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Forced Copulations and Female Contact Guarding at a High Male Density in a Calopterygid Damselfly

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Territorial males of Calopteryx *damselflies court females on territories that contain oviposition substrates. Nonterritorial males try to mate without courtship but very rarely obtain matings because females fail to bring up their abdomen to engage genitalia. Here 1 report the results of observations made on a very high-density population of* Calopteryx haemorrhoidalis *in central Italy. Mating activity was intense, and during 40 h of observation in an 8-m section of the stream, 209 matings were recorded (a maximum of 17 matings* h^{-1}*). Males were continuously disturbing ovipositing females and tried to achieve tandem forcibly. Of 84 cases, males achieved forced tandem in 53, and 49 ended with copulation. Forced tandems were the most common method to obtain a mating in this population (55% of 65 matings). Males guarded females after forced or courtship copulations and, in some cases, maintained physical contact with their mate, by perching on her wings. Confusion was common and males guarded nonmates frequently, which suggests that they were unable to recognize their mate individually.*

KEY WORDS: damselflies; Odonata; Calopterygidae; forced mating; contact guarding; female choice.

INTRODUCTION

Most Odonates achieve the tandem position and mate without a previous courtship. Species recognition occurs in many Zygoptera because only the cerci of conspecific males correctly stimulate some regions of the female prothorax (Robertson and Paterson, 1982). The members of the family Calopterygidae

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are an exception. Males are usually territorial and court females with highly elaborate displays (Haymer, 1973), but secondary genitalia are almost-identical between species (Maibach, 1986), which allows hand-pairing between conspecific as well as heterospecific pairs (Oppenheimer and Waage, 1987). Hand-pairing also allows bypassing of the courtship phase in reproductive behavior, and most females (84% of 81 trials in *Calopteryx maculata) will* mate, which contrasts with the low success of courting males [30% (Oppenheimer and Waage, 1987)]. The same is true for European *Calopteryx* [*C. virgo, C. xanthostoma,* and C. *haemorrhoidalis* (personal observation)].

Female *Calopteryx* are able to reject courting males, and this raises the question why males simply do not capture ovipositing females forcibly in tandem, because the fact that a female is laying eggs indicates that she is receptive (Fincke, 1997). This kind of behavior has been obseved in nonterritorial males of some species, but they rarely obtain matings (Pajunen, 1966; Waage, 1973; Alcock, 1983; Meek and Herman, 1990; Plaistow, 1997). Here I report on the reproductive behavior of a population of *Calopteryx haemorrhoidalis* in central Italy, where males were usually observed capturing ovipositing females in tandem without the characteristic courtship of this species (Heymer, 1973). These observations are useful for discussing female choce in a territorial species.

METHODS

The study site was located in the stream Forma Quesa, a tributary of the river Liri, at Pontecorvo (Frosinone province, Italy; UTM, 33TUF 878873). 1 selected a section of the border, where the stream widened to 4 m and the water current was slow. The water course was totally covered by dense vegetation for at least 500 m upstream. In these shaded sections adults of *C. haemorrhoidalis* were rare, and this fact determined a very high density of individuals at the study site. Males perched in the shore vegetation and females laid eggs in a patch of *Potamogeton* about 50-70 cm wide that covered the left shore. The right shore was covered by *Rubus* with no oviposition substrate and a faster water current. In this area females perched during short periods between visits to the oviposition area. Some males (young?) were also observed there.

On 12 August 1997 I divided the left shore into eight sections of about 1 m and marked the sections with sticks. All males found in the area were netted and marked by writing a number on the thorax with a white pen (Edding 780 paint marker). Both sides of the thorax were marked, to allow reading of the number in perched individuals. No wing marks were made to avoid interference with courtship, because in this species females might choose between males by their wing coloration (M. T. Siva-Jothy, personal communication). Following initial capture, males were liberated and most of them remained in the area. I used a monocular to read numbers, and therefore males were never netted again during the study. From 12 to 21 August (except 18 August) I made continuous observations of adult activity at the site, starting at about 0900 h and ending at 1300-1600 h, depending on activity. In total, 40 h of field observations was made. Very few males were present at the site before 1000 h. On most days, at about 1300 h clouds developed, with an immediate reduction in damselfly activity. In the second half of the study, summer showers started every afternoon. Activity was almost nonexistent after 16 h. These facts suggest that I observed most of the reproductive activity.

