

ADULT SURVIVAL AND MOVEMENT IN MALES OF THE
DAMSELFLY *HETAERINA CRUENTATA*
(ODONATA: CALOPTERYGIDAE)

ALEJANDRO CÓRDOBA-AGUILAR

Instituto de Ecología, A. C., Biosistemática de Insectos. Apdo.
Postal 63. Xalapa, Veracruz. 91000 México

ABSTRACT

During a mark-recapture study of the territorial damselfly *Hetaerina cruentata* (Rambur), several changes in population size, survivorship and birth rates occurred, probably caused by physical conditions and a natural seasonal decline in population size. The average survival rate of males (expected value per day = 0.978) was the highest reported for the Calopterygidae and possibly all Odonata. This value could have been affected by factors that reduced energy expenditures at the end of the season. Analysis of male dispersion showed aggregated distributions, which are expected for territorial species. While most males dispersed, no age-class showed a tendency to move upstream or downstream. Adult females were rare; however, the sex ratio of nymphs was not significantly different from one.

Key Words: Population size, survivorship, movements, age, males, damselfly.

RESUMEN

Durante un estudio de marca-captura de la libélula territorial *Hetaerina cruentata* (Rambur), ocurrieron varios cambios en el tamaño poblacional, sobrevivencia y tasas de nacimiento, motivados probablemente por las condiciones físicas y una disminución natural del tamaño poblacional. La tasa de sobrevivencia masculina (valor esperado por día = 0.978) es la más alta reportada para un Calopterígido y quizás para todo el orden Odonata. Este valor pudo haber sido afectado por factores que redujeron los gastos energéticos al final de la estación. Los análisis de la dispersión de machos indicaron una distribución agregada, lo cual está de acuerdo con el comportamiento territorial de los machos. A pesar de que los machos se dispersaron, ninguna de las clases de edad mostró una tendencia a ir río arriba o abajo. Aunque las hembras adultas fueron raras, la proporción de sexos no fue estadísticamente significativa.

Ecological parameters frequently explain interesting biological variables. Much of community and population structure is well known today because of the study of species abundance and composition. Odonates are excellent models in population ecology, and population studies of some species have been extensive. However, most studies have been made on temperate species, and our knowledge of tropical species is still limited (Garrison & González-Soriano 1988).

The American genus *Hetaerina* is widely distributed in tropical areas, and well studied taxonomically (see Garrison 1990). Nevertheless, diverse aspects of behavior and ecology in this genus have been poorly described (Johnson 1961, 1962, 1963, Bick & Sulzbach 1966; also see Alcock 1982 and Eberhard 1986). Considering the volume of ecological information on other species of odonates, the conspicuousness of *Hetaerina* and the suitability of the rivers for study, it is surprising almost no population data is available except for a few records of *H. cruentata* biology (e.g. Williamson 1923). My aim in this study was to obtain detailed information on the population biology of a species in this interesting genus. Mark-recapture methods were used to

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study demographic parameters of a low-density population of the damselfly *H. cruentata*. Data were compared with those of other calopterygids.

MATERIALS AND METHODS

The study was carried out over 21 days (3-24 September, 1992) at the Sordo River (Fig. 1), which is situated north of Xalapa, Veracruz, Mexico (19°30'N, 96°95'W). The surrounding area is strongly disturbed by agriculture, but some areas still contain virgin forest vegetation. Other odonates found there were *Brechmorhoga vivax* Calvert (very common), *Argia fissa* Selys (common), *Apanisagrion lais* (Selys) (common), *Aeshna psilus* Calvert (rare), *Remartinia luteipennis florida* (Hagen) (rare) and a few species of Gomphidae (rare).

Eighty-nine 2x2 m quadrats were made along the three branches of the river. An indelible ink pen was used to write a distinct number, never exceeding three digits, on either anterior wing. Captures and recaptures were made just once daily, except on days 7, 9, 12, 13, 22 and 23. Sampling activity started at 0900 and ended at 1200-1230 hours. The following data were recorded for each sighting: individual number, sex, age, activity, time, quadrat and date.

