

**MALE TERRITORIAL TACTICS IN THE DAMSELFLY
HETAERINA CRUENTATA (RAMBUR)
(ZYGOPTERA: CALOPTERYGIDAE)**

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Territorial tactics, aggressive interactions, 3 body characters (wing, abdominal and total length), mating success, and the influence of weather conditions were analysed in territorial males. The number of aggressive encounters was positively affected by male abundance and aggression and by weather conditions, also depending on the time of the day. Male abundance was conditioned by territory rank (taken as an index of territory quality). 3 male territorial tactics were discerned, viz. resident, sneaker and floater. Resident males were the most aggressive individuals, and their territories were disputed by sneaker males. Floater males rarely fought. There were no differences in size among individuals using these tactics. A positive correlation existed only between the abdominal and total lengths and the territory rank, but this was probably largely incidental. No size differences were noticed between copulating and non-copulating males. As in other Calopterygidae, the mating system of *H. cruentata* is a resource-defence polygyny.

INTRODUCTION

Odonates have a wide and complex repertoire of territorial behaviors (WAAGE, 1973; CORBET, 1980). Alternative mating tactics have been studied in several species (UEDA, 1979; WAAGE, 1979; TSUBAKI & ONO, 1986; FORSYTH & MONTGOMERIE, 1987; ALCOCK, 1988; FINCKE, 1985, 1992). However, studies on the phenotypic characteristics that confer an advantage to males adopting different tactics are still limited (but see MILLER, 1983; FINCKE, 1984, 1992; HARVEY & CORBET, 1985; TSUBAKI & ONO, 1986, 1987). Possible mating tactics, depending on the species, can include resident, sneaker, and floater males (cf. WALTZ & WOLF, 1984; WATANABE & TAGUCHI, 1990; however, see WALTZ, 1982). These behaviors can be influenced by size (WALTZ & WOLF,

1984; TSUBAKI & ONO, 1987; FINCKE, 1984, 1992), male density (PAJUNEN, 1966; CAMPANELLA & WOLF, 1974), age (FORSYTH & MONTGOMERIE, 1987; TSUBAKI & ONO, 1987) and, probably, by fat reserves (FRIED & MAY, 1983; MARDEN & WAAGE, 1990). Although these mating tactics have been well described in several species, detailed measurements and quantification are still rare.

In this paper, I describe the behavior and territorial competition of the sexually-dimorphic damselfly *Hetaerina cruentata*, at low population density. This species is very common in Mexican temperate rivers and, unlike some other calopterygids, has not been the subject of many studies.

MATERIAL AND METHODS

Observations and field work were carried out from September 3 to October 25, 1992 in the Sordo River, Xalapa, Veracruz, Mexico (19°30'N, 96°95'W). The river has a width of 3-6 m. The study area was 100 m long and it was divided into sections of 2 x 2 m.

Because the territories varied in relation to the availability of aquatic vegetation and the number of males on the site, they were ranked in seven areas. The ranks were assigned according to the preferences exhibited by the resident and the satellite (sneaker and floater) males (see below for more details on these kinds of behaviors; correlation of male abundance with the rank of territory, Kendall's $\tau=0.488$; $P<0.01$), and according to the percent of emergent vegetation within the territory. The latter is related to female oviposition use and to individual perching of males (CÓRDOBA-AGUILAR, 1994a; see WAAGE, 1987). The following method was used to define the ranks according to the vegetation abundance. In each territory that was included in the quadrats, the amount of vegetation was compared to some previously-drawn figures which contained different proportions of covering vegetation by a certain space of quadrats. We had previously assigned six different rank classes (0, 20, 40, 60, 80 and 100 percent) in our figures. This way of measuring gave us an approximate idea of the amount of covering vegetation by territory for a number of quadrats. Besides, in order to prevent any observer's bias when assigning these categories, we also compared different estimates obtained by different observers. According to this method, the first three territories (A, B and C) had either more individuals, or a greater percentage of emergent vegetation. The other four territories (D, E, F and G) had a lower male abundance (Mann Whitney U test = 87.5; $P < 0.002$) or a lower percentage of vegetation cover.

Daily observations started before the beginning of damselfly activity (0800-0900 h) and continued until males abandoned the reproductive sites (1400-1530 h). Males and females observed during the first census were captured and individually marked, using an indelible ink. Females were marked after they had stopped oviposition, and the abdominal, wing and total lengths were measured. Even though some individuals (N=52) left the study site after marking, returning later at different rates, most of them returned within one day to their last territorial position (N=183, save for the females, which normally had distinct daily arrival rates). I assume, therefore, that marking had little observable effect on normal behavior.

