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ORIGINAL PAPER

Male and female interactions during courtship of the Neotropical damselfly *Mnesarete pudica* (Odonata: Calopterygidae)

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Abstract The courtship behavior in calopterygid damselflies is well documented; however, the behavior of the large Neotropical genus *Mnesarete* is still unknown. Thus, here we present the first description of male–female interactions in *Mnesarete pudica*, a common damselfly in the Neotropical Savanna. The male–female interactions were composed of courtship displays, mounting, and chasing. The courtship behavior lasted 5.23±1.65 s and is very different from other calopterygids, consisting of hovering flights and the cross display made in front of females rather than on the oviposition site. The arrival and presence of females on a male territory are not sufficient to initiate sexual interactions; the male usually interacts with the female only after a patrolling flight. The females may present three distinct behaviors in response to male approach: (a) warding off signal (31.53%), (b) escape (28.83%), (c) and wing flipping (39.64%), which seems to stimulate male courtship. Females also may sit still, which induces males to react as if females were signaling they are willing to mate. In this paper, we also suggest that male courtship behavior is mediated by female signals.

Keywords Reproductive behavior · *Mnesarete* · Calopterygidae · Odonata · Mate choice

Introduction

Courtship behavior is an important trait for reproductive success in many animal taxa (Andersson 1994). Sexual selection theory considers that male and female perspectives in sexual interactions may differ (Thornhill and Alcock 1983). These interactions often involve intersexual signals, which regulate the investment of males and females.

Males, for example, have to perceive female receptivity to concentrate efforts in potentially successful interactions (Bonduriansky 2001; King et al. 2005) since courting a non-receptive female would imply a waste of time and energy (Hoefler 2008). Females usually signal their receptivity by several ways, among which we may cite acoustic signals (e.g., Wirmer et al. 2010), pheromones (e.g., Maxwell et al. 2010), and mechanical signals (e.g., Waage 1984). In species with elaborate courtship behavior, females often exhibit unique signals to stimulate courtship (e.g., displays by female collared lizards, Baird 2004), demonstrate receptivity to mounting (e.g., *Calopteryx* damselflies, Waage 1984), or even to show non-receptivity (female whitespotted sawyer, Hughes and Hughes 1985). Furthermore, males modulate courtship behavior according to these female signals (e.g., Waage 1984; Patricelli et al. 2002). For example, male satin bowerbirds

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(*Ptilonorhynchus violaceus*) increase display intensity according to female crouching intensity (Patricelli et al. 2002).

In Odonata, male courtship behavior is well studied (Corbet 1999). The calopterygid damselflies are an intriguing group due to their complex behavioral displays and mating strategies (reviewed by Cordoba-Aguilar and Cordero 2005). The courtship behavior varies greatly among the species, going from simple hovering flights in *Phaon* to elaborated courtship displays in *Calopteryx*, *Vestalis*, and *Mnais* (reviewed by Cordoba-Aguilar and Cordero 2005) and *Neurobasis* (Kumar and Prasad 1977; Günther 2006).

In calopterygids, males are usually territorial, defending oviposition sites and engaging in aerial contests for territories (Waage 1988; Córdoba-Aguilar 2000; Guillermo-Ferreira and Del-Claro 2011). This group also presents a remarkable wing pigmentation, which plays an important role in the complex behavioral displays exhibited during male courtship and territorial contests (Cordoba-Aguilar and Cordero 2005). This wing pigmentation is a condition-dependent ornament that correlates with male fat reserves and immunocompetence (Koskimaki et al. 2004; Contreras-Garduño et al. 2006) and also influences on male–male competition (Grether 1996) and female mate choice (Siva-Jothy 1999).

Although the behavior of Nearctical and Palearctical species is well documented, the behavior of large tropical groups like *Mnesarete*, *Sapho*, and *Umma* is still unknown. Such behavioral studies may provide valuable information about the evolution and ecology of this group, as well as useful data for the distinction of taxonomic groups. For example, since there are insufficient morphological characters that separate the genus *Mnesarete* from *Hetaerina* (Garrison 2006), which presents no courtship behavior (Guillermo-Ferreira and Del-Claro 2011; Cordoba-Aguilar and Cordero-Rivera 2005), behavioral studies of other *Mnesarete* species may present a possible trait that can separate both genera. Indeed, Garrison (2006) predicted that differences in courtship patterns would eventually be found to exist between *Hetaerina* and *Mnesarete*.

