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Male coercion and convenience polyandry in a calopterygid damselfly

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Abstract

Copulation in odonates requires female cooperation because females must raise their abdomen to allow intromission. Nevertheless in *Calopteryxhaemorrhoidalis haemorrhoidalis* (Odonata) males commonly grasp ovipositing females and apparently force copulations. This has been interpreted as a consequence of extreme population density and male-male competition. We studied this behavior at two sites on a river that had different densities over three years. As predicted, at high densities most matings were forced (i.e. not preceded by courtship), but at low density most were preceded by courtship. Courtship matings were shorter at high density, but density did not affect the duration of forced matings. Females cooperated in forced matings even if they had very few mature eggs. Furthermore, females mated more times if they experienced higher male harassment during oviposition, and at low density second and subsequent matings were more likely to be forced. We interpret these results to mean that females engage in "convenience polyandry", because they gain more by accepting copulation than by resisting males. The results also suggest that females might trade copulations for male protection, because under extreme population density harassment by males is so intense that they can impede oviposition.

Keywords: sexual conflict, sexual harassment, Calopterygidae, forced matings, courtship.

Abbreviation:
GLM, generalized linear model

Introduction

Since Bateman's (1948) classical study, the difference in mating rates between males and females is explained by the strong contribution of additional matings to male reproductive success. In polyandrous insect species male fitness increases with mating rate. In contrast, female fitness increases with moderate mating rates but decreases at extreme mating frequencies (reviewed by Arnqvist & Nilsson, 2000). Due to this asymmetry between the sexes, males are expected to attempt to mate indiscriminately (i.e., persistent) while females are expected to avoid superfluous matings (i.e., resistant). Hence, sexual conflict over mating rate might be one of the strongest forces driving the evolution of male and female reproductive strategies (Parker, 1979; Bradbury & Andersson, 1987; West-Eberhard et al., 1987; Rice, 1996; Alexander et al., 1997; Hosken et al., 2001).

In water striders and several crustaceans sexual resistance by females fluctuates depending on different physiological and/or ecological conditions (e.g. Arnqvist, 1992; Rowe, 1992; Jormalainen & Merilaita, 1995; Choe & Crespi, 1997). These data have led to the suggestion that optimal female mating rates should be seen as evolving reaction norms- rather than as fixed optima (Arnqvist & Nilsson, 2000). If so, female mating rate is expected to be plastic and to covary with local environmental conditions. This covariation arises from females modulating their resistance (and therefore their mating rate) in response to several factors that affect the relative costs and benefits of mating. One possibility is that females adjust their mating rate to balance the costs imposed by male persistence (i.e. male harassment). This situation, described as convenience polyandry (*sensu* Thornhill & Alcock, 1983), assumes that males are able to coerce females to accept superfluous matings.

Male coercion has been demonstrated in a wide range of animals (reviewed by Clutton-Brock & Parker, 1995). However, the extent of convenience polyandry remains unclear. The best evidence for females modulating their mating rate as an adaptive response to male harassment comes from studies of water striders (Arnqvist, 1988; Rowe et al., 1994). However, in some other insect orders it has been argued that male coercion and convenience polyandry is highly unlikely. For instance, in odonates, the existence of male coercion is still controversial. Some authors have assumed that it is common (Moore, 1989; Koenig, 1991; Conrad & Pritchard, 1992) while others have argued that this assumption is not well supported

(Fincke, 1997). Evidence against the existence of male coercion in odonates has been based on several behavioral and morphological traits. First, it has been argued that the reproductive anatomy of odonates blocks males from forcing copulations-because females must cooperate by curving the abdomen to contact male genitalia (Waage, 1973; Fincke, 1982; Waage, 1984a; Fincke et al., 1997). Second, some authors have assumed that females carrying no mature eggs invariably resist matings (Fincke, 1997). Consequently, it has been proposed that cooperation in communicating sexual intentions is common in this group, since it would pay the male to heed female rejection signals. Third, in species with pre-copulatory courtship, the non-aggressive signals by the male (i.e., displays) have been used to support the idea that coercion does not occur (Fincke, 1997).

