

Sexual size dimorphism, mating system and seasonality of a Neotropical damselfly, *Telebasis carmesina* (Coenagrionidae)

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Our understanding of mating systems is highly skewed toward temperate examples. This study investigated the mating system, sexual size dimorphism and seasonal variation in local distribution and abundance of male and female *Telebasis carmesina*, a common damselfly in Brazilian tropical savanna. In a natural reserve, daily census and behavioral observations were made throughout 1 year at the edges of a permanent pond. Males were more abundant during the rainy season, when mating and oviposition by females occurred. The operational sex ratio at the pond was heavily male biased, *c.* 1♀ : 19♂. Males were smaller than females but were larger in the dry season than in the wet season, when they were more abundant at the pond. Females were larger in the dry months of July to September than in the rainy season. Both males and females principally used the macrophyte *Eleocharis* sp. as perches and for oviposition. Males exhibited polygynous, scramble mate competition, as in most coenagrionids that have been studied.

Keywords: Odonata; population dynamics; habitat requirements; scramble competition; male-biased sex ratio

Introduction

Although damselflies are abundant and greatly diversified in the Neotropics, aspects of their life history, ecology and behavior are not well known (Cordero-Rivera & Stoks, 2008; Hamilton & Montgomerie, 1989). Studies on reproductive behavior of Brazilian species are few (e.g. Guillermo-Ferreira & Del-Claro, 2011a, 2011b, 2012). *Telebasis carmesina* Calvert, 1909 (Coenagrionidae) is a Neotropical species common in ponds and streams of the Cerrado, the Brazilian tropical savanna. This is one of the most endangered ecosystems in the world (Oliveira & Marquis, 2002), where basic natural history studies are still much needed (Del-Claro & Torezan-Silingardi, 2009). Here we describe the mating system of *T. carmesina*, and investigate how seasonality affected the mating system and body size of adults. We also quantified male and female use of aquatic vegetation at the site.

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Table 1. Average air temperature and humidity (mean \pm SE) from July 2008 to June 2009 in the study site, Cerrado savanna, Brazil (18°59' S, 48°18' W).

		Temperature (°C)	Humidity (%)	Rainfall (mm)*
2008	Jul	19.26 \pm 0.66	64.20 \pm 3.84	0
	Aug	23.20 \pm 0.48	53.50 \pm 3.48	0.5
	Sept	23.75 \pm 1.28	48.00 \pm 4.61	17.5
	Oct	25.45 \pm 1.19	57.17 \pm 5.42	148.2
	Nov	23.80 \pm 0.80	73.00 \pm 3.00	59.9
	Dec	25.20 \pm 0.70	73.50 \pm 0.50	363.3
2009	Jan	26.00 \pm 0.44	69.50 \pm 2.84	256.4
	Feb	25.03 \pm 0.55	75.33 \pm 3.71	202.4
	Mar	23.60 \pm 0.38	78.40 \pm 1.96	103.1
	Apr	23.14 \pm 1.14	70.20 \pm 6.45	70.2
	May	22.30 \pm 0.36	76.20 \pm 4.70	58.8
	Jun	19.74 \pm 1.40	66.20 \pm 4.42	8.5

*Rainfall data were not available for the study site. The values given are long-term means for the city of Uberlândia, about 8 km to the north.

Materials and methods

The study was conducted from May 2008 through to October 2009 at the tropical savanna reserve of the Clube de Caça e Pesca Itororó de Uberlândia (CCPIU), state of Minas Gerais, Brazil (18°59' S, 48°18' W). Data on longevity, size and abundance were collected only from July 2008 through to June 2009; to keep temporal continuity through the study, we divided the latter period into four intervals of 3 months, beginning in July 2008. Our study site typically experiences a wet season from October to March and a dry season from April to September (Table 1; see Réu & Del-Claro, 2005; Arruda et al., 2006, for more details of the area).

