Odonatologica 17(4): 365-378 *December 1, 1988*

REPRODUCTIVE BEHAVIOR OF THE DAMSELFLY *CALOPTERYX DIMIDIATA* BURMEISTER (ZYGOPTERA: CALOPTERYGIDAE)

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Received June 8, 1988 / Accepted July 11, 1988

The reproductive behavior of *C. dimidiata* is described for populations at the northern edge of its range where it is sympatric with *C. maculata*. Like other *Calopteryx* spp. *C. dimidiata* males are territorial, give a pair-forming and postcopulatory display (= cross display) to females at an oviposition site in their territory, and give courtship displays to perched females. Males and females copulate frequently and for short times relative to other damselflies, and sperm removal occurs during the early stages of copulation. Females oviposit into aquatic vegetation, usually in a male's territory. The primary behavioral differences between *C. maculata* and *C. dimidiata* are that in *C. dimidiata:* (1) the cross display is performed while the male floats on the water surface rather than while perched on an oviposition site, (2) females oviposit while totally submerged rather than at the water surface, and (3) there is no clear daily peak in copulation or oviposition frequency. The reproductive behavior of *C. dimidiata* is also compared with published results for other North American, European and Japanese *Calopteryx* spp.

INTRODUCTION

Species of the genus *Calopteryx* are atypical among temperate zone damselflies (Zygoptera) in the complexity of their aggressive and reproductive behaviour. Males are territorial at oviposition sites (emergent aquatic vegetation) along streams, defending these sites with displays and chasing (e.g., BUCHHOLTZ, 1951; HEYMER, 1973; PAJUNEN, 1966; WAAGE, 1974, 1983). Males give distinct pair-forming displays of wing and abdominal coloration to females approaching these sites and continue to display their wings while performing a hovering courtship flight in front of perching females (e.g. HEYMER, 1973; PAJUNEN, 1966; WAAGE, 1974). Unlike most damselflies, which oviposit in tandem, *Calopteryx* exhibit non-contact guarding with the male perching nearby his ovipositing mate, and chasing away another males (ALCOCK, 1979, 1983; WAAGE, 1974, 1979b). Finally, males and females of this genus may mate from one to several times daily and males appear to remove most or all of the sperm of previous mates prior to inseminating a female (WAAGE, 1979a, 1980).

The behavior of three European species, *Calopteryx virgo, C. splendens* and *C. haemorrhoidalis* has been described (BUCHHOLTZ, 1951, 1955; HEYMER, 1973; KLÖTZLI, 1971; PAJUNEN, 1966; ZAHNER, 1960) as has that of three Japanese species, *C. virgo japonica, C. atrata* and *C. cornelia* (MIYAKAWA, 1982; SUZUKI & TAMAISHI, 1981). However, the behavior of only two of the five North-American species has been described: *C. maculata* (ALCOCK, 1979, 1983; JOHNSON, 1962; WAAGE, 1972, 1974, 1978, 1979a, 1979b, 1980, 1983, 1984a, 1984b, 1987, 1988), and *C. aequabilis* (CONRAD & HERMAN, 1987).

In this paper I describe several aspects of the reproductive behavior of a third common North American species, *C. dimidiata*. The description is for populations at the northern extreme of the species range where it is sympatric with both *C. maculata* and *C. aequabilis*. I then compare the pair-formation, copulation and postcopulatory behavior of *C. dimidiata* with that of other *Calopteryx* species, especially *C. maculata*.

METHODS

Most observations were made along the Palmer River in Rehoboth Massachusetts (Bristol County) during the summers of 1977, and 1979-82. These observations were supplemented by occasional notes from other years and other streams in southern Rhode Island taken during an ongoing study of *C. maculata*. This paper is based on about 140 hours of direct observation of *C. dimidiata* and an unknown number of hours of behavioral events seen while watching *C. maculata*. Where possible, individuals were distinctly marked with dots of enamel paint on their wings or with a number written on the clear area of a wing with a felt-tipped pen.