In spite of these arguments, it is known that in odonates male harassment has a negative impact on female fitness (Ubukata, 1984; Waage, 1987), that males have the potential to coerce females and that forced copulations indeed occur (Cordero, 1999). These indirect lines of evidence suggest that convenience polyandry may be found as a female reproductive tactic in some odonates. Our main goal is to test the existence of convenience polyandry in *Calopteryx haemorrhoidalis haemorrhoidalis*, a model species that shows the typical reproductive behavior of calopterygids (i.e. elaborate pre-copulatory courtship, Video 1), but also “forced” copulations without courtship (Cordero, 1999) (Video 2). These copulations are termed “forced” because females cannot choose between accepting or rejecting being taken in tandem, and because a clear rejection behavior is always observed when males try to take a female in tandem (Cordero, 1999). For this purpose, we studied the reproductive behavior of this species under low and high population density over three years. Furthermore, these observations were compared with previous records made on the same population when the population density was higher (Cordero, 1999). This design, allowed us to make three different predictions. First, if males are able to coerce females then undesired (i.e. forced, not preceded by courtship) copulations should be common at high-density spots, where male harassment rate is the highest. In contrast, at low population density forced copulations should be rare. Second, if females copulate to avoid the cost of male harassment, they should sometimes mate multiple times per egg clutch, and females should mate independently of the number of mature eggs they carry. Moreover, the second and following matings should be coerced (not preceded by courtship). If females were to mate mainly to receive sperm from males with better genes or territories, the subsequent copulations should be preceded by courtship. Third, female resistance to forced copulations should decrease as male harassment increases. That is, there should be a positive relationship between the frequency of male harassment and the number of matings by females (Rowe, 1992).

Materials and Methods

Study organism

Calopterygid damselflies are large insects common in rivers that show elaborate precopulatory courtship (Video 1), site fidelity and territoriality. All matings start with a male grasping the females prothorax with their anal appendages which is termed taking them in tandem. Forming a tandem may or may not be preceded by courtship. In most species, males defend a patch of oviposition substrate, court females and guard them from intruders during oviposition (see Heymer, 1972; 1973; Córdoba-Aguilar, 2000, for a description of territorial and reproductive behavior of *C. haemorrhoidalis*). Alternative non-territorial tactics (Gross, 1996) are found in most species (satellite or sneaking males), but these males obtain very few matings (Plaistow & Siva-Jothy, 1996). Females also show two tactics. Some accept mating and guarded oviposition by the resident male, but others simply start ovipositing near a male that is guarding another female without mating with the male (Siva-Jothy & Hooper, 1996).

Study site

We studied a population of *C. h. haemorrhoidalis* at the Forma Quesa river, Frosinone province, in Central Italy (UTM: 33TUF 8787) in August 1999-2001. Results are compared with those reported by Cordero (1999) for the same population. Individuals were netted and marked with an indelible pen on their wings (females) or thorax (males).

Due to the large size of the studied population and the characteristics of the study site, we could not manipulate male density around our observation sites, nor were we able to replicate our treatments at various sites. Observations were therefore repeated over three years on two different river sections, one of high and one of low density. Consequently our experiment is “pseudoreplicated” in time. Pseudoreplication often makes impossible to infer causal relationships. However, we believe that the main conclusions of our experiments hold because they are based on strong predictions (see Oksanen, 2001) and because we were able to use a natural experiment that modified the density of one of the study sites (see below). The first section (site A) was situated at the start of a pool of the stream, where the depth was about 1 m, and a patch of *Potamogeton* (3x0.5 m) was used as oviposition substrate. Males concentrated on the shore and established territories on the *Potamogeton*. The second section (site B) was immediately below a dam (about 3 m high) that created a large sunny area and a very large patch of *Potamogeton* (more than 10x3 m) in a sunny area on one of the riverbanks. Maximum depth at this spot was about 30-40 cm. Marked animals rarely moved between the study sites (4 animals out of more than 700 marked in 1999).