From 13 August females were also netted and marked by writing a large number on their wings, which allowed individual recognition at a distance. Air temperature was measured on a shaded trunk (1 m aboveground), and water temperature at a depth of about 1 cm. The temperature and number of males in territories were recorded at hourly intervals. Air temperature was also recorded at the start of most matings.

On 19, 20, and 21 August I captured one unmarked female, killed it by turning around its head, and presented it to mature males, to test individual recognition of females. Ten males that had recently mated and started to guard their mate were tested. The female was disturbed with a long stem, until she abandoned the ovipositing site, but in two cases this was not necessary because the female spontaneously abandoned the territory. The time elapsed between the end of focal copulation and the substitution of the ovipositing female by the dead model was 2-10 min.

The study site was also visited by *Calopteryx splendens* (rare), *Platycnemis pennipes* (common), *Boyeria irene* (common), and occasional individuals of *Somatochlora meridionalis* and *Orthetrum brunneum.*

I estimated male and female numbers by the Jolly-Seber model using Popan-4 software. All analyses were made with the SPSS program. Means are presented with standard errors and sample sizes.

RESULTS

During the period of observations I marked a total of 95 males and 107 females. Most of them were resighted (56 males and 55 females). By the Jolly-Seber method I estimated that the daily proportion of animals in the population that were marked was 66-97% for males and 66-95% for females. This high proportion of marks allowed estimation of the population size with a high accuracy. The daily male population was 38-62 individuals, with a standard error of only 1-5 males, i.e., a density of 4.8-7.8 males m^{-1} . Females were even more common: population estimates ranged between 53 and 92 individuals (SE, 5-21). Daily survival rate was 0.839 ± 0.035 (7) for males and 0.857 ± 0.047 (6) for females.

When I started observations at about 0900 h, one to three males were already in the shore vegetation (still shaded), but females were rarely observed

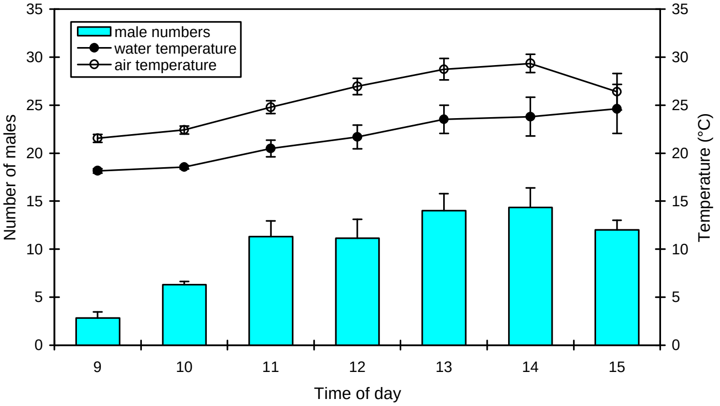

Fig. 1. The relationship among time of day, temperature, and male density. Bars are standard errors of the means.

before 1100 h. Through the morning the male density increased to a maximum of 11-17 individuals at 1100-1400 h (Fig. 1). First-arrived males established territories and defended them from intruders, as is usual in the genus (Heymer, 1972). Females perched in the shore vegetation and were courted by resident males, as described by Heymer (1973). Males that were successful grasped females in tandem, transferred sperm to their secondary genitalia [6.82 ± 0.63 (17) s], and copulated. Copulation was brief, averaging 133.8 ± 64.8 s (118). Copulation duration was negatively correlated with time of day (Spearman r_s = -0.41, n = 118, $P < 0.001$) and with air temperature (r_s = -0.41, n = 109, $P <$ 0.001). Partial correlation analysis suggests that both variables had an independent effect on copulation duration (between copula duration and time of day, controlling for temperature, partial r = -0.20, n = 106, P = 0.042; between copula duration and temperature, controlling for time of day, r = -0.26, n = 106, P = 0.008).

Mating activity was very intense and competition between males extreme. One male was even observed repeatedly to try tandem with an emergent *Potamogeton* leaf. I observed a total of 209 copulations, with a mean of 5-9 matings h^{-1} between 1100 and 1400 h (maximum, 17 matings h^{-1}; Fig. 2). At the moments of highest activity mature males perched at "hot spots" separated by only 10-20 cm and were apparently defending not their territories but their most recent mate. By inducing a guarding male to defend a dead female perched on a long stem, I was able to move the male to a new territory, where he continued defending "his" female. Some males (11 observations by 9 males) even perched on the tip of their mate's wings and maintained this position several minutes to repel intruders (Fig. 3). This "contact guarding" was intercalated with the more "traditional" defenses from a perch.