Therefore, the objective of this study was to make the first description of male–female interactions in a *Mnesarete* species. We then present the case of *Mnesarete pudica*, describing male–female interactions, with special attention to the role of female signals on the stimulation and discouragement of male courtship and mounting behaviors. The behavior of *M. pudica* is also compared with the current data for other calopterygids and pertinent issues are discussed.

Materials and methods

M. pudica is a common damselfly in southeastern Brazil (Costa 1986), and the males of this species are easily recognized by the bright red wing pigmentation (Costa 1986; Garrison 2006). All *Mnesarete* species are confined to South America (Garrison 2006). We conducted our study of *M. pudica* in one stream at the Ecological Reserve of the "Clube de Caça e Pesca Itororó de Uberlândia", Uberlândia, State of Minas Gerais, Brazil (15°57′S, 48°12′ W; altitude 863 m; 640 ha) in March and July 2010, and in another stream in a farm located in Assis, State of São Paulo, Brazil (22°38′S, 50°27′W; altitude 522 m) in July 2010. We made 30 h of behavioral observations from 1000 (when males begin to fight and court females) to 1500 hours (when sexual and fighting activity declines). After this time of the day, the damselflies tend to remain immobile (Costa 1986).

To describe courtship behavior, we used the *sequence sampling* method (Altmann 1974), which consists of behavioral observations focused on the description of behavioral sequences. When a male–female interaction began, we noted the sequence of behaviors exhibited by both males and females until the end of the interaction. The classification of the courtship behavior ($N=111$ male–female interactions) was made according to the following categories: (1) courtship flight (Heymer 1973), when the male hovers in arc in front of the female; (2) cross display (Waage 1973), the male perches and spreads his wings forming an "X"; and (3) float display (Gibbons and Pain 1992), when the male falls to the water and floats with the current. Following Waage (1973) and Robertson (1982), we elaborated flow charts to describe male–female interactions based on 111 behavioral sequences observed using the sequence sampling method. Video recordings (Sony handycam) were used to record male courtship for the description of male and female wing movements. Data for male and female behavioral sequences come from direct observation. A hand chronometer was used to measure the duration of 52 courtship displays.

To study the intersexual signals during male–female interactions, we tethered live females to a line using Duco cement (e.g., Fincke 1994). The line was then glued to a 20-cm wood stick (e.g., Miller and Fincke 1999), and finally, the females were presented to males at the stream by holding and gently waving the stick in front of them. The line was around 2 cm long so that females could move freely but could not fly. The stick was held by one of the observers, who kept the stick around 5 cm away from the male. This method is widely used in Odonata behavioral studies, and it is established as a non-interfering technique to assess female normal behavior.

The males approached the tethered female, and both the female behavior and the corresponding male behavioral response were recorded. Following Waage (1984), we identified three different female signals: (a) wing spread, when the female spreads the four wings, raises the abdomen, and keeps this position until the male retreats, which is a rejection signal, (b) wing flipping, when the female flaps her wings several times in rapid succession, which is a receptivity signal, and (c) sit still, which is a neutral signal. Males usually react to female sitting still as if they were inviting copulation (e.g., *Calopteryx maculata*, Waage 1984).

To simulate female signals, we made a series of manipulations. To simulate a female sitting still, we presented three females with their wings glued to avoid them to spread or flip the wings. We also presented six other females with their wings free, which could display both wing spread and wing flipping. Each of the females was presented to only three different males. After the experiment, we had a final number of 11 male responses to females sitting still (9 manipulated and 2 natural events), 5 male responses to females that presented the wing flipping display, and 11 male responses to female wing spread display. Male behavior was classified as: (a) stop, when the male approached or even grabbed the female but then retreated, (b) courtship, when the male courted the female, and (c) tandem, the male assumed the tandem with the female. The difference between male responses to female signals was compared using the *G* test in the software Statistica 9.0.