Population density and copulation duration

Site A had a very high density of animals in 1997, probably because it was the first sunny place after 500 m of river shaded by riparian vegetation (Cordero, 1999). The riparian vegetation was cleared in 1998, and this provided many sunny areas for male territorial activity. In 1999-2001 male density was clearly lower at this site, while density remained very high in site B. To test if male population density at both study sites was indeed different, we calculated the index of abundance as the number of animals marked per hour during August 1999-2001.

Several studies have reported that copulation duration increases at high population densities or when the sex ratio is male biased (see Cordero, 1990; Cordero et al., 1995; Andrés & Cordero Rivera, 2000, for odonates and Alcock, 1994, for a review). This might be interpreted as a male response to increased intra-sexual competition. However, if females have control over copulation duration, longer copulations might be interpreted as a female strategy to avoid male harassment (Rowe, 1992). Copulation duration was studied at both sites by direct observation in 1999-2000. Given that temperature has a negative effect on copulation duration (Cordero, 1999), we recorded air temperature every 20-60 min in the shade of a tree in 1999. In 2000 we used a datalogger that measured temperature every 10 min. Air temperature was highly predictable by time of day because all observations were done on sunny days ($y= -0.346x^2 + 10.844x - 51.367$; $r^2=0.90$). This relationship was used to estimate air temperature on days when no data were available. The number of pumping movements was counted during the stage I of copulation because these are related to the removal of rivals' sperm (Miller & Miller, 1981; Siva-Jothy & Tsubaki, 1989), and therefore might be related to male paternity.

The reproductive value of females and male coercion

We investigated variation in female reproductive potential during the day to test if females can be forced to mate even if they have no mature eggs. In August 1999 we collected 71 females that accepted copulation at different times of day and counted the number of mature eggs in their ovaries.

If male coercion is common, forced matings should be more likely as second or subsequent matings. If females are not coerced into mating, copulations should be preceded by courtship irrespective of their order. These predictions were tested with an analysis of all matings whose start was observed during 1999-2001.

The number of matings that females accept per egg clutch is the result of the interaction between female resistance and male persistence. Coercion only occurs if females diminish their resistance due to male harassment. The probability that females mate in a particular oviposition event should increase with oviposition duration, because they remain exposed to male copulatory attempts for longer periods. We tested this hypothesis in 2000 by recording the duration of visits and the number of matings of females that arrived to oviposit. Focal females were randomly selected from females that either started oviposition without previous copulation or mated with a resident male. Females were observed until they disappeared from the focal territory. Females that remained in the area less than 10 min were excluded from this analysis.

If females incur costs for resisting males, the number of copulations should be positively related to male disturbance rather than oviposition duration. We tested this prediction with a second experiment done in 2001. We observed 60 females that arrived to oviposit and recorded the duration of their visits, number of harassments and number of matings. For ovipositing females, harassments were defined as any male approach that interrupted oviposition (courtships and attempts to obtain forced tandem). Once females interrupted oviposition, harassments were defined as male attacks and chases that prevented females from perching on the desired oviposition substrate. Females were observed until they disappeared from the focal territory.

Means are presented with their standard errors and sample size. Statistical analyses were done with GenStat 4.2, 5th edition (GenStat, 2000).