Two small scale mark-recapture studies were done in 1979 and 1980. In 1979, 47 males and 34 females were individually marked along a 100 m section of the Palmer river. In 1980, 34 males and 47 females were marked in the same area. Recaptures were limited to sightings of individuals in the marking area and to occasional censuses of 600-800 m upstream from the study area.

The reproductive potential of females was assessed by capture and dissection of solitary females and mating pairs in various contexts. Ovaries were removed and mature (dark yellow) eggs counted (see WAAGE, 1980 for details and a comparison with *C. maculata*).

Data presented in this paper are: mean +/- standard error (sample size). For significance tests either analysis of variance or non-parametric tests (Chi-square and Wilcoxon tests) were used.

RESULTS

TERRITORIAL BEHAVIOR

Quantitative data on territorial behavior and the dynamics of intermale contests for territories are not yet available for *C. dimidiata*. However, qualitative comparisons can be made with *C. maculata* and other species. *Calopteryx dimidiata* males localized at and defended territories centered on emergent or barely submerged aquatic vegetation, usually *Sparganium* spp. Territories also contained one or more perch sites on emergent vegetation or adjacent to it on shore. Territory size, as defined by reaction distances to approaching males, was quite variable and ranged from 1 to 4 m in diameter. Male-male interactions were clearly aggressive and involved chasing and spiraling flights typical of other *Calopteryx* (PAJUNEN, 1966; RÜPPELL, 1985; WAAGE, 1983, 1988) as well as occasional prolonged escalations that involved intense spiraling and chasing over 3-12 m of stream.

Territorial males were resident at the same oviposition sites for periods of <1 to 29 days (mean=6.6, median=3, for 10 males seen at the same site on two or more days). Some males changed locations daily and several males might localize at the same oviposition site for several days, with occasional fights among them.

PAIR FORMATION

Figures 1 and 2 show the results of 317 male-female encounters in two contexts: (a) the female flew into a male's territory or toward the oviposition site where he was located, and (b) the female flew above the oviposition site from a perch on shore within a male's territory, usually during a feeding flight. The interactions from encounter to copulation were similar for both contexts, but different with respect to the relative frequency of various components. I will first describe the typical pattern for encounters leading to copulation in each context and then examine the differences between contexts.

When a female flew within 1-2 m of a male's oviposition site and was less than 1 m above the water surface, the male would fly rapidly to the oviposition site and drop to the water surface with his wings slightly spread and the distal part of his abdomen curled dorsally (Cross Display — Figs 1, 2). He floated on the water surface for 10-50 cm and if the female continued to fly around the oviposition site, he would repeat the floating cross display. Receptive females would fly to shore and perch (Female Lands). Non-receptive ones would leave the territory (Female Flies) or attempt to oviposit.

The males would follow the female to shore and hover before her in courtship flight (Male Courts) characteristic of the genus (BUCHHOLTZ, 1951; HEYMER, 1973; PAJUNEN, 1966; WAAGE, 1974). The duration of courtship flight varied from several to as many as 45 s. Unlike *C. maculata* males, *C. dimidiata* males were able to relocate perched females on shore if courtship was interrupted by the approach of another male or when the courting male flew down to his oviposition site and back to the perching female. A receptive female