The study pond was *c.* 5 m deep at maximum, with 70% of its surface occupied by emergent macrophytes such as *Pontederia parviflora* Alexander (Pontederiaceae) and *Eleocharis* sp. (Cyperaceae) and submerged macrophytes such as *Heteranthera* sp. (Pontederiaceae). The margins of the pond (Figure 1) were divided into three sections, A, B and C, that differed in orientation, water depth and vegetation cover. Margins A and C were both situated along shallow margins of the pond (\sim 30 cm deep) in contact with grasses and shrubs of the open Cerrado vegetation (*sensu* Oliveira-Filho & Ratter, 2002). Margin A (70 m long), had surface macrophytes comprising mostly *Pontederia* (5.1% cover) and *Eleocharis* (2.2%). Margin C (40 m) also had *Pontederia* (2.1 % cover) and *Eleocharis* (6.3%). The third margin, B (70 m, between A and C), had a 2-m wide field road at its edge and formed an inclined plane with deeper waters (2–4 m deep) and denser macrophyte cover, again of *Pontederia* (20.5%) and *Eleocharis* (9.1%). Macrophyte coverage was measured in both wet (February 2009) and dry (September 2009) seasons. Along each of the three pond margins, an area of 10 m² was established for measurement of vegetation coverage. Those in sections A and C were 5 m long and extended 2 m into the water, toward the center of the pond; along section B the steep bank restricted access to the water, so the study area in that section, the area demarked, was 10 m long and extended 1 m into the water, so encompassing the same area as along A and C. In each designated vegetation area, 10 quadrats (0.5 \times 0.5 m) were randomly selected to measure the vegetation structure (species and abundance) using a plastic (PVC) square frame with a 10 \times 10-cm mesh. Quadrats with vegetation cover of > 60% were designated as “covered”; quadrats with less than 60% vegetation cover were designated as “not covered”.

Transects, where damselflies were collected, marked and recaptured, were established at 5, 10 and 15 m from the edge of the pond (Figure 1), after previously searching for the insects up to 500 m from the pond; *T. carmesina* were rarely observed > 15 m from the border of the pond.

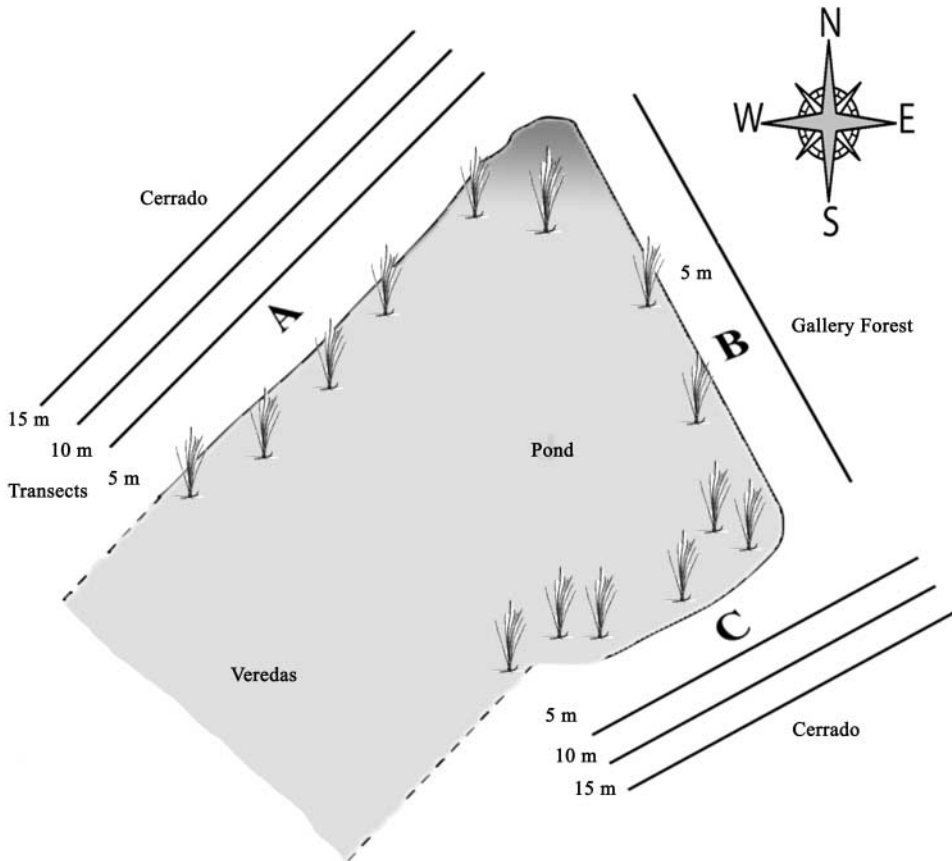


Figure 1. Schematic drawing of the study pond showing the margins and position of transects. Margins A and C were surrounded by tropical savanna (Cerrado), and B by gallery forest. The pond is in the end of a Vereda (flooded clay soil covered by grasses and palm trees).