Results

Population density and copulation duration

At site A in 1997 population density was high (Cordero, 1999), but after riverine vegetation was cleared in 1998 males distributed themselves over a larger area and therefore this site showed lower density of males than site B over 1999-2001 (Fig. 1). For the period 1999-2001 density was significantly different between sites (ANOVA, $F_{1,24}=62.28$, $p<0.001$), but not between years ($F_{2,24}=1.23$, $p=0.310$), and there was no significant interaction site x year ($F_{2,24}=1.73$, $p=0.199$). At both sites, males obtained copulations by courting females (Video 1) or by forcibly taking ovipositing females in tandem (Video 2, Cordero, 1999). During 1999-2001 most copulations at site A were preceded by courtship (77% of 96 matings), while at site B most were forced (60% of 161 matings; $\chi^2_1=31.1$, $p<0.001$). In contrast, in 1997 most matings were forced at site A (55% of 65 copulations, Cordero, 1999).

Courtship-preceded copulations lasted an average of 1.85±0.09 (73) min and forced copulations 1.66±0.11 (40) min. We compared the duration of both types of mating using a generalized linear model (GLM), with copulation duration as the response variable (square-root transformed), and type of copulation, site, and air temperature as predictor variables. Year was not included due to insufficient data. Results indicate a significant effect of site (p=0.017) and type of copulation (p=0.008) and a negative effect of temperature (p<0.001). The interaction site x type of mating was also significant (p=0.044). Courtship-preceded copulations were longer at site A (Fig. 2), but both types of copulations had a similar duration at site B (high density).

The first part of copulation was characterized by pumping movements of the male genitalia (stage I of Miller & Miller, 1981). There was a positive relationship between copulation duration and the number of pumping movements during stage I (Fig. 3). The average number of stage I movements was 63±6.0 (21) and 46±3.7 (21) for courtship-preceded and forced matings respectively.

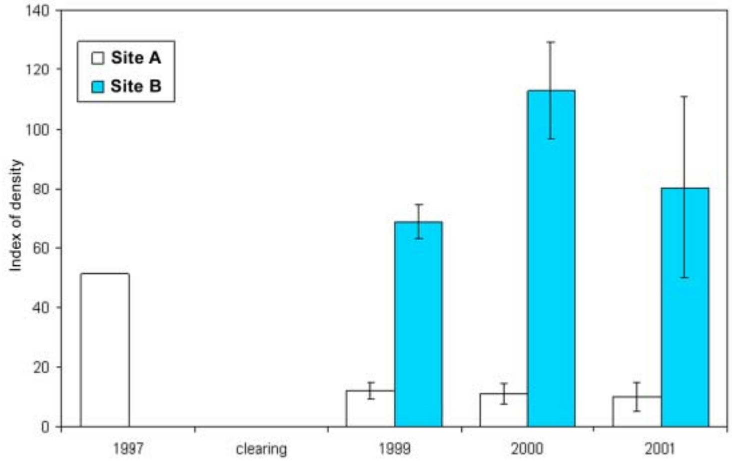

Figure 1. An estimate of population density of *Calopteryx haemorrhoidalis haemorrhoidalis* (individuals marked/hour±SE) in both study sites. In 1997 only site A was studied (no SE is available for this estimate). In 1998 clearing of the riverine vegetation provided many sunny areas and males dispersed over greater shore distances. Consequently density was lower in site A over 1997-2001.

The reproductive value of females and male coercion

Mating activity was most intense during the mid morning, although copulations were observed between 9:23 and 17:54 h. Postcopula females had an average of 202.3±10.6 (71) mature eggs but some accepted mating with as few as 11 eggs (Fig. 4). The effect of time of day and body size on the number of mature eggs present in females captured after having accepted copulation was tested with a GLM with Poisson errors and log link (Crawley, 1993). The reproductive value of females did not change over the day (p=0.233), but