Results

Male courtship behavior and female response to male courtship

The males and females are usually found at the water, but some individuals were found fighting and courting up to 5 m away from the stream margins. When a female approaches a territory, the male usually does not respond until patrolling the territory, when the male finally flies towards the female and approaches her. With a male approach, the female may immediately present three distinct behaviors: (a) the females spreads her wings in a refusal display (35/111, 31.53%), which makes the male retreat; (b) the female leaves her perch and escapes from the male (32/111, 28.83%), or (c) the female starts to flap her wings rapidly (44/111, 39.64%), which leads the male to give his full courtship display as shown in the video (Electronic supplementary material 1).

The courtship display starts with the (1) courtship flight; however, the male does not hover in arc in front of the female (like other calopterygids do), but flies rapidly in circles around the female (Fig. 1). After the courtship flight, the male perches near the female and spreads his wings (Fig. 2a), swinging the body alternatively to the right and to the left (Fig. 2b) and occasionally spinning around the perch while holding it (*N*=5). This behavior may be considered the (2) cross display in this species. The male usually repeats this sequence of courtship flight and cross display for up to five consecutive and uninterrupted times to the same female. At no time did we observe a (3) float display. After the courtship display, if the female sits still, the male grabs the female wings and clasps her prothorax with his abdominal appendages to form the wheel position.

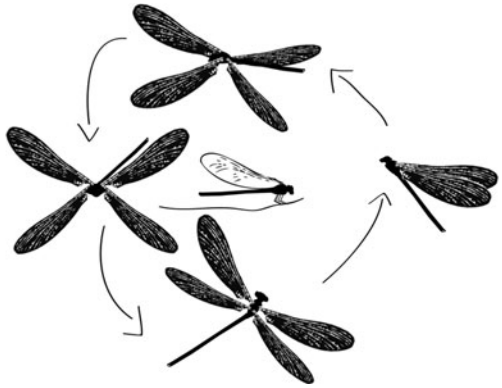

Fig. 1 A male *M. pudica* hovering around a female and showing his wings. The male is represented by the *dark* winged damselfly and the female by the *clear* winged damselfly. The *arrows* indicate the male movements and the *line* the female perch. The wing positions during the flight were determined by analyzing video footage

This display lasts 5.23±1.65 s (*N*=52; range, 1–9 s), and the male usually stops courting the female and stays immobile on the same perch occupied by the female. The male may also try to mount and chase the female without any courtship. The male–female encounters (Fig. 3) may be divided into: (a) type I, when the encounter initiates with the male finding a female after patrolling the site; (b) type II, when a male tries to mate with a female during a territorial contest; (c) type III, when the female lands and the male approaches. Of the 111 courtship events observed, 93 were classified as type I, 12 as type II, and 6 as type III. Interestingly

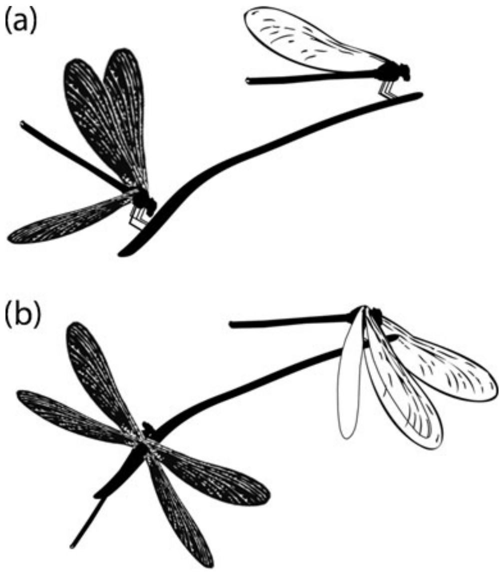

Fig. 2 The male *M. pudica* perches near the female and spreads his wings (**a**), swinging from the middle of the perch to the left and to the right, while the female flaps her wings (**b**). The male is represented by the *dark* winged damselfly and the female by the *clear* winged damselfly. The *line* represents the perch