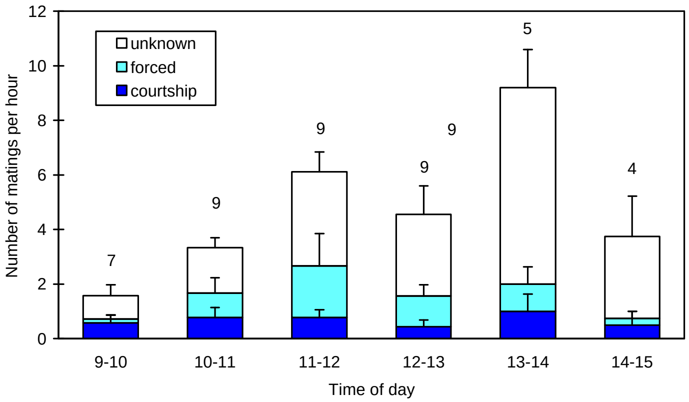

Fig. 2. The mean number of matings observed per hour (+SE). Numbers above bars indicate sample size. Note that forced copulations occurred all day long.

The reason males maintained physical contact with their mates became apparent from the first hours of observation. Contrary to other *Calopteryx* species, ovipositing females were commonly disturbed by males, which on 84 occasions tried to achieve tandem without previous courtship. Mated males attacked intruders but were outnumbered by them and rarely were able to impede forced tandems when the density was high. At 1100-1200 h most males had abandoned territorial defense, even males that were strongly territorial during the first half of the morning. Females always refused forced tandems by opening their wings and impeding tandem formation (Fig. 4). Two females were observed to submerge partially or completely after several male attempts to obtain a forced tandem. Most abandoned oviposition and moved to the shore vegetation, to return after several minutes. Nevertheless, if the male was successful in grasping the female in tandem, the pair moved to the shore vegetation and mated. One female was observed to mate 11 times in 2 h, and 9 were forced matings! (on the remaining 2 occasions she was already discovered in copula). Of 84 male attempts, 53 resulted in forced tandem and 49 ended with copulation. The only exceptions were separated due to male attacks (two cases; one tandem fell to the water and separated after 1 min) or female refusal. One female refused to fly and mating occurred on the *Potamogeton* leaves.

Forced tandems were the most common method to obtain a mating in this population: of a total of 65 copulations whose start was observed, 36 (55%) were forced and 29 (45%) were preceded by courtship (only copulations from 15 to 21 August are included, because I did not record whether a copulation was preceded by courtship before that date). Figure 2 presents the mean number of matings observed in 1-h intervals. Even if all matings whose start was not observed were courtship matings, forced copulations represented at least 23%