Individuals were placed into one of three age classes: teneral, juvenile mature and old mature. Tenerals were those individuals recently emerged. In general, they were of soft, fragile construction, difficult to manipulate and flew in a zig-zag pattern. Teneral males did not possess the same blackish color as mature adults and the red spots at the bases of the wings were not intense. In teneral females, color was not as distinct as in the other age classes, but the fragility and weak flight was easily seen. Juvenile mature (**JM**) animals were identified by their color (principally the red basal wing spots in males and brilliant greenish body color in females). In old mature (**OM**) animals, body color was well developed and the wings were opaque. Some individuals showed wing damage. A fourth type, mature (**M**), was frequently assigned to those individuals in transition between juvenile and old mature. Only some of the population parameters for females could be obtained because they were very scarce at the study site.

Jolly's (1965) multiple capture and recapture method was used to estimate the number of marked animals in the population, population size, survivorship and the recruitment into the population. Jolly's population survivorship is a relative value ranging from 0 to 1 (values higher than 1 make no sense). The recruitment estimate is assumed to be the net increase resulting from birth and migration. Average daily survivorship (Garrison & Hafernik 1981) was also calculated by averaging daily sur-

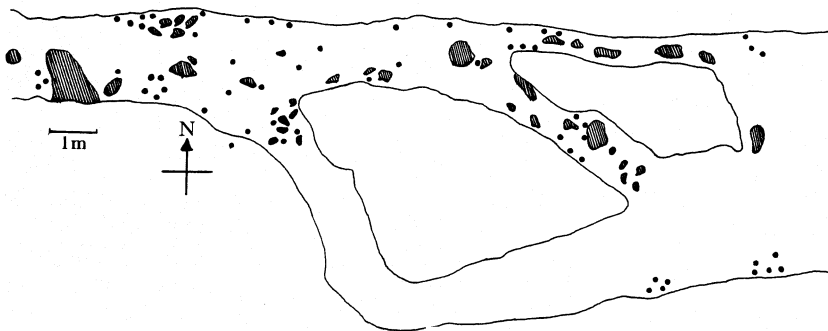


Fig. 1. Central portion of the study site (Sordo River, Xalapa, Veracruz, Mexico). Shaded areas are rocks. Points indicate distribution of individuals.

vivorship values. Values for missed days between recaptures were estimated as follows (Garrison & Hafernik 1981):

$$\text{one day survival rate} = (\text{survival rate})^{1/d}$$

where, d is the number of missed days taking into account the last day of recapture. The survival rate was translated into expected life-span by the method of Cook et al. (1967), which according to the average of daily survival rate, indicates a potential expected life-span in the population

$$\text{expected life-span} = \frac{-1}{\log_e (\text{average daily survival rate})}$$

Velocity patterns were calculated by Scott's (1974, 1975) procedure to obtain averages of total distance travelled in meters (D), time in days (T) and velocity ($V=D/T$). Adult velocity is used here as the distance travelled per time by an individual. For this species, this parameter is important because changes in velocity can reflect differences in territorial tenure. Damselfly movements were separated according to the direction travelled (upstream or downstream) and the age of the individual, looking for net changes in total displacement (not daily movements). These estimates of movements and velocity were made carefully only after checking the number of days elapsed between recaptures to avoid mistakes when assigning ages.

Morisita's (1959) index of dispersion, Lloyd's (1967) mean crowding index and the variance-to-mean ratio (Southwood 1979) were used to analyze population dispersion. For each method, values less than one indicate a uniform distribution, values greater than one indicate an aggregated distribution and a value of one indicates a random distribution. All χ^2 analyses include Yate's correction factor.

RESULTS

A total of 208 individuals was marked (Table 1). Recaptures differed greatly between sexes, showing, as in other studies, a greater percentage of males. An important factor in the study was that female numbers were low, probably because of a natural seasonal decline. Results referring to females must be interpreted carefully.