Once each week, one observer looked for *T. carmesina* adults by slowly walking and inspecting the transects between 8:00 a.m. and 2:00 p.m., the period of highest activity of *T. carmesina*. To estimate adult microhabitat use, abundance, operational sex ratio and sexual size dimorphism, adults were captured using an aerial insect net. For each adult caught, we recorded the time, its exact position on the transect or pond, and its behavior (flying or resting on a perch/plant species). All caught individuals were marked by writing a consecutive number on the wing with an indelible paint pen, measured with a digital caliper (0–150 mm; accuracy of ± 0.03 mm) from head tip to abdomen end, and sexed. Marking apparently had little or no effect on the behavior of individuals, because after release the marked animals flew in the same manner as unmarked ones (e.g. Guillermo-Ferreira & Del-Claro, 2011a, 2012). These insects have slow flight and are easy to catch. Rarely did the observer miss a catch, and in this case the individual was not considered. Relative longevity was estimated as the time between the day an individual was marked and its last appearance (Hamilton & Montgomerie, 1989).

Observations of sexual behaviors were made between 7:30 a.m. and 2:30 p.m., only at the pond margins, from May 2008 to October 2009. Initial observations used all-occurrence sampling, followed by sequence sampling (*sensu* Altmann, 1974; Del-Claro, 2010) to characterize each phase. Agonistic interactions consisted of aggressive behavior displayed between a male occupying a substrate and an approaching male. We quantified agonistic behaviors using all occurrence sampling and animal focal sampling (*sensu* Altmann, 1974; Del-Claro, 2010). In general, each

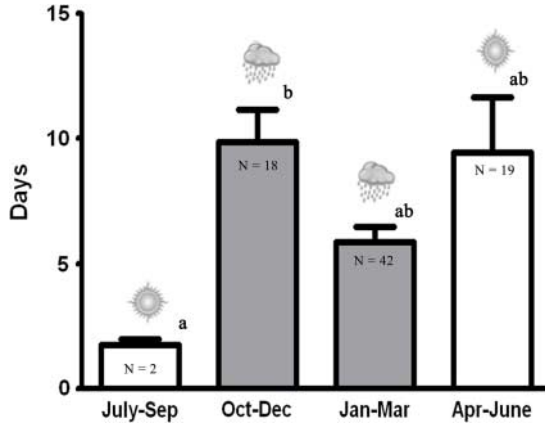


Figure 2. Male longevity (days) among four 3-month periods of the year (July 2008 to June 2009) varied significantly (Kruskal–Wallis test). Different letters indicate statistical difference among periods (Dunn’s multiple comparison test). Sun figure over white bars indicates the dry periods and the clouds over the grey bars indicate the wet periods. The *N* inside the bars represents the number of males sampled in each period.

focal sampling session lasted 30 minutes, although it might be extended to observe the end of mating. After each observation both individuals were caught, marked and released. To verify whether male size affected agonistic interactions, we compared the size of the first male on a perch with the size of the approaching male.

Voucher specimens were deposited at the Museu de Biodiversidade do Cerrado (MBC/UFU).

Statistical analysis

Statistical analyses followed Zar (1999), using BIOESTAT 5.0[®] software. When possible, parametric analyses were performed. We used non-parametric analyses when data were not normally distributed, even after being transformed (\log and $\sqrt{+ 0.5}$). We considered $P < 0.05$ as significant. Specific tests are indicated as appropriate in Results.

Results

Abundance and distribution of individuals

From July 2008 to June 2009, a total of 1133 individuals (1078 males, 55 females) were marked. Ninety-seven males (8.6%) and no females were recaptured on a different day. Both males and females were captured or observed within 15 m of the pond edge. There was no statistically significant relation between the distance from the pond and the number of males (Spearman rank correlation, $r_s = -0.2315$, $t = -1.0641$, $P = 0.244$) or females ($r_s = -0.2389$; $t = -0.9206$, $P = 0.412$) caught. We previously checked out to 500 m from the permanent pond but rarely found a male or female beyond 15 m from the pond shore, and never farther than 30 m.