Daily focal observations of two and three hours were made on a pair of individuals (one resident and one intruder each time) in all the study areas (not just the ranked territories). Using a different set of males, one-hour observations were carried out to time general activities, especially flight activity, which included patrolling, chasing and interactions, feeding, perching and copulation. Resident males were identified as those that successfully defended the territory after several aggressive contests against intruders. Satellite males (sneakers and floaters) were those which, despite fighting, did not acquire a territory. Likewise, every hour, from 0900 until 1400 h, visual counts were performed along the river to record the displacements and new positions, reproductive activity, aggressive interactions, recogni-

tion of residents and satellites in a territory, and the abundance of individuals on the river. I used a personal audio recorder (Broksonic, model TSG-45) to facilitate the data recording.

To determine the effect of the weather on daily activity, weather conditions were arbitrarily divided into four classes: (a) clear, without any clouds; (b) clear-cloudy, with some clouds but territories were not shaded; (c) cloudy-clear, mostly cloudy with no observable probability of rain; and (d) cloudy, the sky mostly cloudy with a high probability of rain.

Body measurements are given in cm. Statistical tests were performed using SYSTAT statistical package (WILKINSON, 1986). Means \pm SE are presented unless stated otherwise.

DAILY ACTIVITY

Males arrived at their territories between 0912-1046 h, depending on the weather conditions. Individuals had different arrival times, but the residents were consistent (residents = 0912-0930 h, satellites = 1020-1046 h). The end of activity was less variable (1336-1427 h).

TERRITORIES AND AGGRESSION

Territories were clearly demarcated along the banks of the river, but it was difficult to recognize their limits in the middle of the river (between two opposite banks). More interactions occurred between the neighbours of adjacent territories along the same border (91.7%) than between the males on the opposite banks of the river (8.3%, binomial test $z=-4.79$; $P<0.001$). On several occasions ($N=12$), some males flew in the middle of the river, but were not chased. Territories varied in width along the banks from 4-6 m (measured as an average of distance patrolled by residents).

There were some areas without any individuals, and these had fewer oviposition sites. The three highest-ranked territories had the greatest number of interactions (Mann Whitney U test=479; $P=0.004$). The number of males in some territories varied $\bar{x} = 4.9$ males, range 1-8, $N=43$), but in each, one male was dominant. We recorded a total of 354 male contests, involving 165 different males. Residents were frequently, but not always, the dominant individual after a contest against a satellite (179 contests won and 30 lost by residents; binomial test $z=-9.68$; $P<0.001$). 67 contests were carried out between resident males and 8 between satellites. In 43 contests, we could not identify the winner, and another 27 encounters were collective contests (see below). Contests were mostly carried out against individuals in flight (90%), although sometimes the residents interacted with the perching individuals as well (10%).

MALE TACTICS AND AGGRESSION

Three types of males were recognized, based on their behavior (number of movements, displacements and activities in territories). These were designated as sneak-

ers, floaters (see WATANABE & TAGUCHI, 1990) and residents. Although the sneaker and floater males have been considered as satellites (WALTZ, 1982; WALTZ & WOLF, 1984), here I treat them separately. Sneakers were present for several days in a territory or in adjacent territories. When sneakers arrived at the territories, the residents vigorously interacted with them, but the sneakers did not leave the site, perching instead a short distance away. Sneaker males participated in collective contests (see below), in which several males were fighting. Sneakers almost never started a contest (49 cases, including 30 where sneakers displaced the residents), and they lost most contests against the resident males (167 lost fights, $N=197$).

Floaters were considered the males that travelled among different territories on the same day, without staying more than one or two hours at a given territory. As with sneakers, when floaters arrived at territories, they were intensively attacked by the residents. However, when a resident interacted with a floater, the latter left the territory quickly ($N=12$). In fact, floaters rarely interacted with resident males ($N=4$ occasions).

A collective contest began with a fight between either two neighbouring residents or between a resident and a sneaker. Afterwards, other neighbouring residents or sneakers joined in the fight. These contests consisted of up to five individuals in flight ($\bar{x}=3.29$, range 2-5, $N=27$ collective contests). Some males only approached the contest and then left quickly, while others interacted strongly, sometimes with physical contact. Contests between neighbouring residents did not end in displacement of either, and both returned to their respective positions. Contests between sneakers and floaters were rare ($N=8$), and were followed by interactions between the resident males. Longer interactions ($N=24$) took place between residents (15.37 ± 3.25 s). An individual remained as resident in a territory for 14.35 ± 4.6 days ($N=17$, range 5-21).