Population Size, Survivorship and Recruitment

The results of the estimates by Jolly's method are summarized in Table 2. There are two population peaks (see Fig. 2) on days 10 and 17 (about 1080 and 2700 individuals, Table 2). After day 17, the population decreased sharply. Population estimates probably increase on sunny days after a few days of rain, as could have been the case for days 7, 12 and 13 when strong rains fell on the river. However, this does not explain the peak on day 10 because it did not rain on day 9 (however, it should also be noted that one of the largest standard errors also occurred on day 10).

TABLE 1. RECAPTURE INDEXES OF *HETAERINA CRUENTATA*. N = TOTAL CAPTURED INDIVIDUALS, RC = NUMBER OF INDIVIDUALS RECAPTURED, %RC = PROPORTION OF MARKED INDIVIDUALS RECAPTURED.

Sex	N	RC	%RC
Male	182	118	64.8
Female	26	6	23.07
Totals	208	124	59.6

TABLE 2. POPULATION PARAMETERS OF *HETAERINA CRUENTATA* ESTIMATED PER DAY BY JOLLY METHOD (1965). M = MARKED POPULATION ESTIMATES, N = POPULATION SIZE, SURV = SURVIVORSHIP, B = NUMBER OF ANIMALS ENTERING INTO POPULATION, AND SE = STANDARD ERRORS.

Days	M	N±SE	Surv±SE	B
3	----	----	----	----
4	291	385±34	1.44±0.18	64
5	437	621±101	0.95±0.15	-4
6	427	588±104	0.77±0.09	41
8	341	496±58	2.61±0.71	-216
10	933	1083±295	0.35±0.09	73
11	337	462±61	2.44±0.79	-344
14	849	786±242	0.86±0.32	219
15	732	898±192	1.54±0.64	-98
16	1145	1288±479	1.91±1.27	237
17	2204	2708±1511	0.57±0.38	46
18	1279	1611±608	0.45±0.21	162
19	582	888±280	1.25±0.69	-141
20	757	976±465	0.38±0.23	23
21	293	395±162	-----	-----
24	----	-----	-----	-----

Survivorship fluctuated greatly. On several occasions, values higher than one were obtained; such values make no biological sense. The daily survival rate reflects the differences in the number of recaptures. High recapture rates were associated with high daily survival rates. The estimated survival curve for males captured on the first day, is shown in Fig. 3. This survival curve included individuals of all ages except tenerals (**JM** n = 9, **M** n = 7, **OM** n = 43). The curve clearly shows a decline throughout the study. No analysis of females was made due to their infrequent recaptures.

Average survival rate was 0.978 per day, which, when converted to life expectancy by Cook et al.'s method is 44.9 days. This result is compared with the survivorship and life expectancy of males of other species in Table 3.

Dispersion, Movements and Velocity

Morisita's index of dispersion for males was 3.63 which is statistically different from one ($p < 0.05$). Lloyd's mean crowding index was 2.19 ± 0.01 (S.E.) while the variance-to-mean ratio (Southwood 1978) was 2.75. All three indices indicate aggregated distributions. Aggregations of individuals in the central portion of the study site can be seen in Fig. 1.

The same number of **JM** males moved up the river as down. In **M** males, more individuals moved downstream, but the difference was not significant ($\chi^2 = 0.02$, d.f. = 1, $p > 0.05$). More **OM** males moved upstream than down, but this difference was also not significant ($\chi^2 = 0.93$, d.f. = 1, $p > 0.05$). There was, however, a significant difference when the number of individuals of each age dispersing was compared with those remaining in the same quadrat among recaptures. More **OM** and **JM** males remained in the same quadrats (or very close) ($\chi^2 = 16.6$, d.f. = 1, $p < 0.001$ for **OM**, $\chi^2 = 5.66$, d.f. = 1, $0.05 > p > 0.01$ for **JM**). Nevertheless, among **M** individuals none remained on the same quadrat for all recaptures (n = 25). Although there were more animals (regardless of age) that moved upstream (64%) than downstream (36%), the