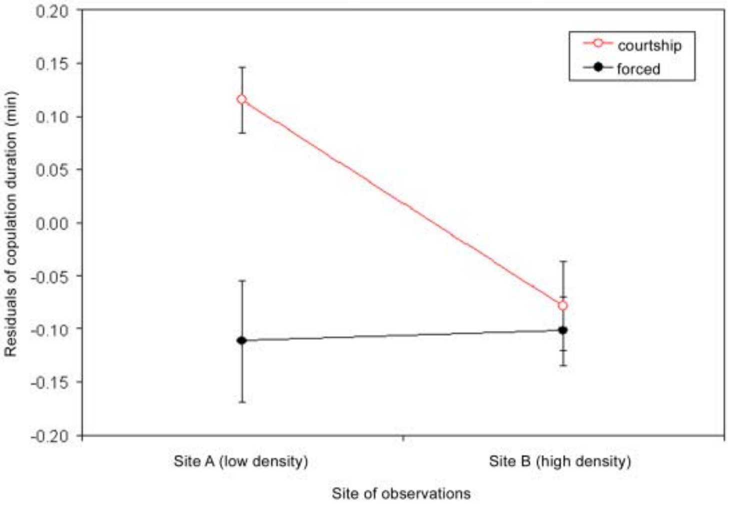

Figure 2. The effect of site and type of copulation on mating duration. Values are mean duration after the removal of the negative effect of temperature ($p<0.001$). The interaction is significant ($p=0.044$).

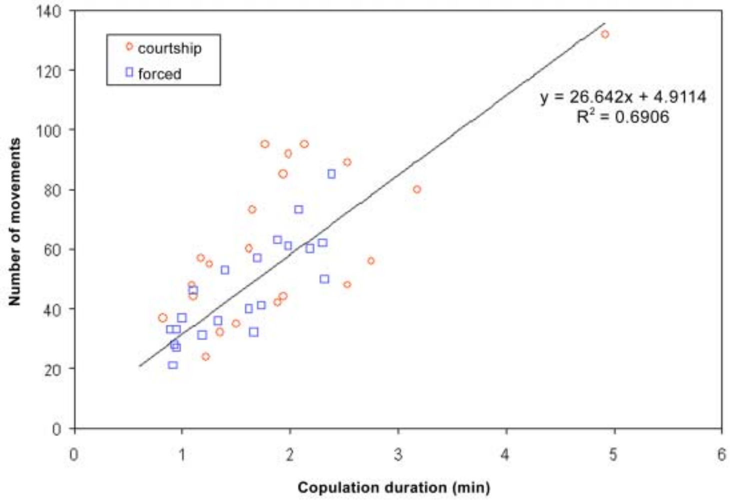

Figure 3. The relationship between copulation duration and the number of pumping movements during the stage I of copulation in courtship and forced matings.

body size had a negative effect on egg load ($p=0.016$). Females needed at least 30 min to lay most of their eggs (Fig. 5), and abandoned oviposition with an average of 54.4±11.5 eggs remaining unlaid (22).

During 1999 to 2001 at site A females were very rarely forced in their first mating (Fig. 6), but 38% were forced in their first mating in 1997 (when male density was higher). In contrast, most matings were forced at site B, irrespective of mating order. At both sites many females were able to lay eggs without males attempting to mate at all, and for this reason the mean number of matings was 0.95±0.223 (19) at site A, and 0.98±0.180 (41) at site B (data for focal females observed in 2001). Females that oviposited for at least 30 minutes mated 0.63±0.183 (8) times at site A and 1.30±0.300 (20) at site B. In 2000, females that oviposited over a longer period mated more times. A GLM with Poisson errors and log link, with number of matings as the response variable and visit duration as the predictor variable, was significant ($p=0.011$) (Fig. 7a). The effect of male disturbance, population density (site) and oviposition duration on female mating frequency was tested with a GLM with Poisson errors and log link in 2001. These results indicate that neither density ($p=0.474$) nor oviposition duration ($p=0.147$) had a significant effect. In contrast, male disturbance had a strong positive effect on female mating frequency ($p<0.001$, Fig. 7b).

