

**COPULATION BETWEEN THE DAMSELFLIES *HETAERINA AMERICANA* (FABRICIUS) AND *CALOPTERYX MACULATA* (PALISOT DE BEAUVOIS) (ZYGOPTERA: CALOPTERYGIDAE)**

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Males of *H. americana* were seen in tandem with females of *C. maculata* 4 times during the summers of 1982 and 1983. Copulation followed by apparent oviposition was seen in 2 of these pairs. The behavior of the copulating pairs was more similar to that of conspecific *H. americana* than to *C. maculata* pairs.

**INTRODUCTION**

BICK & BICK (1981) have summarized published records of 93 heterospecific pairings in the Odonata. Actual copulation was recorded for only 19.4% of these pairings. Three observations of copulation, two followed by oviposition, are reported for *Calopteryx maculata* (Palisot de Beauvois) females and *C. aequabilis* Say males by WAAGE (1975), but intergeneric copulation in the damselflies has been seen between coenagrionid genera only (PARR, 1976). This short communication describes and discusses the first observations of intergeneric copulation followed by apparent oviposition in the Calopterygidae, between *Hetaerina americana* (Fabricius) and *Calopteryx maculata*.

During the summers of 1982 and 1983 I recorded territorial and reproductive behavior of individually marked *H. americana* along the Little Huron River, a small stream in Livingston Co., Michigan, U.S.A. Individuals were marked with spots of Testor's Enamel on the wings and abdomen, as shown on male No. 0243 in Figure 1. In the summer of 1983 I also recorded the reproductive activity of unmarked *C. maculata* at the same site. Both species were sexually active at the same time, often ovipositing on the same aquatic plants simultaneously.

In both species a male grasps the prothorax of a female with his terminal

abdominal appendages before copulation, creating the tandem configuration. After tandem formation, the male bends his abdomen down and forward and by opposing his ninth and second abdominal segments, transfers sperm from the primary genitalia on his ninth abdominal segment to the secondary genitalia on his second abdominal segment. Cooperation of both sexes is then required to achieve the copulatory position. The male lifts the female up and forward by raising his abdomen and the female bends her abdomen down and forward until the genitalia behind her eighth sternite engage the secondary genitalia of the male. The pair is then in copula. In this position the male performs a series of regular undulatory movements of his basal abdominal segments known as pumping. These movements are associated with removal of sperm from the spermatheca and bursa copulatrix of the female in *C. maculata* (WAAGE, 1979). Pumping usually continues until just before the end of copulation, at which time sperm is transferred from the male's secondary genitalia to the female. Females usually oviposit shortly after copulation, inserting their eggs into submerged vegetation in the stream, where the larvae will hatch and mature. Males and females of both species may mate repeatedly with different individuals throughout their adult lives.

No courtship behavior has been observed in *H. americana* prior to tandem formation. Copulation normally lasts an average of 5 min 14 sec ( $n=18$ , maximum = 13 min 9 sec, minimum = 1 min 27 sec). After copulation the pair (still in tandem) invariably flies about the water's edge. In most cases the male releases the female only when she has begun her descent into the water to begin submerged oviposition. Each bout of oviposition lasts on average 33 min 12 sec ( $n=16$ , maximum = 57 min 5 sec, minimum = 4 min). Copulation and oviposition are over more quickly in Texas (JOHNSON, 1961) and Oklahoma (BICK & SULZBACH, 1966). Males frequently remain near the point where the female entered the water as she oviposits, and may chase conspecific males away from the immediate area. This behavior is called guarding.

Males of *C. maculata* usually court females by hovering nearby before clasping them in tandem (WAAGE, 1973). The average duration of copulation in *C. maculata* is 1 min 41 sec ( $n=90$ , maximum = 5 min, minimum = 30 sec; WAAGE, 1973). Immediately after copulation the female is released. She then finds her way to a nearby oviposition site. Females normally oviposit with only the distal end of their abdomens beneath the surface of the water. Each bout of oviposition lasts an average of 9 min 11 sec ( $n=363$ , maximum = 55 to 60 min, minimum = < 1 min; WAAGE, 1978). During oviposition the male usually chases conspecific males away from the oviposition site. More complete accounts of the normal reproductive behavior of these species can be found in JOHNSON (1961), BICK & SULZBACH (1966) and WAAGE (1973).

## OBSERVATIONS

Males of *H. americana* and females of *C. maculata* were seen in tandem four times in the summers of 1982 and 1983. A description of the behavior of each heterospecific pair follows. The first two pairs were seen copulating, while the second two were not.

On August 16, 1982, at 1522 EDT, a male of *H. americana* (No. 1452) was perched in tandem with a female of *C. maculata*. The pair approached the copulatory position, the male raising his abdomen and the female bending hers down and forward. One min 7 sec after the initial sighting, copulatory position was achieved and the male began pumping irregularly. Copulation lasted 4 min 25 sec. In the 1 min 56 sec immediately following copulation the pair flew and perched four times. The last two perches were at water level, the female touching the surface. At the end of this period the female was released by the male who then perched alternately on and next to the female. Two min 47 sec after release the female was entirely under water and made weak probing movements with the end of her abdomen as if to oviposit among the submerged vegetation of her support. After 2 min 6 sec underwater she released the vegetation and drifted 33 meters downstream until grasping some debris.