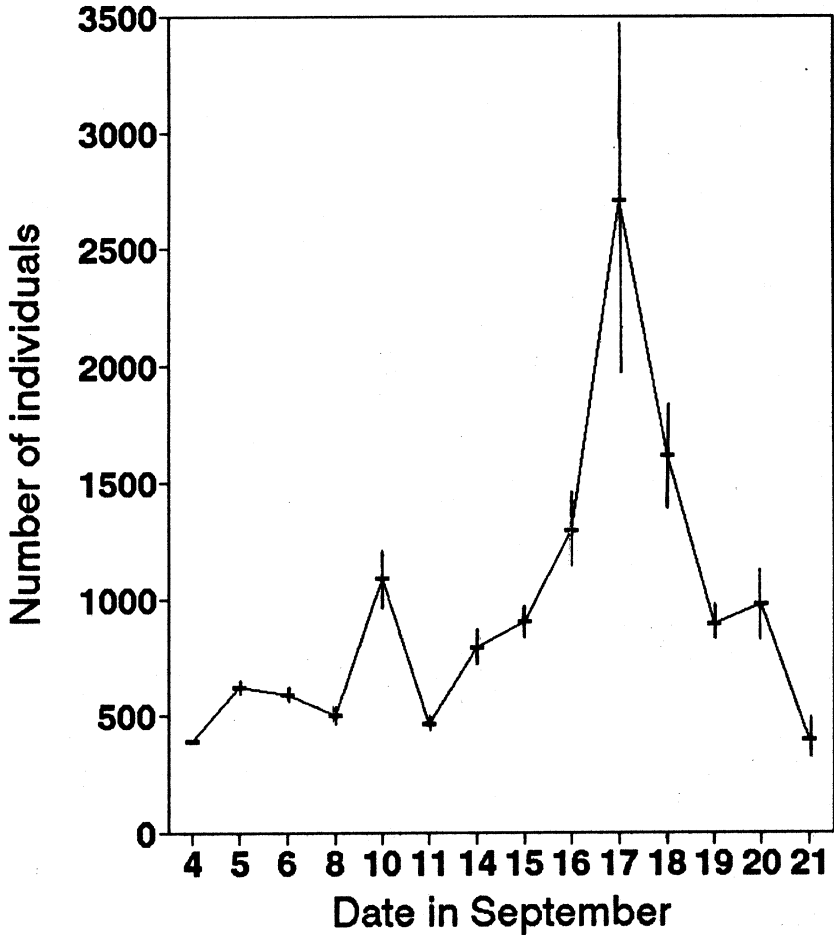


Fig. 2. Estimated population size in *Hetaerina cruentata* as estimated by Jolly (1965) method in the study. Vertical lines are standard errors.

TABLE 3. AVERAGE SURVIVORSHIP COMPARISONS AMONG MALES IN SEVERAL SPECIES OF CALOPTERYGIDAE AND THEIR EXPECTED VALUE IN DAYS. 1 = CORDERO (1989), 2 = CONRAD & HERMAN (1990), 3 = HIGASHI (1976 IN CORDERO, 1989), 4 = NOMAKUCHI ET AL. (1988), AND 5 = THIS STUDY. ESTIMATES IN PARENTHESES IN *CALOPTERYX HAEMORROIDALIS* AND *MNAIS PRUINOSA* (4) REFER TWO COMPARATIVE AVERAGES.

Species	Avg	Days
<i>Calopteryx virgo</i> (1)	0.86	6.6
<i>C. haemorroidalis</i> (1)	0.94 (0.91)	16.2 (10.6)
<i>C. xanthostoma</i> (1)	0.66	2.4
<i>C. aequabilis</i> (2)	0.767	3.8
<i>Mnais pruinosa</i> (3)	0.943	-----
<i>M. pruinosa</i> (4)	0.944 (0.947)	17.6 (18.4)
<i>Hetaerina cruentata</i> (5)	0.978	44.9