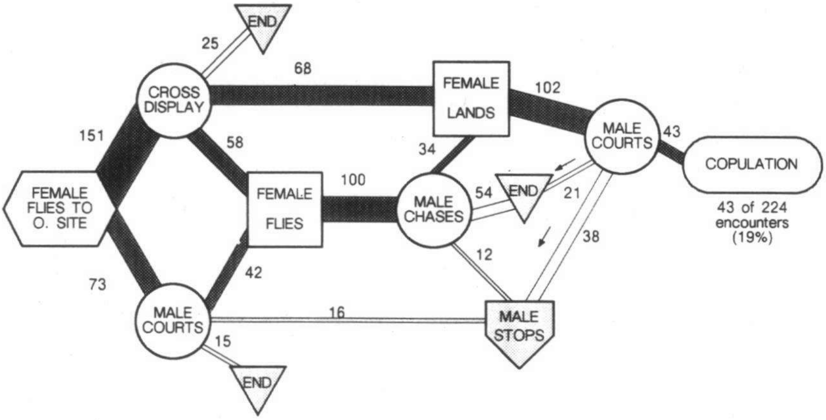

Fig. 1. Flow diagram for 224 male-female interactions when a female flew into a male's territory. Circles indicate male actions and squares are female's. "Male stops" means a male stopped his pursuit or courtship of a female and returned to his perch. "End" means the interaction was terminated by: the female flying away or submerging to oviposit, or interference from other males. Numbers and width of lines indicate the number of events following a given path. All flow is to the right except where indicated by arrows. See text for explanation of overall pattern.

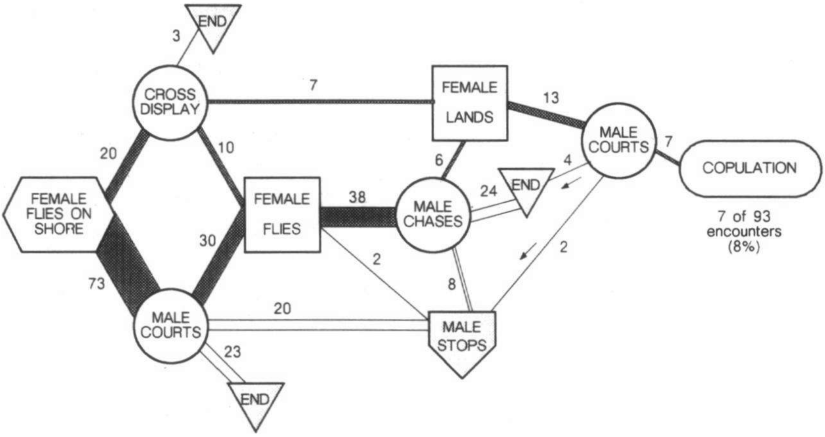

Fig. 2. Flow diagram for 93 male-female interactions when a female was discovered flying on shore or out from a perch on shore. See Fig. 1 for explanation of diagram.

would flip her wings several times while being courted and the male would then land on the forward edges of her wings, form the tandem position and copulate. Following copulation the male would return to his territory and wait for his mate to return for oviposition.

The major variant for this encounter context (Fig. 1) involved the male flying out to an approaching female using courtship flight (rapidly whirring wings — Male Courts). He would then pursue the female (Flies-Chases-Lands) along the shore where, if she landed, additional courtship and occasionally copulation would occur. Male-female interactions were terminated (Male Stops, End), when (a) a male stopped spontaneously and returned to his perch, (b) other males joined the pair and a fight resulted, (c) the female flew away from or was lost by the male and (d) when the female submerged to oviposit.

Males also discovered females flying on shore (Fig. 2), either during a chase by another male or during a feeding flight by the female. Females often perched in bushes near male territories to feed. Pair formation in this encounter type primarily involved pursuit and courtship of the flying female, sometimes for several meters along the shore. This second encounter type led to significantly fewer matings (7 of 93 versus 43 of 224 encounters, χ^2=6.74, df=1, P=0.009).

The major difference in behavioral sequences between the two contexts was the frequency with which the cross display was given. It was given significantly more often to females flying near the water and along the stream (first context) (151/194 times) than the females flying out from shore (20/93 times, χ^2=55.74, df=1, $P < 0.001$). There were no differences between encounter types in the likelihood that males would stop courting or pursuing a female (66 of 224 times for the first type and 32 of 93 times for the second encounter context — χ^2=0.74, df=1, $P > 0.10$).