Discussion

We have shown that *C. h. haemorrhoidalis* males have two different reproductive tactics: courting and coercive mating. On the other hand, females seem to show an adaptive response to this shift by modulating their mating rate. In fact, our results suggest that females are modulating their mating rate to balance the costs and benefits of multiple matings with the costs imposed by male harassment (i.e., convenience polyandry). Four predictions result if the convenience polyandry hypothesis is valid. First, that forced copulations should be common at high density whereas at low density most initial copulations should be preceded by courtship. This prediction is supported by the data. The fact that density is the crucial factor for this behavioral change is supported by the comparison of site A in 1997 (high density) and 1999-2001 (low density) and by the difference between sites A and B in 1999-2001. Second, that some females should mate more than once per egg clutch and that they should

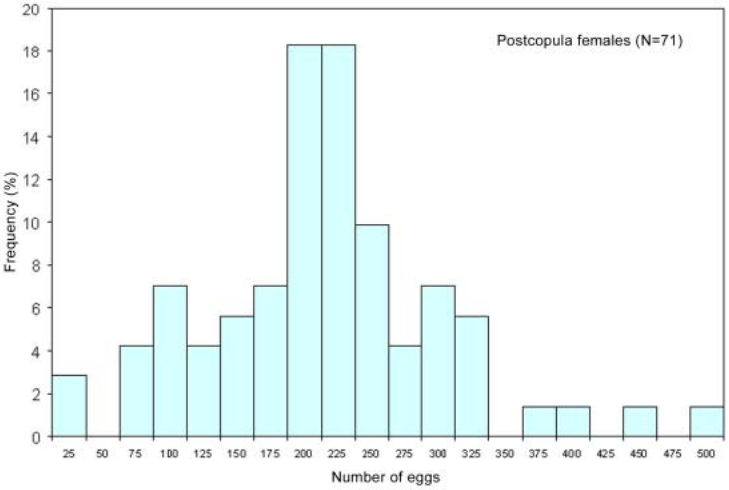

Figure 4. The number of mature eggs in females that accepted copulation. Note that some females mated even though they had very few eggs.

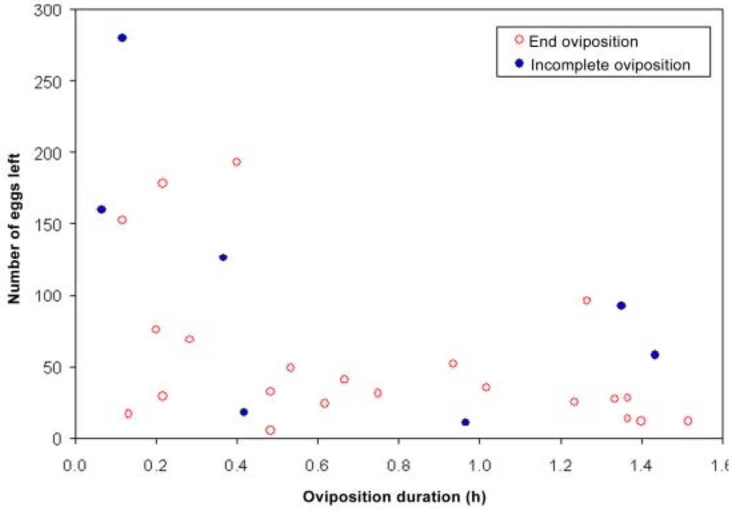

Figure 5. The relationship between oviposition duration and the number of eggs remaining in the abdomen of females that spontaneously abandoned oviposition or females that were ovipositing and accepted a new mating (incomplete oviposition).

copulate even if they had very few mature eggs to lay. Some females indeed mated five times, but female mating rate was lower than expected (see below). Female mating rate was positively correlated with male disturbance, but not with the time that the females spent at the oviposition patches. The third prediction is that females are forced to mate multiply. The data show that most of the subsequent matings were not preceded by courtship as the female choice hypothesis predicts, and there was a consistent difference between sites and years (Fig. 6).