Male longevity varied as shown in Figure 2. Average longevity during the main reproductive season (October to April) was 7.1 ± 0.72 days. The range of individual persistence in the field varied between a maximum of 27 days for male number 587 in January, and a minimum of 1 day for several individuals between April and September. In the dry season individuals lived for 1–9 days and in the wet periods for 3–27 days.

Sex ratio

No females were caught in July, November or December 2008, or in February 2009. Based on the average daily count of marked individuals, males greatly outnumbered females (55 females/1078 males), resulting in an operational sex ratio of $1\text{♀} : 19\text{♂}$ (maximum observed ratio of $1\text{♀} : 27\text{♂}$; in the morning of 16 March 2009). The habitat used by females when they are not at the pond is still a matter for investigation. Due to the fact that females arrived at and disappeared from the pond and its shores at much shorter intervals, the number of females may be underestimated.

Size

Males were smaller than females (male body length, mean = 2.70 ± 0.003 cm; $n = 1005$; female body length, mean = 2.78 ± 0.017 cm; $n = 41$, Mann–Whitney: $U = 29$, 128.500, $P < 0.0001$). The average size of males (analysis of variance: $r^2 = 0.161$, $F_{3,1001} = 64.207$, $P < 0.001$) and females (analysis of variance: $r^2 = 0.347$, $F_{3,37} = 6.549$, $P < 0.001$), varied significantly with time of year (Figure 3). Moreover, male size was negatively related to abundance ($r^2 = 0.547$, $F_{1,10} = 12.099$, $P < 0.05$).

Abundance in relation to air temperature and season

Like other insects, *T. carmesina* is influenced by season and temperature (Figure 4; Table 1). Analysis of covariance (ANCOVA) showed that period of year was a significant predictor of male abundance (Table 2). Males were also marginally more abundant with higher air temperature (Table 2). Before running ANCOVA, we found that covariates temperature and humidity were weakly correlated. Data for females was insufficient to perform an ANCOVA.

Perching surface

At the reproductive site, *T. carmesina* males disproportionately perched on *Eleocharis* sp. stems whereas females did not show a preference for any macrophyte species (Student's *t*-test with 999 randomizations of the perching frequencies, $P < 0.001$ for males, $P = 0.664$ for females). Both sexes were found mainly in areas covered by macrophytes (Mann–Whitney: $U = 12.50$, $P = 0.0016$ for females; $U = 167$, $P < 0.001$ for males). In total, *T. carmesina* perched principally on *Eleocharis* sp. stems (63% of observations), *Pontederia parviflora* leaves (5%), grasses (24%), and other vegetation (9%).

The pond vegetation cover, represented by the dominant species *Eleocharis* sp. and *Pontederia parviflora*, did not change between rainy and dry seasons (Wilcoxon: $Z = 0.9878$, $df = 83$, $P > 0.05$, for *Eleocharis* sp., $Z = 0.7821$, $df = 84$, $P < 0.05$ for *P. parviflora*). However, *Eleocharis* sp. cover differed between sections “A” and “C”, (Kruskal–Wallis: $H_{2,29} = 16.9025$, $n = 30$, $P > 0.001$), and *P. parviflora* cover differed between section “B” and both “A” and “C” ($H_{2,29} = 53$, 3890, $n = 30$, $P < 0.001$). *Eleocharis* sp. was less available than other macrophytes and had the lowest abundance in relation to overall macrophyte coverage ($U = 7576$, $n = 180$, $P < 0.001$).

Mating behavior

Reproductive behaviors of *T. carmesina* were observed mainly between October and April, between 7:30 a.m. and 2:30 p.m. (maximum). Copulations were sighted most often near mid-morning (10:08 a.m. ± 27 min; mean \pm SE, $n = 19$). A small number of adults were also observed