COPULATION, SPERM DISPLACEMENT AND POSTCOPULATORY INTERACTION

Once in copula, the behavior of *C. dimidiata* was indistinguishable from that of *C. maculata* (WAAGE, 1979a). Sperm translocation lasted several seconds (not timed) and was followed by copulation lasting from 48-274 s (mean=140.6 +/- 7.3 s, n=61). During copulation rocking and pumping movements, characteristic of sperm removal, occurred during the first 1-1.5 min. I compared volumes of sperm stored by females collected at one of three stages in copulation (before, during and after, see WAAGE, 1979a, 1984a) to determine the extent of sperm removal.

Sperm volume indices for a sample of 54 females are shown in Table I. Since relatively few pairs were caught in tandem but prior to copulation, I used sperm volumes of females collected in the morning as a sample of the females likely to mate. Since all females collected during copulation had some sperm, I assumed that the sperm volume values for females collected either early in the day were reasonable estimates of the amounts of sperm carried by mating females. These females had significantly more sperm than those from interrupted copulations. Thus there was considerable removal of sperm during mating.

Comparing average postcopula sperm volume with that of interrrupted copula (Tab. I) revealed that an average of 98% of the sperm carried by postcopula

Table I

Sperm displacement during copulation by *Calopteryx dimidiata*. Values are an index of sperm volumes for females captured in various contexts (see WAAGE, 1979a). Means followed by different letters are significantly different at the $P < 0.05$ level (ANOVA)

Context	N	Mean	S.E.	
Precopula	10	610.0	154.8	A
Interrupted Copula	5	32.4	9.7	B
Postcopula	12	1372.8	175.3	C
Post oviposition	14	1258.1	144.1	C
On stream	13	1495.2	196.3	C

females belonged to the last male to mate with her. Post-oviposition females had sperm volumes that were 92% of that in postcopula females. Females collected early in the day had only 41 to 48% as much sperm as those collected later (postcopula, post oviposition and on stream). These differences were significant (Tab. I) but there were no significant differences between sperm volumes carried by females in the postcopula, post oviposition and on stream (afternoon) contexts.

Following copulation a male would return to his territory and fly over the oviposition site there one or a few times. He then perched near it until his mate flew down from shore. Females usually returned within a min of the end of copulation, but sometimes remained as long as 3 min (occasionally they would not return at all — see below). When his mate returned, or when a second female approached the oviposition site prior to his mate's return, the male repeated the initial floating cross display as the female attempted to land on the oviposition site. If the vegetation was below the water surface, males would continue to repeat the cross display as long as the female remained in the area and tried to grab hold of the vegetation.

OVIPOSITION

C. dimidiata females were never seen to oviposit while at the water surface. Instead they would first land on emergent vegetation (mostly *Sparganium* sp.) and walk down a leaf until completely submerged before beginning to probe with their ovipositor. Usually a female would walk to the base of the plant before beginning to oviposit. When vegetation was just below the surface they would fly back and forth until a leaf broke the surface or would dive into the water to grasp a leaf just below the surface.

Oviposition duration, including moving about and probing, ranged from 1 to 40 min (mean=17.3 +/- 1.0, n=68). the average number of eggs oviposited by

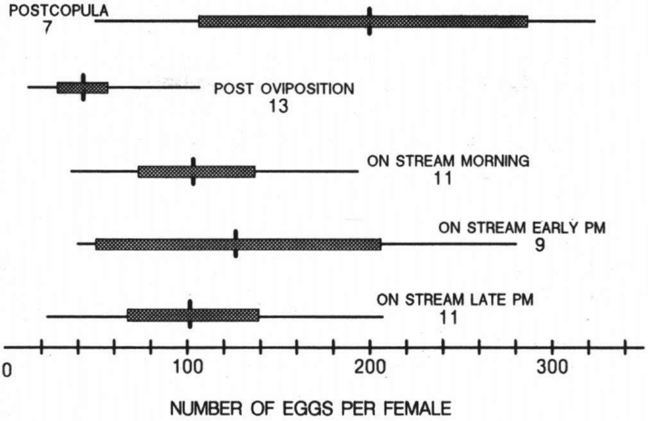

Fig. 3. Number of eggs per female *Calopteryx maculata* collected in seven different contexts (cf. text). Vertical line, solid box and horizontal line are, respectively, mean, 95% confidence limits and range. Sample sizes are given below each label.