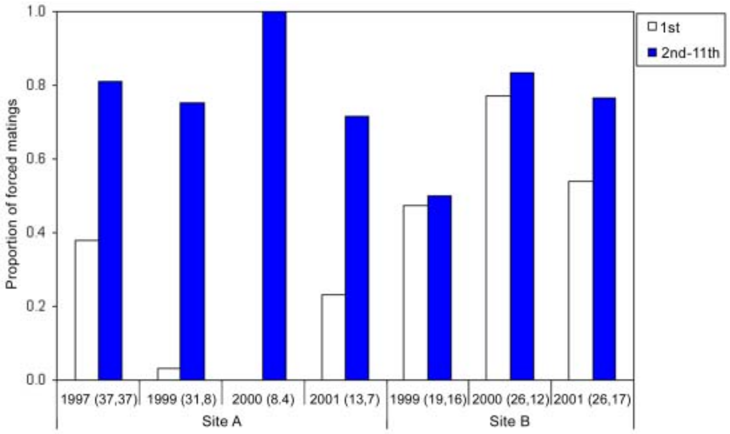

Figure 6. The proportion of forced matings in first and subsequent matings of marked females. Numbers after years indicate sample size.

Finally, if males coerce females the female mating rate per egg clutch would be expected to be significantly greater than one. Our results do not support this prediction. However, it is likely that females moved between oviposition sites when disturbed, and therefore additional matings at different places might have been under-recorded. Under a very high density, Cordero (1999) observed a female that mated 11 times in 2 hours. It is also important that a significant proportion of the focal females were able to find a refuge at the oviposition places, thereby avoiding being detected by males. Many of them were observed to lay eggs without any mating at all. In fact, ovipositing without mating with resident males is a well-known reproductive tactic in calopterygids (Siva-Jothy & Hooper, 1996). This behavior could reduce the frequency of forced matings.

Females always resist forced attempts to take them in tandem (Video 2), but nevertheless cooperate if successfully grasped (see also Thornhill & Alcock, 1983), even if they have very few mature eggs. This suggests that costs of resisting male coercion are greater than costs of accepting a new mating, and that as a result, females engage in convenience polyandry.. Furthermore, females probably benefit from new matings because males defend their mates with the same probability after both forced or courtship matings (Cordero, 1999). At high male density females were so often chased by males that they had great difficulty starting to oviposit. Males usually guard females by defending their territories but at very high density males sometimes switched to a contact guarding strategy (Video 3, Cordero, 1999). Therefore by accepting forced copulations, females might also benefit from some minutes of guarded oviposition. The costs of forced matings are probably minimal because copulation is short, especially at high density.

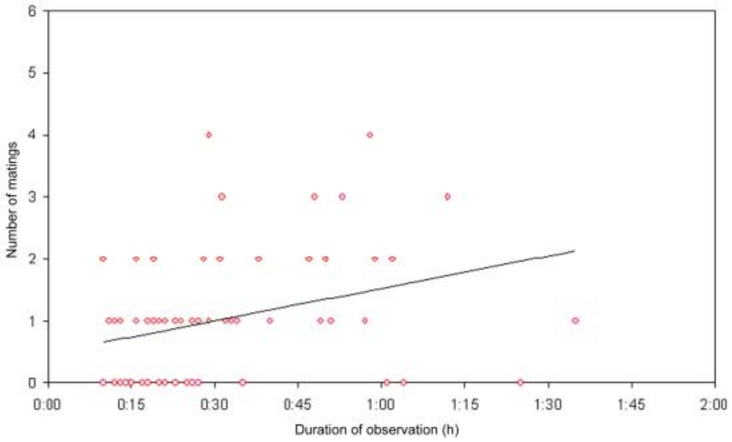

Figure 7a. The relationship between duration of oviposition and number of matings for females observed in 2000.