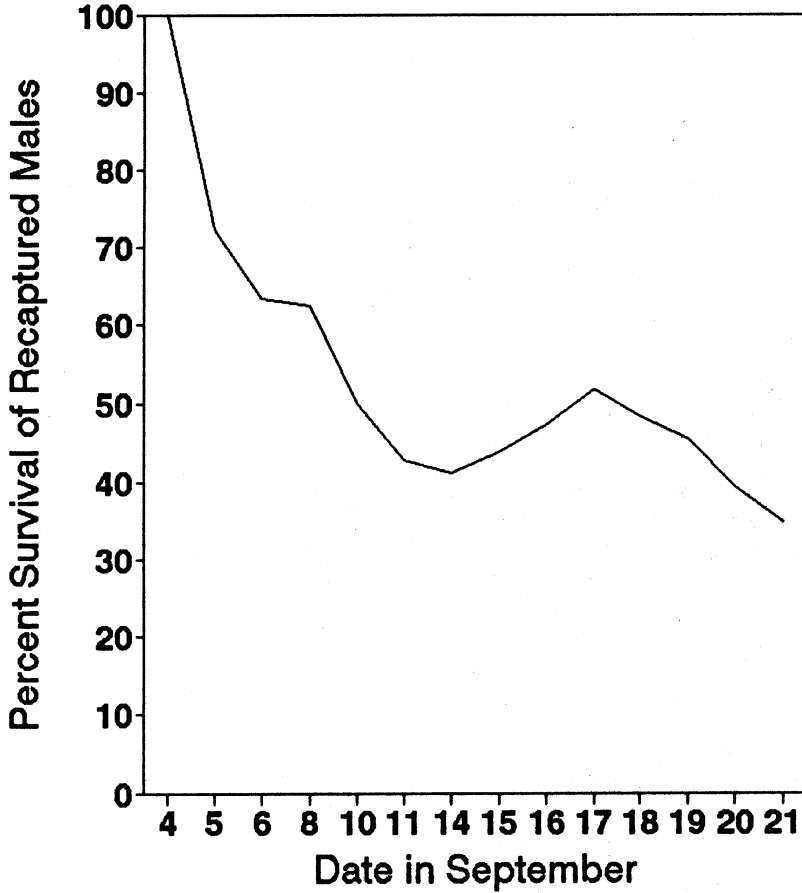


Fig. 3. Estimated percent of survivorship in males of *Hetaerina cruentata* captured in the first day of study ($n = 59$).

difference was not significant ($\chi^2 = 1.05$, d.f. = 1, $p > 0.05$). Movement patterns of teneral and females could not be estimated.

Scott's velocity indices were as follows: time in days between first and last recapture in males was 11.4, mean of total distance travelled in m was 44.3, and the mean velocity was 3.9 m per day. For individual velocities, males only and different age classes were analyzed separately. The procedure used was to take the quadrat of the first recapture (after capture) and calculate the number of days between captures. This short interval among captures meant age did not change much between captures. There were no velocity differences among age classes (one-way ANOVA, $p > 0.05$). Distances travelled between males and females differed significantly (t test = 2.13, d.f. = 29, $p < 0.025$). Females had higher velocity patterns as in other species of *Calopteryx* (see Cordero 1989, Conrad & Herman 1990, Waage 1972). The differences among teneral and the other age classes is probably great because a teneral was never recaptured within 15 m of the river. Two males travelled 66.9 m between successive recaptures while other males remained in the same quadrats for several days. This fact has been reported previously for other calopterygid species [*He-*

taerina americana (Fabricius), Johnson 1962; *H. vulnerata*, Alcock 1982; *H. macropus* Selys, Eberhard 1986].

Sex Ratio and Mortality

Operational sex ratio always was notably skewed toward males (182 males, 26 females), but these estimates do not reflect the primary sex ratio and result mainly from behavioral differences between the sexes. Estimates of sex ratio were obtained also by sexing larvae. In spite of a slight deviation toward females (43 females, 36 males), the ratio was not significantly different from 1:1 ($\chi^2 = 0.455$, d.f. = 1, $p > 0.05$).

During the study, no attacks by vertebrates like birds, frogs or fishes were noted although they are usually regarded as common predators of other odonates. On one occasion an ovipositing female was attacked by a giant aquatic bug (Family Belostomatidae). Some newly emerged individuals were found in spider webs. Although the sampling quadrats increased spider density by providing new, favorable places for webs, no adults of *H. cruentata* were observed in these webs.