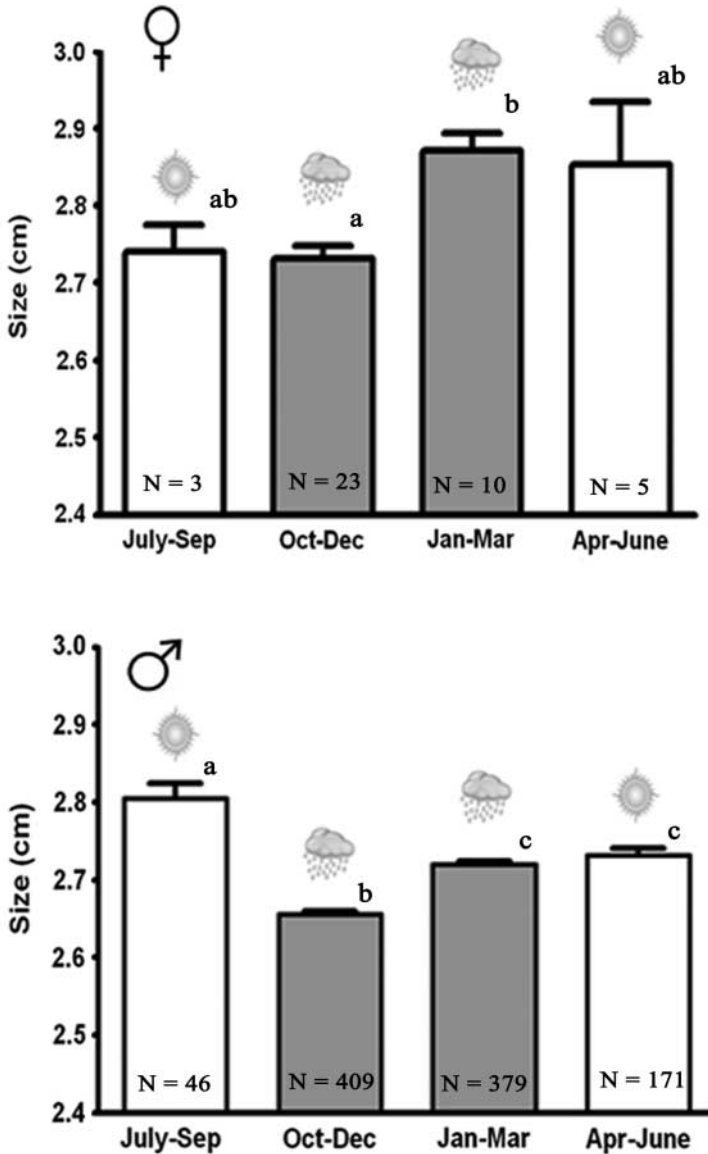


Figure 3. Adult damselflies size among four 3-month periods of the year (July 2008 to June 2009). Error bars represent ± 1 SE. Different letters indicate significant differences ($P < 0.05$; analysis of variance/Tukey post hoc test; $\alpha = 0.05$ for males; and $P < 0.05$; Kruskal–Wallis/Dunn’s multiple comparison test; $\alpha = 0.05$ for females). Sun figure over white bars indicates the dry periods and the clouds over the grey bars indicate the wet periods. The N inside the bars represents the number of males sampled in each period.

breeding outside this season, always within 15 m of the pond’s edge. These individuals exhibited all normal behaviors of the species, including reproductive behaviors.

Telebasis carmesina showed a mating sequence similar to other Zygoptera. When a male located a perched female on a stem, it hovered over the female and grabbed her, almost immediately assuming the wheel position (when the male’s anal appendages grasped the female’s prothorax, the male moved his abdomen ventrally, leading the female’s genital pore to his genital ligula, $n = 33$ observations; Figure 5). This first step lasted on average $19:33 \pm 3:43$ min ($n = 6$). When

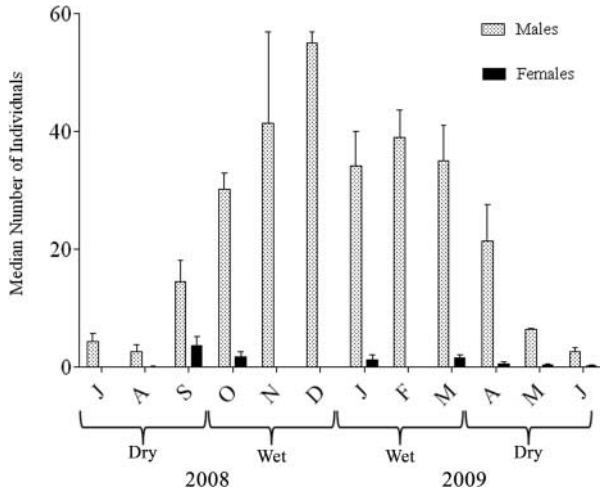


Figure 4. Damselfly (*Telebasis carmesina*, Coenagrionidae) abundance (males, hatched bars; females, black bars; mean \pm SE) in a Brazilian tropical savanna. The dry periods had lower temperatures and humidity, than wet periods (Table 1).