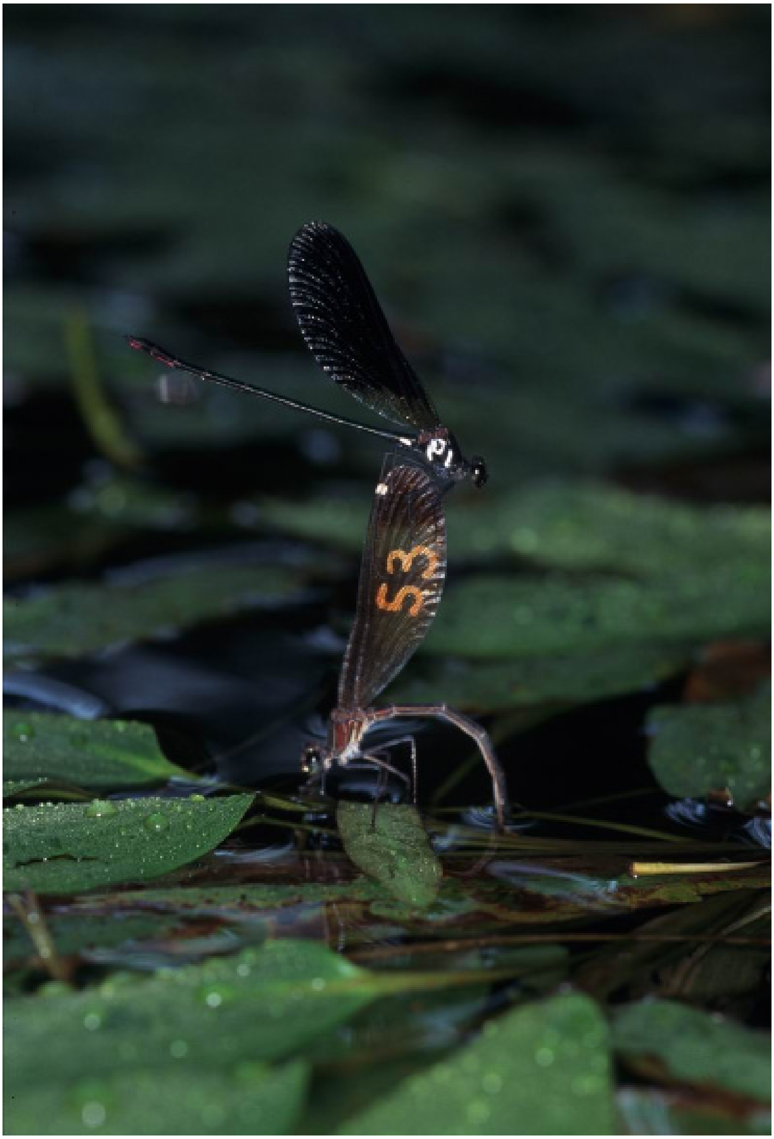

Fig. 3. Contact guarding by male C. *haemorrhoidalis.* Males perched on their mate and repelled intruders from this point. Some males defended nonmates in the same way.

Fig. 4. One male tried forced tandem with an ovipositing female while her mate tried to impede it. Note the refusal position of the female (wings opened and head oriented to the water surface).

(49/209). Forced copulations peaked at 1100-1200 h, 1 h before the number of males was maximum (Fig. 1), but occurred as early as 0951 h. Nevertheless, there were no significant differences in the hourly distribution of forced and courtship copulations (Kolmogorov-Smimov two-sample test, $z = 0.799$, $n = 36$ forced and 29 courtship matings, $P = 0.547$). Both types of copulations were not significantly different in duration (ANOVA with air temperature and time of day as covariates, $F = 0.217$, $P = 0.644$). Individual males showed both types of behavior, even during the same morning (the most successful male obtained 3 forced, 3 courtship, and 16 matings of type unknown). Males were as likely to defend their mate after a forced copulation (13/16) as after a courtship mating (16/18; $\chi^2 = 0.394$, $P = 0.530$).

To test if males were able to distinguish their mate from other females, I selected 10 guarding males and substituted their mate (always marked) by an unmarked dead female. Therefore males could use the conspicuous number that I had put on their mates to detect that the model was a different female. In 9 of 10 cases, the guarding male defended the unmarked dead female as it did its mate, a result at variance with the individual recognition hypothesis (I retired the model female after one to five defensive behaviors by the test male). The dead female was highly attractive to other males, which tried and sometimes obtained tandem with her. The only male that did obtain tandem with the dead female, nevertheless, defended her after 13 min in a second presentation. These results suggest that males did not recognize their mates. Confusion was common in this crowded situation, and males defended nonmates from a perch or even shortly perched on them (15 observations of 10 males; Fig. 3).

DISCUSSION

Males of C. *haemorrhoidalis* behaved in an unusual way at the stream Forma Quesa. The most common way to obtain a mating was not courting the female, as is typical for the species (Heymer, 1973; Cordero, 1989), but capturing her forcibly in tandem while she was ovipositing. This is not a new behavior for calopterygids, although it seems to be absent from some species (Waage, 1988). Pajunen (1966) indicates that nonterritorial males of C. *virgo* can sometimes clasp females without preceding courtship. Waage (1973) observed the same in nonterritorial males of *C. maculata*, but only 3 of 15 obsevations ended in copulation. Two forced tandems were also observed by Alcock (1983) in the same species. Nonterritorial males of *Calopteryx splendens xanthostoma* also take females in tandem without prevoius courtship (Plaistow and Siva-Jothy, 1996), but this behavior is extremely rare: five successful tandems and copulations in 400 h of observation, and only one of them guarded the female (Plaistow, 1997). Meek and Herman (1990) observed frequent male harassment of unguarded ovipositing females of three *Calopteryx* species, some males trying to take females in tandem or to drive them from the water by flying at them and bumping their wings. In C. *amata* such behaviors led to courtship or copulation in 6 of 52 cases. In *Mnais* damselflies nonterritorial (hyaline-winged) males mate without courtship, but territorial males (orange-winged) court females [see Higashi (1981) for *Mnais pruinosa*, Watanabe and Taguchi (1997) for *Mnais pruinosa costalis*, and Higashi and Nomakuchi (1997) for *Mnais nawai]*. The difference in the present population is that forced mating was the rule rather than the exception and was used as a mating tactic by all males.