females can be estimated from the data shown in Figure 3. Postcopula females averaged 202 eggs and post oviposition ones 43 eggs. Thus about 159 eggs were laid on average in 17.3 min for an estimated oviposition rate of 9.2 eggs min for submerged *C. dimidiata* females. The fact that post oviposition females had very few eggs (see Fig. 3) suggests that a 15-20 min bout of oviposition was sufficient to deposit most of the female's eggs on a given day. Females were rarely seen to oviposit more than once on the same day, although it was relatively easy to miss females going underwater and they were hard to find if not seen entering the water.

Two categories of ovipositing females were observed: those ovipositing following copulation with the resident male and those coming from elsewhere without an immediately preceding copulation. There was no significant difference in oviposition duration for these two contexts ($F=0.721$, $df=1.54$, $P > 0.25$). Nor was there any significant relation between the duration of an oviposition and the time of day it occurred ($F=2.22$, $df=5.52$, $p > 0.05$).

When females resurfaced from a bout of oviposition, they often appeared weakened and had trouble breaking free of the water surface or flying to shore. Males displayed to or courted these females, but only 1 of 11 observed resurfacings led to a mating. The other females gave a refusal display which resulted in the male stopping (7 of 10 times) or they flew away when the male approached (3 of 10 times).

TIME OF DAY FOR COPULATION AND OVIPOSITION

Figure 4 shows the number of observed copulations and ovipositions initiated per hour of observation. This includes data from all years and at a variety of densities of *C. dimidiata*. Thus it is only an indication of a general pattern. There was no clear daily peak in either copulation or oviposition behavior as was found for *C. maculata* (WAAGE, 1980 and Fig. 5). There was a tendency for more oviposition activity early and late in the day, but the way the data were collected does not allow a statistical test of the significance of this trend. In contrast with a comparable data set for *C. maculata* (Fig. 5, from WAAGE, 1980) copulations and ovipositions by *C. dimidiata* were less frequent than the relative population densities would predict (see Tab. III in WAAGE, 1980). *C. maculata* were about 1.4 to 2.7 times as numerous in censuses done in 1976 and 1977, but never 4 to 6 times as numerous as would be suggested by comparing the average number of copulations or ovipositions per hour in Figure 5. However, since *C. dimidiata* females do not leave the water between matings (WAAGE, 1980) the census data may overestimate the number of receptive females available. Thus the data in Figure 5 are only a suggestion that reproductive interactions in *C. dimidiata* may be less frequent than in *C. maculata*.

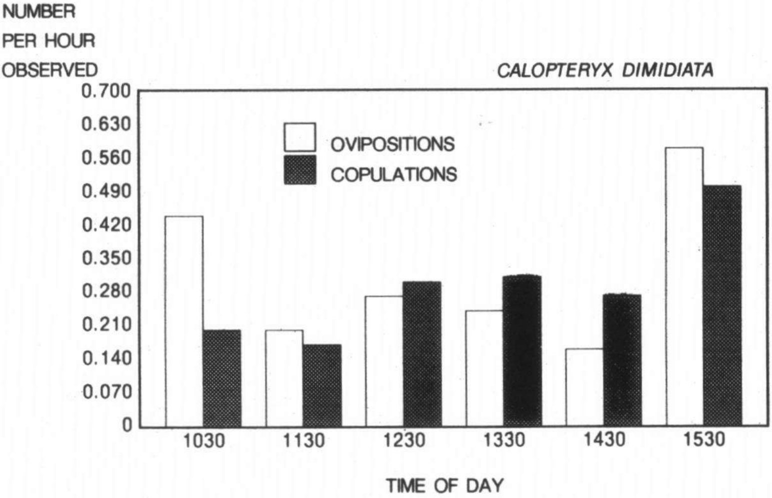

Fig. 4. Number of copulations and ovipositions seen per hour of observation at various times of day (EST) in Rhode Island and S.E. Massachusetts populations between 1979-1982. 140 hours of observation are involved, see text.