Table 2. Analysis of covariance of the variables associated with male abundance over 1 year (2008: July–Sep, Oct–Dec; 2009: Jan–Mar, Apr–Jun) period of study ($n = 54$; $r^2 = 0.678$).

Variable	df	F-ratio	P-value
Temperature*	1	3.741	0.059
Humidity*	1	1.596	0.213
Season [†]	3	12.525	<0.001

*Covariates

[†]Factor

copulation was initiated, the male performed abdominal contractions, probably indicating the removal of sperm previously deposited by other males. During the last minutes of the copulation, these movements ceased. Then, presumably, transfer of sperm to the female occurred (e.g. Cordero & Miller, 1992). Usually, other males approached the couple and in 33.3% of cases ($n = 33$) these males broke up the tandem pair. However, in most observations (66.7%), intruder males did not dislodge the pair and the couple remained together moving to an oviposition site. During oviposition, the female and male remained in tandem. Often, the male perched, while the female laid eggs only in *Eleocharis* sp. ($n = 28$ observations). It was possible to quantify oviposition time from beginning to end in only one observation, which lasted 33 minutes. During an oviposition, a female either: (1) kept her body partially submerged and changed the oviposition site ($n = 26$, 92.8% of observations) or (2) remained totally submerged at the same point during egg laying while the male was partially submerged ($n = 2$, 7.2% of observations). In both cases, males escorted females in tandem.

Agonistic behaviors observed in *T. carmesina* were (1) pursuit (one male chased the other, then went back to its original position, or its position was taken by the other); (2) warning signal (wing-spread – a male perceived the approach of another, and opened its wings), and (3) attack (males hit each other with their bodies, legs and abdominal appendages or mouthparts). Agonistic behaviors were mostly aimed at conspecific males but sometimes also at heterospecific individuals, including *Acanthagrion truncatum* Selys, 1876, *Argia* sp. and *Homeoura nepos* Selys,



Figure 5. *Telebasis carmesina* in wheel position. Photo: Kleber Del Claro.

1876. The most frequently recorded agonistic behaviors were conspecific (56.34%, $n = 41$) and heterospecific (18.31%, $n = 13$) pursuit, followed by conspecific attacks (9.86%, $n = 7$) and warning signals (8%, $n = 5$).

We noted that males recaptured at the same point on different days ($n = 52$, i.e. 52.52% of recaptured males) were more aggressive than males recaptured in different points of the pond, especially with conspecific males. There was no statistically significant difference in size among the perching males and the approaching males ($t = 0.939$, $df = 78$, $P = 0.351$).

Discussion

Variation in abundance of *Telebasis carmesina* males and in adult body size was strongly seasonal. Over the 1-year study period, the greatest abundance of individuals occurred during the rainy season, and the operational sex ratio was highly male biased. Similar patterns are observed for some other tropical damselfly species, as in Costa Rica (Hamilton & Montgomerie, 1989).

Corbet (1999), in a review of longevity of Odonata, showed that the average life expectancy for adult zygopterans is 7.6 days, with maximum longevity ranging from 17 to 64 days; at least one tropical zygopteran can live as long as 150 days (Fincke & Hadrys, 2001). Hence, mean survival duration of *T. carmesina* adults during the reproductive period – approximately 7 days – was close to the average for most Zygoptera, although their longevity was higher during Oct–Dec (approximately 10 days).

The primary sex ratio (i.e. sex ratio at fertilization) should be 1:1, except under local mate competition or other unusual situations (Cordero-Rivera & Stoks, 2008). Some studies on sex ratio at emergence (Corbet & Hoess, 1998; Lawton, 1972) found that males are slightly more frequent than females in Zygoptera, but this slight male bias in emergence sex ratios could not explain the heavily skewed operational sex ratios we found in *T. carmesina*. More likely, females stay farther from the pond than we monitored or were hidden in the top of tall trees in the middle of Vereda.