Territorial behavior allows males to defend a resource (the oviposition substrate) that is needed by females. By defending a territory, the resident male obtains a very high mating success (Plaistow and Siva-Jothy, 1996), which has been documented in many insect species (Thornhill and Alcock, 1983). Nevertheless, territorial defense is advantageous only if males can defend resources in an economical way (Conrad and Pritchard, 1992). Ecological theory predicts that under very extreme competition, males should abandon territorial behavior, and this seems to have occurred in the study population. The estimated density of males (4.8-7.8 males m^{-1}) is very high compared to that in other populations of the same or similar species. Cordero (1989) estimated a density of 0.6 male m^{-1} in a Spanish population of C. *haemorrhoidalis* and densities of 0.03 to 0.4 male m^{-1} for *Calopteryx virgo* and C. *xanthostoma.* Similar densities are reported for *Calopteryx cornelia, C. atrata,* and C. *virgo japonica* [0.12 to 0.32 male m^{-1}, calculated from data of Higashi and Uéda (1982)]. Only Pajunen (1966) observed densities of 3.3-4.7 males m^{-1} in C. *virgo.*

To my knowledge, this is the first time that contact guarding of the female has been observed in a Calopterygid damselfly (Fig. 3). By perching on the female, males were able successfully to impede forced tandems, which was impossible if they perched in the territory. Males perching only 20 cm from the female had a great risk of losing their mate to another male (Fig. 4), because forced tandems were extremely fast. In fact, when guarding males were absent, ovipositing females were immediately captured in tandem by rival males. In one case five females were captured from a territory when the owner disappeared for a few minutes. Nevertheless, there were no observations of tandem oviposition, which could have been expected under this extreme competition for mates. This plasticity in mate guarding has been observed in males of *Sympetrum* dragonflies (Uéda, 1979, 1996, and references therein).

It is generally assumed that female odonates cannot be forced to mate because they must raise the abdomen to achieve copulation (e.g., Fincke, 1997). Observations of female behavior indicate that they always refused forced tandems (Fig. 4) and sometimes impeded tandem by opening their wings and immersing their heads in the water (most tandems were in fact impeded by other males). But if the female is captured she cooperates in copulation. This suggests that females can obtain benefits from forced copulations. In fact, males that obtained forced copulations defended their females during oviposition as did courting males. Unguarded females were unable to oviposit at a high male density. By accepting forced copulations, females can continue to oviposit for at least some minutes. Therefore these matings were forced in the sense that females could not choose their mate, but they obtained clear fitness benefits. Given the short mating duration, the only cost that females had in forced matings is some minutes of interruption of oviposition.

C. haemorrhoidalis males seem unable to distinguish their recent mate from other females. Mate-guarding males defended mates and nonmates spontaneously, and they did not try mating with an unmarked dead female that I put in the place of their mate (while other males did). It could be argued that males suffered reduced sexual motivation immediately after copulation (Alcock, 1983), and therefore they were not interested in *any* female. However, this seems unlikely because tested males were sexually motivated: five of them courted a new arriving female between 4 and 16 min after the end of the focal mating. Furthermore, 14% of copulations *(n* = 86) by the same male in 1 day were separated by less than 10 min (34% by less than 20 min) and one male remated with the same female less than 1 min after having released her, indicating that reduced sexual motivation after copula seems unlikely. Hooper (1995) suggests that male C. *splendens xanthostoma* recognize their mates. Hopper's experiment consisted of mating tethered females to two territorial males and introducing both females into one territory. Females were left in the territory for 1 min in every 3 minutes. After 20 min the territorial male had mated with the nonmate in nine trials and the recent mate in two trials. This suggests individual recognition, but it is also possible that females behaved in a different way when they were in the territory of their mate or not, and males used this cue to select which female to court. In my experiments all model females were unmarked, while the males mate was marked. I deliberately used this experimental design to help males to identify their mate, but they did not try mating with the unmarked female. I propose that male C. *haemorrhoidalis* cannot recognize their recent mate but guard the first female that starts to oviposit near him. This behavior allows males to guard their recent mate at the usual population density of this species and recognize any newly arriving female as a nonmate [males usually courted any new arriving female but were not interested in females already in oviposition near their mate (see also Pajunen, 1966)]. At a very high density, confusion should be common, as in the present population. More experiments are needed to test this hypothesis.

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