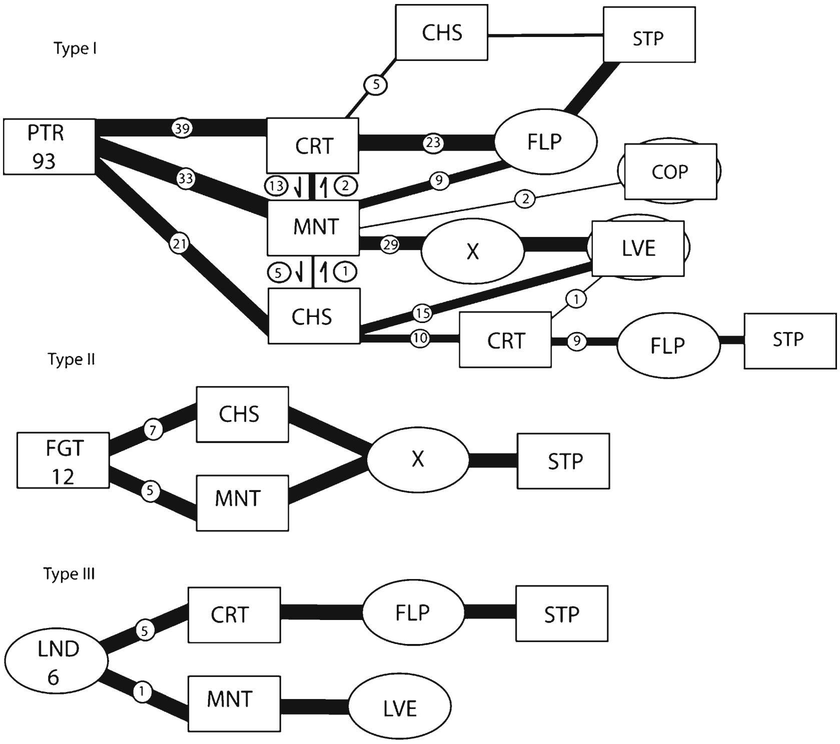

Fig. 3 Flow chart for male–female encounters in *M. pudica*: type I, male patrols and finds the female; type II, during a male–male contest, the male interacts with the female; type III, the female lands on the territory and the male approaches. *Squares* indicate male actions and *circles*, female actions. The flow is from *left* to *right*, and the *numbers in the lines* and the *relative thickness of the lines* indicate the number and percentage of encounters following a particular pathway. *Numbers within the symbols* indicate the number of times that the event occurred. *CHS* Chase female, *COP* copulation, *CRT* courtship, *FGT* male–male fighting, *FLP* female wing-flipping display, *LND* female lands on the territory, *LVE* female leaves the territory, *MNT* the male tries to mount the female, *PTR* patrol the territory, *STP* the male stops courting the female, and *X* the female spreads her wings in a refusal display

though, in such a vast number of courtships only two copulations could be observed, and these females did not oviposit inside the territory, being released by the male right after copulation. As for the males, they returned to their territory, fighting rival males and courting females. One male was observed to court the female he had just mated five consecutive times. We found no ovipositing female, and seven males defended areas with no apparent oviposition resource. Other two males defended a site 5 m away from water, and they were still visited by females.

Male response to female signals

Male responses differed according to female signals (*G* test, *df*=4, $p<0.0001$). Six males grabbed those females whose wings were immobilized without any courtship attempt and assumed the tandem, while the other three males retreated (Table 1). Five females with free wings made the wing-flipping display and were courted by males. None of the courtships proceeded to tandem. Eleven females made the wing-spread display, leading ten males to retreat and one to assume the tandem. Two females with free wings sat still, leading males to assume the tandem.