Among Odonata there is a gradient from simple, aggressive behavior, without either site attachment or residentiality, to ritualized display, with site attachment and pronounced residentiality (Corbet, 1980). We found that male *T. carmesina* exhibit aggressive behavior and most males were recaptured at the same point after several days. We also found, however, that males did not defend a discrete oviposition site, as most territorial species do (Guillermo-Ferreira & Del-Claro, 2012; Waage, 1988). Such evidence suggests that this species adopts a polygynous system of interference competition (scramble competition), behaving aggressively in a variable way according to the density of males nearby. We found no statistical difference in size among first landed males (males recaptured at the same place) and approaching males (recaptured at a different place); even highly territorial species, however, do not necessarily show a significant size difference between successful and unsuccessful territory holders (e.g. Marden & Waage, 1990).

Telebasis carmesina reproductive behavior was similar to other non-territorial coenagrionids (e.g. Bick & Bick, 1963; Fincke, 1982; Banks & Thompson, 1985; Sirot & Brockmann, 2001). Males cannot force copulations on unreceptive females because females must actively form the wheel position (Fincke et al., 1997; Sirot & Brockmann, 2001). *Telebasis carmesina* males always guarded ovipositing females with which they had mated. This is expected if other males are likely to attempt to interrupt oviposition and mate with the female (Corbet, 1980), as appeared true here. As in many Odonata, guarding of a recently inseminated female by her most recent mate should enhance the probability that the male actually fertilizes the eggs being laid. In addition, male presence during oviposition enhances the time that females can expend laying eggs. Due to their very low abundance at the site of reproduction, *T. carmesina* females can be considered as limiting resources for males, resulting in adaptations by the latter to ensure fertilization like scramble competition and oviposition in tandem.

Differences in body size between males and females are common in many animals (Andersson, 1994). The direction and magnitude of selection on body size may differ between sexes and generate sexual size dimorphism (Thornhill & Alcock, 1983; Wong-Muñoz et al., 2011). Females of *T. carmesina* are larger than males, i.e. sexual size dimorphism is female-biased. Non-territorial males that use scramble competition reproductive tactics are generally smaller than females, as corroborated by other studies (reviewed by Bick & Bick, 1963; Banks & Thompson, 1985; Cordoba-Aguilar, 1993; Fincke et al., 1997). This may occur because (1) larger females are more fecund (Honeck, 1993); (2) the differential use of niches reduces competition for resources between the sexes, promoting morphological differences (Shine, 1989); and (3) natural selection favors small males in species in which competition between males takes place in the air (Székely et al., 2007), if small body size enhances aerial agility (Blanckenhorn et al., 1995) as may happen with *T. carmesina*. Indeed, seasonality influenced individuals' abundance and body length such that size was smaller at times when male–male interactions were most likely.

As in other ectotherms, both daily and seasonal patterns of activity and abundance of Odonata are influenced by temperature (Corbet, 1999). In male *T. carmesina*, however, activity, and consequently, abundance at the breeding site, are strongly influenced by season and only very weakly by air temperature. Hence, we speculate that the effects of time of year on larval life and emergence success are more important in determining adult activity than are the immediate effects of temperature and other environmental parameters, even though a few adults are always present. Because season and temperature co-vary, however, the possibility of a larger direct effect of temperature than indicated here cannot be altogether discounted.

The outcomes of this study showed that some specific breeding site features are important. The availability and identity of macrophytes influenced individuals' behavior, mainly their reproductive acts. Despite the fact that *Eleocharis* sp. is less available than other macrophytes, *T. carmesina* preferred it for perching, mating and oviposition. This bears out earlier studies. According to Nessimian and Carvalho (1998), the genus *Telebasis* prefers water bodies with macrophytes. Aquatic macrophytes are important habitat components in the life cycle of many

Odonata (Buchwald, 1992; Wildermuth, 1994), and several studies have described a correlation between the abundance of certain species of dragonflies and macrophytes (e.g. Gibbons et al., 2002; Hofmann & Mason, 2005; Schindler et al., 2003). Changes in distribution and cover of aquatic vegetation, either naturally or because of human interference, are likely to have significant impacts on odonate populations (Batzer & Wissinger, 1996). As well as acting as oviposition sites and perches for both adults and larvae, the type of vegetation present at a site may also indicate present or future ecological conditions of the larval habitat (Buchwald, 1992), because plant communities are strongly dependent upon the long-term chemical and physical condition of the aquatic system. Hence, it seems reasonable to speculate that macrophytes influence the reproductive success of *T. carmesina* and consequently its population distribution. However, further studies are needed to confirm this and to elucidate the nature of interactions that lead to this result.

Acknowledgements

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