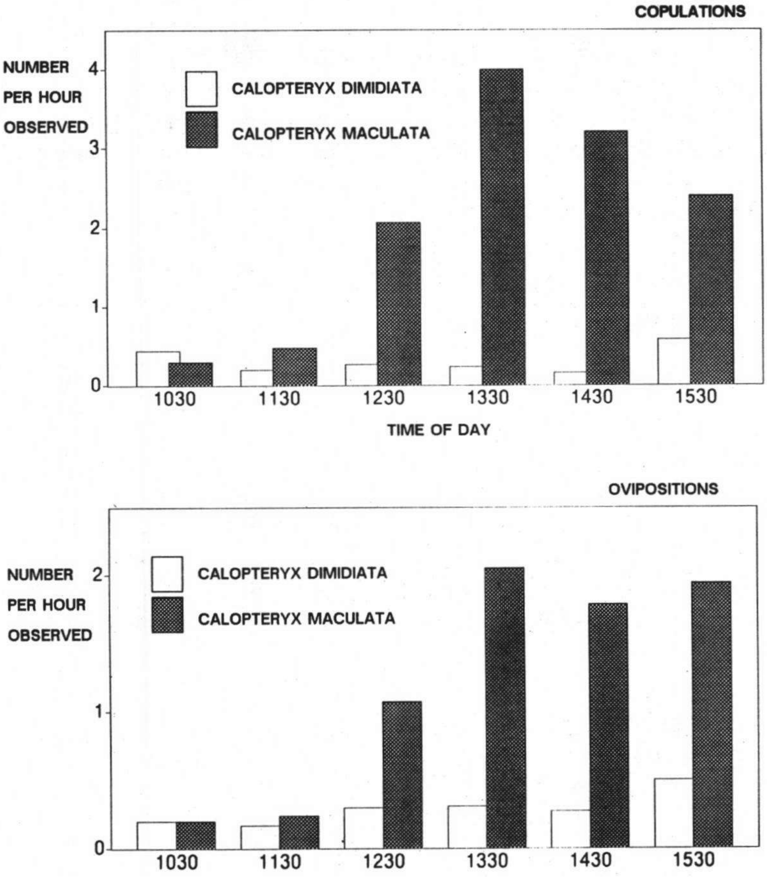

Fig. 5. Comparision of activity (number of events seen per hour of observation) for *Calopteryx maculata* and *C. dimidiata* at various times of day (EST). The *C. maculata* data are from WAAGE (1980) and those for *C. dimidiata* are from Fig. 3. Population densities of *C. maculata* were 1.4 to 2.7 times those of *C. dimidiata*. — (A): Number of copulations per hour of observation; — (B) Number of ovipositions per hour of observation.

FREQUENCY OF MATING FOR MALES AND FEMALES

Despite the small samples of marked males and females it is clear that both male and female *C. dimidiata* mate more than once per lifetime. Of 9 marked males seen mating, 3 mated once, 5 mated three times and 1 mated four times. For 12 marked females, 9 mated once and 3 mated twice. Of 13 marked females seen ovipositing, 11 were seen once and 3 twice (all oviposited on consecutive days).

LONGEVITY ESTIMATES FOR MALES AND FEMALES

Mark-recapture data from 1979 and 1980 provide rough estimates of male and female longevity (Tab. II). Since both males and females remain at the water from emergence until death (WAAGE, 1980). there is less chance of bias against recapture of females, but more chance of including males and females not yet sexually mature. In addition, sampling intervals and sampling areas were not regular. Given these limitations, the average time between marking and last resighting of individuals seen at least once was 4.65 +/- 0.8 days for males (n=59 of 81 marked in the two years) and 7.35 +/- 0.9 days for females (n=42 of 81 marked in the two years).