Aggressive interactions increased towards noon (Kendall's tau= 0.733 ; $P<0.01$) and decreased in the afternoon (after 1300 h). The time when the owners were most likely to lose their territories was between 1000 and 1200 h, which could be called the peak hours of aggression. These coincided with the greatest female arrival (between 1100 and 1200 h). The abundance of males increased from morning to midday, and directly affected the number of interactions in the territories (Kendall's tau= 0.467 ; $P<0.01$). There was also a significant correlation between the number of interactions where the resident lost the contest and the number of interactions a resident had previously had against other individuals (primarily sneakers) that disputed his territory (Kendall's tau= 0.685 ; $P<0.001$). In these contests, sneakers initiated the attack, meaning that aggression could be initiated by residents as well as by non-residents.

On the other hand, interactions between residents and sneakers were significantly more numerous than between residents alone ($\chi^2=38.9$; $P<0.001$). Aggressive interactions between residents ($N=67$) occurred when a resident was in a collective contest in a nearby territory, or when a resident male, patrolling the border

of his territory, was assaulted by a neighbouring resident.

ACTIVITY OF RESIDENT AND SNEAKER MALES IN TERRITORIES

The activities of residents and sneakers consisted of five distinct behaviors: patrolling, chasing or aggressive interactions, perching, copulating and feeding. The time allotted to each activity is expressed as a percentage of the total time spent in all activities. Floaters were not considered, since they were very passive in the territories. Copulatory activity, compared with other odonates, was relatively rare (only one complete copulation was recorded), therefore it was excluded from statistical analysis. Time allotted to chasing and other interactions ($2.57\% \pm 2.13$) was significantly longer than that spent in territory patrolling ($1.15\% \pm 1.07$, Mann Whitney U test=1233; $P < 0.0001$). Relatively less time was devoted to feeding ($0.08\% \pm 0.03$) than to patrolling (Mann Whitney U test = 87.3; $P = 0.01$), or to all aggressive interactions (Mann Whitney U test=103.7; $P = 0.006$). Most of the time was spent on perching ($92.99\% \pm 12.10$, Kruskal Wallis ANOVA = 86.45; $P < 0.0001$). On the other hand, the residents spent, in general, more time in flight than the sneakers (Mann Whitney U test=79.4; $P = 0.002$).

SIZE, MALE TACTICS AND COPULATION

Table I

Measurements of males using the different mating tactics. Differences are not significant (one-way ANOVA; $P > 0.05$) – [Numbers in parenthesis are sample sizes]

Characters	Residents (13)	Sneakers (17)	Floaters (18)	F
Wing	2.69 ± 0.11	2.72 ± 0.13	2.70 ± 0.08	0.18
Abdomen	3.68 ± 0.13	3.60 ± 0.16	3.61 ± 0.18	0.89
Total	4.62 ± 0.17	4.53 ± 0.15	4.52 ± 0.21	0.75

-way ANOVA; $P > 0.05$). However, a positive correlation existed between total and abdominal length of residents with territory rank (Kendall's tau=0.027 and 0.31, respectively; both $P < 0.05$), but not with wing length (Kendall's tau=0.067; $P > 0.05$). The same correlation did not exist for any character in sneakers (Kendall's tau=0.02, 0.09, 0.1, total, abdominal and wing length, respectively; all $P > 0.05$).

Twenty copulations were seen, and all

Size did not differ significantly among males practising the three types of territorial tactics (Tab. I; one-way ANOVA; $P > 0.05$). No differences in size existed among residents of high and low rank territories (Tab. II; one-

Table II

Measurements of males in high (N=20) and in low-ranked (N=15) territories. Differences are not significant (one-way ANOVA; $P > 0.05$)

Characters	High rank	Low rank	F
Wing	2.71 ± 0.09	2.69 ± 0.10	2.09
Abdomen	3.59 ± 0.23	3.63 ± 0.17	2.89
Total	4.67 ± 0.16	4.54 ± 0.16	1.02

Table III
Size differences in copulating (N=20) and non-copulating males (N=131). Results are not significant ($P>0.05$)