Discussion

The courtship behavior in *M. pudica* can be considered as complex as the behavior of related species such as *C. maculata* (Johnson 1962; Waage 1973), *Calopteryx aequabilis* (Waage 1973), *Calopteryx virgo* (Pajunen 1966), *Calopteryx haemorrhoidalis* (Cordoba-Aguilar 2000), *Calopteryx dimidiata* (Waage 1988), and *Calopteryx amata* (Meek and Herman 1990). In these species, the males also show the wings to females during courtship. However, *M. pudica* males present certain differences that must be considered: (1) *Calopteryx* males fly in arc in front of the females, while *M. pudica* fly in circles around the female; (2) *Calopteryx* males make the cross display perching or hovering over the oviposition site, while *M. pudica* makes it perched near the female,

Table 1 Male responses (stop, tandem, and courtship) to female signals (wing flipping, wing spread, and sitting still) in *M. pudica*

	Stop	Tandem	Courtship
Wing flipping	0	0	5
Wing spread	10	1	0
Sit still	3	8	0

spreading his wings in front of her; (3) in *Calopteryx*, there is the float display, that we did not observe in *M. pudica*; (4) in *C. maculata* (Waage 1973) and *Platycypha caligata* (Robertson 1982), the courtship initiates mainly when the male intercepts the female, while in *M. pudica* the courtship initiates when the male patrols the territory and finds a female perched inside it.

Interestingly, the males court the female after patrolling or fighting. The females may spend hours perched near a male, and he does not court them until he flies in a patrol or engages in a fight. This suggests that males only court females when they fly in search for them. After courtship, the male just stops courting the female with no apparent reason in most cases, and does not proceed to copulation, which is also different from other species with high mating rates (e.g., Waage 1973, Cordoba-Aguilar 2000).

We also observed males courting the same female several times during the day. Some studies suggest that in species where male courtship has multiple traits, females require repeated displays to assess male quality (Borgia 1995; Sullivan 1994; Patricelli et al. 2002). Thus, repeated courtship in *M. pudica* may occur because females need cumulative input signals from males to exert mate choice.

During the cross display, *M. pudica* males swing to the right and to the left, a behavior that has never been observed in Odonata. Because the wing color reflection may vary with angle of view (Schultz and Fincke 2009), we suggest that this behavior could be interpreted as an adaptation to enhance the output of the color signal according to the female angle of view and sunlight direction, similar to the adaptation that occurs in peacocks (Dakin and Montgomerie 2009).

Sexual selection may favor the ability to adjust courtship effectively in response to female behaviors (Patricelli et al. 2006). In this scenario, females provide information for males about their willingness to mate and male courtship effectiveness, and males use this information to enhance their reproductive success (West and King 1988; Patricelli et al. 2002, 2006).

Male courtship behavior in *M. pudica* seems to be dependent on female signals. The results showed that females flip their wings to stimulate male courtship. Without the wing-flipping display, the males tend to grab the females without previous courtship and assume the tandem, similar to what occurs in *C. maculata* (Waage 1984). The males also avoided interactions when the females made the wing-spread display, just like in *Calopteryx* (Waage 1984). These results corroborate Waage (1984) and show how male and female behavior may have co-evolved to create mutual signals of attraction and repulse.

Since females suffer from male harassment and forced copulations, which decrease female longevity (Cordoba-Aguilar 2009) and prevent females from assessing mates, selection should favor females that exhibit behaviors that regulate male courtship and mounting attempts. Thus, we suggest that in *M. pudica* selection may have favored a display that signals female receptivity to courtship but not to copulation, which avoids forced copulations but does not repulse potential mates (e.g., Patricelli et al. 2004). Through this signal, females have the opportunity to assess male quality and exert mate choice. Male courtship would then evolve in response to this female signal in a way they could show their quality to females.

The fact that *M. pudica* has a complex courtship behavior is surprising since the close related genus *Hetaerina* (Garrison 2006) presents no courtship behavior (Guillermo-Ferreira and Del-Claro 2011; Cordoba-Aguilar and Cordero-Rivera 2005). Therefore, as Garrison (2006) predicted, behavioral studies of other *Mnesarete* species may present a possible trait that can separate both genera, if they also present such complex behaviors like *M. pudica*. The study of other Neotropical *Mnesarete* and *Hetaerina* species may also provide important data on the evolution of courtship behavior and male–female signals in Calopterygidae.

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