This difference between sexes was significant and largely attributable to a higher probability of encountering a marked female more than twice in the area surveyed. Table II shows that a significant (χ^2=8.48, df=3, P< 0.04) excess of females over males was seen more than once (where at least a day separated each sighting). This suggests a bimodal distribution of male movement and a short tenure of males at a given site relative to females. A few males remained for more than a week at the same or nearby sites, but most seemed to disperse from the area after a few days. Subjectively, females were less localized within the sampling area, but tended not to move out of it as much.

Table II
Recaptures — years pooled (1979 +1980)

Sex	N	No. times seen again				
		0	*1*	*2*	*3*	*4+*
Male	81	24	29	14	7	7
Female	81	30	13	14	13	1

χ^2 = 9.45, df = 4, P = 0.0508; — For just those seen again: χ^2 = 8.48, df =3, P = 0.037

FEMALE REPRODUCTIVE POTENTIAL

Samples of females collected for an analysis of sperm displacement were also examined for the number of mature eggs females carried. This gave an estimate of the reproductive potential of females in various contexts (WAAGE, 1980). Mating females carried an average of 202 eggs (Fig. 3), nearly twice the number carried by females collected at the water at various times of day (means = 104, 126, and 102 for females collected in the morning, early afternoon and late afternoon). These differences between the number of eggs carried by mating females and those captured at random on the stream were significant ($P < 0.05$, ANOVA). There was no difference in egg number among females captured along the stream at different times of day. Post oviposition females had significantly fewer eggs (mean = 43) than either copulation females or those collected along the stream.

DISCUSSION

COMPARISON WITH *C. MACULATA*

WAAGE (1980) suggested that *C. dimidiata* males and females are always at the water while in *C. maculata* females tend to remain away from the water between ovipositions. The present study supports this distinction in several ways. First, the lack of difference in mean egg number for *C. dimidiata* females collected at different times of day (Fig. 3) is in contrast to data from *C. maculata* (WAAGE, 1980) which showed a decrease in average egg number with time of day. Second, the ranges for the number of eggs per *C. dimidiata* female overlapped considerably for the five contexts. Both trends are expected if *C. dimidiata* females remain at the water during their lives. Thus samples of copulating and post oviposition females probaly represent tails of the distribution of eggs per female in the entire population. In contrast, in *C. maculata* the females sampled at the water are a sample from the upper end of eggs per female in the population (WAAGE, 1980).

WAAGE (1984b) has shown that the interspecific difference in female oviposition behavior, surface versus submerged oviposition, appears to affect the dynamics of male-female interactions during courtship in *Calopteryx maculata* and *C. dimidiata. C. dimidiata* males do not have much control over the access of females to their territories. In turn, *C. dimidiata* females tended to re-mate less often while completing oviposition at more than one site. These differences were reflected in the dynamics of pair-formation (contrast Figs 1 and 2 with those in WAAGE, 1984) and in the apparent tendency of *C. dimidiata* females to enter matings with relatively less sperm (contrast Tab. I with Tab. I in WAAGE, 1979).

C. dimidiata male-female interactions are further affected by the lack of male control over female access to oviposition sites and by the fact that females do not leave the water after oviposition. A greater proportion of females were not receptive or not ready to oviposit than was true for *C. maculata* females at the water (WAAGE, 1980). Finally, *C. dimidiata* female reproductive activities were spread fairly evenly throughout the day and may have been less frequent in general relative to population density. This further decreased male mating expectancies at any place or time.

