Odonatologica 42(2): 97-108 *June 1, 2013*

THERMOREGULATION AND MICROHABITAT CHOICE IN *ERYTHRODIPLAX LATIMACULATA* RIS MALES (ANISOPTERA: LIBELLULIDAE)

L.B. CALVÃO[1], M.V.C. VITAL[2], L. JUEN[3], G.F. LIMA FILHO[4], J.M.B. OLIVEIRA-JUNIOR[5], N.S. PINTO[6] and P. DE MARCO Jr[7]*

[1] Programa de Pós Graduação em Ecologia e Conservação, Universidade do Estado do Mato Grosso, Nova Xavantina, Mato Grosso, Brazil; – lenizecalvao@hotmail.com

[2] Setor de Biodiversidade e Ecologia, Instituto de Ciências Biológicas e da Saúde, Universidade Federal de Alagoas, BR-57.010-020, Maceió, Alagoas, Brazil; – marcosvital@gmail.com

[3] Instituto de Ciências Biológicas, Universidade Federal do Pará, Rua Augusto Correia, nº 1 Bairro Guama, BR-66.075-110, Belém, PA, Brazil; – leandrojuen@ufpa.br

[4] Universidade Estadual de Goiás (UEG), Av. Rio Araguaia esq. Av. Paranaíba, Itapuranga, Go, BR-76680-000 Goiás, Brazil; – ecoufg@yahoo.com.br

[5] Programa de Pós Graduação em Ecologia e Conservação, Universidade do Estado do Mato Grosso, Nova Xavantina, Mato Grosso, Brazil; – maxbio@hotmail.com

[6] Programa de Pós Graduação em Ecologia e Evolução, Universidade Federal de Goiás, Goiânia, Goiás, Brazil; – nelsonsilvapinto@gmail.com

[7] Laboratório de Ecologia Teórica e Síntese, Departamento de Ecologia, Universidade Federal de Goiás, BR-74.001-970 Goiânia, Goiás, Brazil; – pdemarco@icb.ufg.br

Received July 2, 2012 / Revised and Accepted September 27, 2012

It was assessed whether solar incidence affects the spatial distribution, microhabitat choice, territorial defense, time spent in behavioural categories, activity patterns, and abundance of *E. latimaculata*. The study was conducted in a semi-lotic area in the Cerrado in Aparecida de Goiânia, Goiás, Brazil, using the scan procedure with a fixed area, sampling 3 environments, viz. shade, partial shade, and an area with constant solar incidence. There was a higher abundance and activity concentration of this sp. in areas with higher solar incidence than in other areas (H = 19.180; P <0.001). This can be explained by the ecophysiological requirements of *E. latimaculata*, in which individuals need to be exposed to solar radiation to warm their bodies, allowing the beginning of their activities. Diurnal variation did not affect the behavioural pattern, indicating that individuals are ectothermic and need direct solar incidence on their bodies (H = 12.193; P = 0.160). They spend most of the time perching with wings dropped (41.448 ± 21.781; mean ± SD) and displaying a territorial behaviour, making defense flights around the perch. In lenthic water bodies ♀♀ seem only to mate and oviposit (exophytic, directly into the water).

* **Corresponding author**

INTRODUCTION

The distribution of odonate species in a given landscape is determined by their ability to thermoregulate, which may be influenced by climate, body size, behaviour, and microhabitat choice (MAY, 1976; CORBET, 1962). CORBET (1962) classified anisopterans as fliers or perchers and considered differences in their thermoregulation and behaviour. Fliers tend to have larger body size and can produce endogenous heat, controlling their inner temperature, flying most of the time and regulating their body temperature by controlling haemolymph flow (MAY, 1976; CORBET & MAY, 2008; CORBET, 1999). On the other hand, perchers have smaller body sizes, remaining perched most of the time and are classified as thermal conformers or heliotherms. Thermal conformers have a higher surface: volume ratio and are thus more susceptible to thermoregulation by convection (DE MARCO & RESENDE, 2002). As they have high conductance, they can quickly gain or lose heat to the environment. Consequently, they can start their activities as ambient temperature increases. However, this restricts their activities to a certain period of the day (CORBET & MAY, 2008). Because of their lower conductance, heliothermics need direct sunlight to warm their bodies and start their activities, i.e. they are influenced by the solar irradiation on their bodies (CORBET & MAY, 2008; MAY, 1976). Perchers remain resting, close to sites visited by females for oviposition, usually defending spots against conspecifics, displaying territorial behaviour (CORBET, 1999).