Our observations indicate that females might have three alternative tactics to avoid the costs of male harassment. First, they might try to "hide" from males thereby avoiding mating during oviposition. Second, if they are unsuccessful in hiding, they might accept superfluous copulations. A third possibility is to join a defended female and oviposit close to her (Waage, 1979). Males are apparently unable to distinguish between recent mates and non-mates (Cordero, 1999; but see Hooper, 1995), and will readily defend non-mates. For this reason groups of 4-5 females defended by one male were common (Video 3), even though only 1-2 females had been previously mated by the resident male. The behavior of *C. haemorrhoidalis* is very similar to that of *Calopteryx maculata* (Waage, 1979; 1984b), and clearly suggests that calopterygid females have many behavioral tactics that modulate the mating rate, in spite of apparent male control of oviposition substrates.

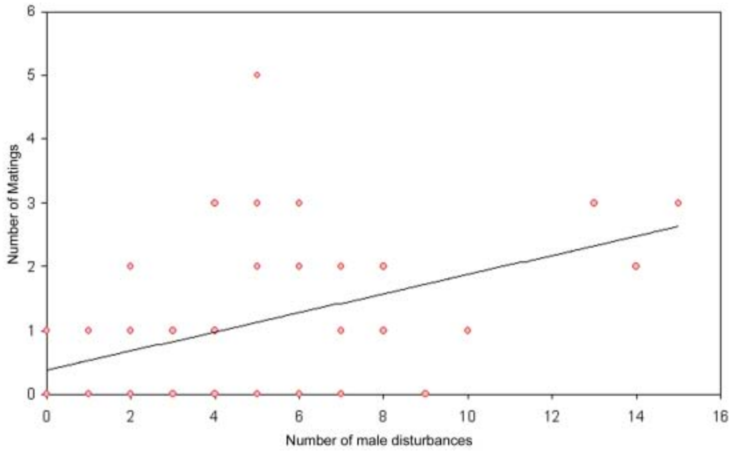

Figure 7b. The relationship between the number of male disturbances of ovipositing females (including chases when females tried to start oviposition) and the number of matings per clutch. Disturbances that ended in copulation are not included.

Previous studies of water striders whose mating systems are characterized by convenience polyandry have shown that copulation duration covaries positively with population density or a male-biased operational sex ratio (see Arnqvist, 1988; Rowe et al., 1994). In these species, long copulations might not only be male adaptation to avoid sperm competition (Alcock, 1994), but also result from a female strategy to avoid additional male harassment (Arnqvist, 1988; Rowe, 1992; Rowe et al., 1994). In contrast, in our study, we found that copulation was shorter at high density. In these species in which longer copulations occur at high density, females may control copulation duration. In contrast, in odonates copulation duration seems to be controlled by males (Miller, 1987), and in calopterygids mating has no guarding function. Given these conditions, copulation duration is expected to be shorter at high population density because searching time decreases and males will be "selected" to increase their mating frequency at the expense of the time dedicated to each mating (Nuyts & Michiels, 1993). That is, males are constrained and cannot maximize both mating and fertilization success. As a result, males might optimize their reproductive success in two alternative ways. At low density, males could maximize their fertilization success (i.e., increase copulation duration to reduce the risk of sperm competition) while at high density males could maximize their mating success. In fact, at high density, the amount of rival sperm removed was reduced as a consequence of shortened copulations (Cordero et al. unpublished data), suggesting that this is the case in *C. h. haemorrhoidalis*. A second explanation is that males are investing less time in forced matings because females whose mating is forced have been taken while in oviposition, and might have fewer eggs to lay, and also are likely to mate again under conditions of high male density. Both factors reduce the number of eggs that a male could expect to fertilize, and might contribute to shorten copulations. Additional data are needed to test these hypotheses.

In conclusion, female coercion is common in *C. h. haemorrhoidalis* under high population density, and females seem to respond adaptively by increasing their mating rate. In species in which females have control over copulation duration females also respond by increasing copulation duration, to avoid further male harassment. However, in species like *C. h. haemorrhoidalis* in which males seem to have control over copulation duration, females might avoid further male harassment by finding secretive places for oviposition or if males defend their mates by joining a group of defended ovipositing females.

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