Characters	Copulating	Non-copulating	t-test
Wing	2.68 ± 0.03	2.72 ± 0.01	1.59
Abdomen	3.62 ± 0.04	3.65 ± 0.01	1.41
Total	4.52 ± 0.05	4.59 ± 0.01	1.87

and floaters in their territories ($\bar{x}=4.75$, range 3-7) than the two males that copulated only once ($\bar{x}=2.16$, range 1-4, Mann Whitney U test = 67.5; $P = 0.002$). A t-test, carried out for each character, comparing the size of copulating males against those non-copulating, was not significant (Tab. III; $P>0.05$).

occurred between 1100 and 1200 h. Half of the matings were by males of unknown status, since they came from outside my study site. After marking (after copulation) they were not seen again. Two copulations were by sneakers and eight by residents. The three resident males that copulated twice, also had a significantly higher number of sneakers

WEATHER CONDITIONS AND MALE ACTIVITY

Variation in weather conditions affected the daily abundance of individuals exhibiting the three tactics (sneakers and floaters Kendall's tau=0.987, residents 0.901; both $P<0.001$). Likewise, during the day, the activity patterns and individual abundance were also affected by meteorological conditions (Kendall's tau=0.518; $P<0.01$). Cloudy and cloudy-clear conditions affected the start of daily activity. On some days, the damselflies remained inactive until 1100 h. However, activity generally ended around 1400 h, regardless of the weather.

DISCUSSION

As in other odonates (see WAAGE, 1973; CONRAD & PRITCHARD, 1992; FINCKE, 1992), the mating system in *H. cruentata* is a resource-defence polygyny (EMLEN & ORING, 1977; THORNHILL & ALCOCK, 1983). CONRAD & PRITCHARD (1992) have considered many calopterygid mating systems as resource-limitation systems, in which the males are unable to control all the female access to oviposition sites. The male ability of defending distinct, female-preferred territories can promote different male territorial behaviors (EMLEN & ORING, 1977; CONRAD & PRITCHARD, 1992).

Male competition for territories was intense in *H. cruentata*, mostly around 1100 h, when male aggression coincided with female arrival and high male abundance. It was during these hours that displacements of the original residents occurred. Therefore, aggression appears to be density-dependent (PEZALLA, 1979; WOLF & WALTZ, 1984; VAN BUSKIRK, 1986).

The resident males remaining until midday have a higher possibility of gaining copulations. It is very probable that the defence of a territory is coupled with high

energetic costs (MARDEN & WAAGE, 1990). These could be particularly high in the territories with a greater male density. Taking into account that a resident *cruentata* male can retain a territory for a period of 14-15 days, spending daily 5 to 6 hours in defending it against intruders (CÓRDOBA-AGUILAR, 1994a), the consideration of the energetic demand is interesting. This period is relatively long compared with the related species (e.g. 1-8 days in *Calopteryx maculata*; WAAGE, 1973), and could be perhaps attributed to the low population density during a particular season. Likewise, it is possible that the territorial tenure period in *H. cruentata* is influenced by longevity (emergence to maturation 15 to 18 days; CORDOBA-AGUILAR, 1995) and by the expected lifespan (44.9 days; CÓRDOBA-AGUILAR, 1994b).

Although weather conditions affected the male activity, males left the territories early, even on clear afternoons. This could be explained in two ways: either the males go off for feeding, or the female arrivals cease early, even though weather conditions are appropriate. Either explanation is feasible, considering how little time was spent on feeding while the males were defending their territories, and we never saw a female at the water side after 1400 h.

The influence of size on male alternative reproductive tactics has been recorded only in three odonate species, viz. *Orthetrum chrysostigma* (MILLER, 1983), *Megaloprepus coerulatus* (FINCKE, 1984, 1992), *Pyrrosoma nymphula* (HARVEY & CORBET, 1985), although it is a common pattern in other insect orders (cf. ALCOCK, 1979; BORGIA, 1980; THORNHILL, 1980; OTRONEN, 1984; CONNER, 1988). The different territorial tactics employed by the *cruentata* males were apparently not conditioned by their size. This is interesting, since in territorial contests, the winners were larger in wing length (CÓRDOBA-AGUILAR, 1994a). Although a positive relationship existed between the territory rank and the abdominal and total lengths in the resident *cruentata* males, this could have been largely incidental, since there is neither a relationship between a male's size and his mating success (CÓRDOBA-AGUILAR, 1994a), nor between the territory rank and the size of the sneakers. Although the wing length has been used as an index of body size (FINCKE, 1982, 1984; TSUBAKI & ONO, 1986, 1987), it did not correlate with the territory rank in *H. cruentata*, and it was not associated with the different tactics. In the same way, there were no size differences between the copulating and non-copulating males. The factors affecting different behavioral decisions in odonates still remain insufficiently known.

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