacement rate was even higher at larger intervals. For example, only 17% of the total of 83 marked individuals observed at 11:00 and 17:00 were seen at both inspections (percentages differ significantly by the binomial test, $p < 0.05$). Day to day variations in individuals present at a given time (11:00) were somewhat smaller however; the percentage of individuals observed on successive days during the period 11-15 March (the total numbers of marked individuals resighted on successive days during this period differed by less than 5) averaged 34% of the number (179) of sightings of marked individuals (this percentage differs significantly from the 17% mentioned above, $p < 0.05$ by the binomial test). This suggests that given individuals may have preferred times as well as preferred sites.

DISCUSSION

The behavior of *H. macropus* can be compared with published accounts of *H. americana, H. vulnerata,* and *H. titia* on several points. Aggressive interactions between males, including circle flights and chasing were similar to those of these three species (JOHNSON, 1961, 1962; ALCOCK, 1982), but no *H. macropus* behavior corresponded to the male "display" flights described for *H. americana* and *H. titia* (JOHNSON, 1961). BICK & SULZBACH (1966) also failed to observe such flights in *H. americana.* Wing warning similar to that of *H. macropus* occurs in *H. americana* and *H. titia* (JOHNSON, 1961, 1962). Female aggression, in which females occasionally displaced each other and males from perches, rarely involved short circle flights as in *H. americana* (BICK & SULZBACH, 1966).

Other *Hetaerina* species show variability in the events immediately preceeding copulation, even within the same species (JOHNSON, 1961; BICK & SULZBACH, 1966), and *H. macropus* seems to follows this pattern. Sperm translocation sometimes occurred just before copulation, but sometimes did not. Copulation was slightly shorter than in *H. americana, H. vulnerata,* and *H. titia.* Male wing flicking just before copulation as in *H. vulnerata* (ALCOCK, 1982) was not seen.

Oviposition by completely submerged females also occurs in *H. americana* and *H. vulnerata* (BICK & SULZBACH, 1966; ALCOCK, 1982). In apparent contrast to *H. vulnerata,* females of *H. macropus* used only living plant material (mainly rootlets) as oviposition sites. On at least two occasions male *H. macropus* failed to guard submerged females as they do in *H. americana* (JOHNSON, 1961; BICK & SULZBACH, 1966) and sometimes in *H. vulnerata* (ALCOCK, 1982).

The distributions of *H. macropus* males and females were not the same along the banks of the stream, but the significance of the differences is uncertain. The distribution of the females may reflect where they fed rather than where they bred. The 103-116 m stretch of stream (Fig. 1) was probably especially attractive for

predatory activity because it had many exposed sunny perches with a dark background on both sides of the stream. Two of the five observed copulations, on the other hand, occurred in areas where females were seldom seen. Females of *H. americana,* which were probably also feeding when observed, were also more clumped along the stream than the males (JOHNSON, 1962). Male and female site preferences differ in other damselflies (WAAGE, 1980).

The tendency for males to perch low, near the stream surface has been noted in *H. americana* (JOHNSON, 1961), and ALCOCK (1982) found that territorial males of *H. vulnerata* perched especially close to the water. *H. macropus* males which were perched low near the water usually flew a short distance up into nearby vegetation when disturbed, suggesting that low perches may be more dangerous.

The frequent aerial pursuits of unreceptive females that BICK & SULZBACH (1966) described for *H. americana* did not occur in *H. macropus.* Territorial *H. macropus* males responded only to low flying individuals. They never chased the many females commonly present higher above the water in some parts of the stream; the only two seizures I witnessed were of low flying females. It appears that all of the seizures observed by BICK & SULZBACH also occurred close to the surface of the water (1966, p. 156), and the same may be true in *H. vulnerata* (ALCOCK, 1982, p.102).

The tendency for males to stay in more or less the same stretch of stream bank was also noted in *H. americana* (JOHNSON, 1962) and *H. vulnerata* (ALCOCK, 1982). Female fidelity to a given site has not been well documented in other species of this genus, although BICK & SULZBACH (1966) saw one *H. americana* female return to the same site four times in a 19 day period.

H. macropus appears to be unusual in this genus in not remaining close to water during its entire adult life, or even perhaps during a single day. WILLIAMSON (1923) stressed that *Hetaerina* species are exceptionally strongly associated with water. The suggestion by BICK & SULZBACH (1966) that the lack of variation in the numbers of individuals of *H. americana* present during the day along a given stretch of stream implies that this species spends all its time near the water should be treated cautiously since they did not take into account the possibility of population turnover during the day such as that found in *H. macropus.*

ACKNOWLEDGEMENTS

I thank MIKE MAY for identifying specimens and JOEL WEICHSEL for other favours. The Vicerrectoría de Investigación of the Universidad de Costa Rica provided financial support.

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