At 1633 EDT on July 26, 1983, a male of *H. americana* (No. 0243) and a female of *C. maculata* were in copula, the male pumping. Despite my very close approach to photograph the pair (Fig. 1), copulation continued without interruption for 8 min 22 sec. At the end of copulation the pair flew along the stream margin for 1 min 46 sec before perching 5 cm above the water. The abdomen of the female was partially in contact with the water which she probed with the end of her abdomen. After 16 sec the pair flew again, was chased by two *H. americana* males, and landed almost immediately at the surface of the water. Two min 5 sec later the male flapped his wings as in flight, releasing his hold on his perch without releasing the female. The female held on to her perch and the pair wobbled as the male continued to flap his wings. In 1 min 2 sec the male fell sideways into the water and 18 sec later so did the female. The male released the female 16 sec later, left the water, and perched 7 cm above the water, 60 cm downstream. The female submerged and occasionally made weak probing motions with her abdomen as if to oviposit. After the females had been submerged for 4 min 1 sec she was lost to view.

No attempt was made to look for eggs laid by these two females because both species oviposited frequently in this area and their eggs could not have been distinguished from those laid by other females. Hybrids between these two species have never been observed. Both copulation duration and post-copulatory behavior of these two pairs were more similar to *H. americana* than to *C. maculata* conspecific pairs. These observations do not allow the post-copulatory behavior of the males to be classified clearly as guarding or non-guarding.

At 1743 EDT on August 4, 1983, a male of *H. americana* (No. 0231) was perched in tandem with a female of *C. maculata*. The pair flew about 15 meters downstream 10 sec after the initial observation, chased part of the way by two males of *H. americana*. After 28 sec of flight the pair separated.

At 1342 EDT on August 7, 1983, a male of *H. americana* (marked, but No. unrecorded) was in tandem with a female of *C. maculata*. The pair flew from perch to perch for 1 min 18 sec. Five times in the next 1 min 38 sec, while on the last perch, the male lifted the female, who bent her abdomen down and forward. At one point the secondary genitalia of the male and the female's genitalia came into contact, but the position was held for only 11 sec. At the end of this period the pair flew for 12 sec and perched. After the male lifted the female up once again, he released her. Thus, in three of these four pairs, the female was not simply held passively in tandem, but actively participated with the male in behavior which normally leads to copulation.

In 524 hours of observation at this site during the summers of 1982 and 1983, I encountered 168 tandem pairs (0.321/hr) of *H. americana*. In the same period I encountered the 4 heterospecific tandem pairs described above (0.008/hr). In 253.5 hours of observation in 1983 I encountered 71 tandem pairs (0.280/hr) of *C. maculata*. Thus, the rate of encountering mixed pairs of *H. americana* with *C. maculata* in this study was 1.25% of the rate of encountering all sexually active pairs of both species.

All three of the known males were observed in tandem with conspecific females, No. 1452 twice before, No. 0243 three times after, and No. 0231 twice before the heterospecific pairing. The latter was the only male observed to copulate with a conspecific and was also the only male whose female of *C. maculata* did not copulate or bend her abdomen down and forward in the manner which precedes copulation. The greyish appearance of the terminal abdominal segments of the female copulating with male No. 0243 (Fig. 1) is probably due to dried debris which adhered after immersion of these segments during an earlier normal bout of oviposition.

## DISCUSSION

Some damselfly females are known to reject potential conspecific mates following tandem formation on the basis of stimulation received from the terminal appendages of the male (KRIEGER & KRIEGER-LOIBL, 1958; LOIBL, 1958; ROBERTSON & PATERSON, 1982). Males of *H. americana* and *C. maculata* have differently shaped appendages (cf. JOHNSON, 1972, p. 70), but none of these mixed pairs were collected so neither the appendages nor the thoraces of the females can be examined for abnormalities.

Visual discrimination of species and sex has been demonstrated in a number of odonates (WAAGE, 1975, and refs therein). The color patterns of Nos 1452,



Fig. 1. *Hetaerina americana* male (No. 0243) in copula with a *Calopteryx maculata* female. The color pattern of each insect is typical, but note that the male has been individually marked by the researcher on the wings and abdomen.

0243 and 0231 were normal, as shown for male No. 0243 in Figure 1. I have no record of the color pattern of the marked but unrecorded male. The normal color patterns of *H. americana* and *C. maculata* are very different, so visual discrimination between the species was theoretically possible for the males and females discussed here. The cooperation of the female in these interactions is perhaps more puzzling than the male's attempts, because most female insects have more parental investment to lose than do males (THORNHILL & ALCOCK, 1983). Coercion by the males, undetected abnormalities in either partner or abnormally low ability to make parental investment on the part of the females may have led to the cooperation observed.

No one has ever reported seeing a male of *C. maculata* or a female of *H. americana* in tandem with anything but a conspecific. I did see two other non-copulating mixed tandem pairs involving *H. americana* males at this site, one with a lepidopteran in 1982 and one with a coenagrionid in 1983. BICK & BICK (1981) also report a male of *H. americana* in tandem with a coenagrionid. As noted, *C. maculata* females have copulated with *C. aequabilis* in addition to *H. americana*.

The relatively high incidence of *C. maculata* females in heterospecific copulating pairs may simply reflect the large amount of attention given to this species by researchers, but it is also possible that females of *C. maculata* are more likely than other species to mate with a non-conspecific. Behavior suggesting relaxed sexual discrimination in females of *C. maculata* in a context of persistent conspecific males has been discussed by WAAGE (1984). Eventual understanding of the basis of heterospecific copulation will hopefully lead to insights into the mechanism of normal mate choice between conspecifics.

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