DISCUSSION

Population size (Fig. 2) may have changed during the study as a result of strong rains, which affected afternoons and occasionally whole days. The rains may also have been responsible for the highly fluctuating survivorship (Table 2). However, other reasons exist for these changes (predation, migration, among others) that could not be measured. As the study progressed, captures decreased and this affected several additional parameters, including the Jolly's estimates (especially the S.E.'s).

Cordero (1989) found that recaptures (% RC) in three species of *Calopteryx* (*haemorroidalis*, *xanthostoma* and *virgo* L.) did not exceed 53% for both sexes. The highest percentage was for *C. virgo* (54%). In this respect, *H. cruentata* males showed a relatively high percentage (64.8%, Table 1) of recaptures. The highest frequency of recaptures for a damselfly is that of *Ischnura gemina* (Kennedy) (Garrison & Hafernik 1981) with 84% for both sexes and 90% for males alone. In addition, if it is assumed that during the study the population was at low density when compared with other months (pers. obs.), then the high recapture rates (higher than other species of Calopterygidae) could result because males are better able to successfully defend territories for several days when there is relatively little competition for sites. Comparisons within the calopterygids and with other species are needed to test this hypothesis.

Primary sex ratio was not different from one in *H. cruentata*. The same occurs in other members of the calopterygids as *Calopteryx virgo*, *C. haemorroidalis*, *C. xanthostoma*, *C. virgo* (Cordero 1989), *C. maculata* (Beauvois), *C. dimidiata* (Waage 1980). Waage (1980) has pointed out that the sex ratio should be 1:1 among all odonates.

Survivorship estimated by Jolly's method was quite variable (Table 2), but shows a general decline over the month. Some of the variation probably results from including several age classes in the analysis. The curve declines mainly due to the mortality of **OM** animals. **JM** individuals presumably experience different mortality pressures. It is interesting to note that the survival rate by Cook et al.'s method was the highest (44.9 days) in the suborder, and perhaps for odonates in general. Corbet (1958) has pointed out that adult life-span of neotropical damselflies is longer compared with those of temperate latitudes, presumably due to less variable abiotic conditions in the tropics. However, reduced energetic expenditures may have also lengthened life in *H. cruentata*. These factors could include reduced activity in rainy

days because of cooler temperatures or reduced competition for territories due to low density conditions.

H. cruentata is a territorial species with behavioral biology similar to other calopterygids (Córdoba-Aguilar 1994). Several males perch, aggressively defending certain areas (oviposition sites) against other males, where females arrive, searching for copulation and oviposition. These sites have high male density in relation to others where oviposition sites do not exist. Under low density conditions, movement of mature males are minimal, and presumably male velocity diminishes due to the availability of many defensible territories, as has been demonstrated in *Calopteryx aequabilis* Say at low density by Conrad & Herman (1990). Likewise, when density is modified, other behavioral parameters are modified too. For example, fights among territorial males in *Mnais pruinosa* Selys at the transitional period (when there were mature and immature individuals in the population and at, presumably, low density) influenced movements on the stream of individuals that could not win a territory (Nomakuchi & Higashi 1985). Once these males established their territories, and density was higher, they moved infrequently (Nomakuchi & Higashi 1985). This result was similar to territorial males of *H. cruentata*. However, other conditions can influence dispersal and movements. In general, animals experiencing poor feeding or mating opportunities are usually more likely to disperse than those with good conditions (Lomnicki 1978, Lawrence 1987).

On the other hand, the few differences among age classes in movements and velocities are interesting. Eberhard (1986) observed that *Hetaerina macropus* Selys periodically left the river but had a low tendency to disperse, in general. Cordero (1989) found that in *Calopteryx haemorroidalis*, juvenile males moved greater distances than mature males, and movements in *C. xanthostoma* were up river probably resulting from strong winds. Likewise, Higashi & Ueda (1982) found similar results in a greater percentage of individuals of *C. cornelia* (Selys). Nevertheless, *H. cruentata* males did not display significant upstream or downstream movements. More studies are needed to examine dispersal at high densities.

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