These aspects of *C. dimidiata* female behavior may also influence male-female interactions relative to *C. maculata.* Qualitatively, males of *C. dimidiata* seemed to be less localized, more tolerant of intruders and to exhibit lower degrees of site tenure than males of *C. maculata* on the same streams. This and the fact that they stop courting females more frequently than *C. maculata* males (WAAGE, 1984b) may reflect the fact that *C. dimidiata* males have less control over female access to oviposition sites and cannot harass submerged females. The apparent advantages to *C. dimidiata* females of submerged oviposition and the occasional observation of prolonged submerged oviposition by *C. maculata* females raises the question of the adaptive significance of submerged versus surface oviposition. This is currently being investigated for these and other *Calopteryx* species.

COMPARISONS WITH OTHER *CALOPTERYX* SPECIES

MIYAKAWA (1982) summarized the pair-forming, copulation and oviposition behavior of *Calopteryx* species from Japan, Europe and North America. Territorial males of all *Calopteryx* species so far studied (N=9) perform a characteristic pair-forming (cross) display at an oviposition site to incoming females. The display is repeated when the female returns to oviposit after mating with the resident. There seem to be three forms of the display: (a) male perched on the oviposition site, hind wings spread and tip of abdomen curled dorsally — *Calopteryx maculata,* (b) male hovering at the water surface above an oviposition site with hind wings extended and held toward the water surface, abdomen straight — *C. aequabilis, C. atrata,* and (c) perching on or floating above the oviposition site with wings partly spread and abdomen curled dorsally — *C. dimidiata, C. virgo, C. virgo japonica, C. cornelia, C. haemorrhoidalis, C. splendens* (references: CONRAD & HERMAN, 1987; MIYAKAWA, 1982; WAAGE, 1974, this paper). There is no strong correlation between display type and whether or not oviposition is at or below the water surface. For example, in *Calopteryx maculata* both the display and oviposition occur on plants at the water surface; but in *C. haemorrhoidalis* and *C. atrata* where oviposition is similar, the display involves hovering above or gliding over the oviposition site. Once the display patterns for the remaining *Calopteryx* species have been determined, it should be possible to investigate whether similar displays represent convergence due to habitat, divergence due to the presence of other *Calopteryx* species, or homology within different lineages of *Calopteryx* species.

The duration of copulation for *C. dimidiata* falls within the range reported by MIYAKAWA (1982) for other *Calopteryx* species: 77 s (*C.atrata*) to 254 s (*C. cornelia*). These are short copulations for zygopterans and probably reflect the fact that *Calopteryx* species tend to be territorial and to mate frequently (WAAGE, 1984a). In North America the recorded durations of copulation tend to be longer for *Calopteryx* species with lower mating frequency: *C. maculata,* mean = 101 s, range = 30-300 (WAAGE 1974); *C. maculata,* mean = 141 s, range = 48-274 (present study); and *C. aequabilis,* mean = 169 s, range 73-356 (CONRAD & HERMAN, 1987). However these data involve different locations, population densities and sample sizes.

Calopteryx dimidiata, at least in the northeastern U.S., appears to oviposit exclusively underwater. Sympatric populations of *Calopteryx aequabilis* also oviposit while submerged, but several populations in North America are known to show mixed surface and submerged oviposition (J.K. Waage, pers. obs. and

CONRAD & HERMAN, 1987). In Europe and Japan, *C. virgo, C. virgo japonica, C. cornelia* and *C. splendens* exhibit mixed oviposition. It is not clear why such variation occurs within and between species, but it may relate to stream flow, oviposition site location or the degree of male harassment during oviposition. Submerged oviposition may also have physiological costs as is evidenced by the apparently weakened condition of some *C. dimidiata* females following a long period of submerged oviposition (see also FINCKE, 1986). The duration of submerged oviposition is difficult to time and there are few samples for comparison among species. However, *C. dimidiata* oviposition durations are similar to those cited by MIYAKAWA (1982) for other *Calopteryx* species.

ACKNOWLEDGEMENTS

I thank GEORGE BICK and KEN TENNESSEN for their useful comments on drafts of this paper. The work was supported by NSF grants DEB 77-15904, DEB 80-04282, and BSR 8400171 to the author.

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