According to SAMWAYS (2006), dragonflies are sensitive to habitat quality and ambient light. This is in agreement with the results of SILVA et al. (2010), suggesting that dragonfly communities are more sensitive to landscape changes (e.g., deforestation, grazing, loss of habitat integrity) than to the physicochemical parameters of water. Environmental disturbance can cause serious problems to species with strict ecological requirements, which can be replaced by those that are more generalist. FERREIRA-PERUQUETI & DE MARCO (2002) found that species living in areas with some kind of environmental change can invade pristine areas, but not the contrary. This suggests that anthropogenic changes homogenize the environment, and consequently decrease resource availability and oviposition sites (PAULSON, 2006; FERREIRA-PERUQUETTI & FONSECA-GESSNER, 2003).

The environment in which behavioural interactions occur is wider than the range of environmental conditions that may affect an odonate species. This environment also includes other species that can compete for perches, forcing individuals to occupy sub-optimal habitats. For example, DE MARCO & RESENDE (2004) showed that, when *Planiplax phoenicura* Ris is present, males of *Orthemis discolor* (Burm.) tend to use lower perches due to competition for high perches. Thus, behavioural studies of single species can benefit from information about the biotic environment in which the species occurs, fostering the interpretation of mechanisms responsible for patterns of microhabitat use and other associated behaviours.

Erythrodiplax latimaculata Ris belongs to the intrageneric group *famula* (Libellulidae). Species of this group are widely distributed in South America (BORROR, 1942; HECKMAN, 2006). In general, males of *E. latimaculata* remain perched most of the day, defending breeding areas in lakes. This activity pattern is consistent with that of percher's species (RESENDE, 2010; CORBET & MAY, 2008). Considering the thermoregulation constraints (DE MARCO et al., 2005; CORBET, 1999) and the competition between males in territory defense, we analyzed the ethological patterns of males of *E. latimaculata*, to test the hypothesis that the spatial pattern of distribution, microhabitat choice, territorial defense and activity patterns of *E. latimaculata* are directly affected by the solar incidence and temperature fluctuations throughout the day. We also analyzed the species composition in areas where males of *E. latimaculata* defended territories.

METHODS

STUDY AREA – The study was conducted between April and June 2009 in Aparecida de Goiânia, Goiás, Brazil (16º49'54.6" S; 49º15'10.3" W). The region is covered by a typical Cerrado vegetation, and has two distinct seasons: a rainy (October-March) and a dry (April-September) season (KLINK & MACHADO, 2005).

The study site was a 97 m long farm dam. We divided it into three sections. Section 1 was 22 m long, with dense vegetation that shaded the sampling area throughout the day. Section 2 was 28 m long in a pasture area, with grasses (*Brachiaria* sp.) that covered up to the edge of the dam; this area received constant solar irradiance during the day. Section 3 was 48 m long, it was located between the other two and had intermediate characteristics. Some parts of section 3 were predominantly covered by grasses; in the morning (up to 10:00 h), the pond margins remained shaded but, later in the day, they received some sun.

SAMPLING – We made ten days of field observations, once a week from 10:00 h to 14:00 h. Air temperature was recorded hourly in each shaded place. A scan procedure within a fixed area was used to estimate species abundance (FERREIRA-PERUQUETTI & DE MARCO, 2002; FERREIRA-PERUQUETTI & FONSECA-GESSNER, 2003). In sections 1 and 2, 22 sticks were placed per section, at 3 m intervals. In section 3 we put 25 sticks spaced 1 m apart because of the higher dragonfly density. Thus, in total 69 stretches were marked.

Entomology nets were used for sampling. Specimens were identified with keys (BORROR, 1942; GARRISON et al., 2006) and by comparison with museum specimens. They were deposited in the collection of the Laboratory of Theoretical Ecology and Synthesis of the Federal University of Goiás.

ANALYSIS OF THE BEHAVIOUR – The focal animal method was used in behavioural observations (DE MARCO & VITAL, 2008; DE MARCO & RESENDE, 2002; ALTMANN, 1974). The observations were limited to one minute and a half. The classification of activities was based on CORBET (1962) and further subdivided according to DE MARCO (1998) and DE MARCO et al. (2005). The following types of behaviour were observed: copulation (CO), – oviposition (OV), – transition flight (TRA), patrolling (PAT), – open wings posture (OWP), – obelisk perching (OP), – dropped-wings perching (DP), – wings in different positions (WDP), and – flying (FL).

STATISTICAL ANALYSIS – Species richness was estimated using the first order jackknife method, which allows the correction of bias and calculates a confidence interval to compare different

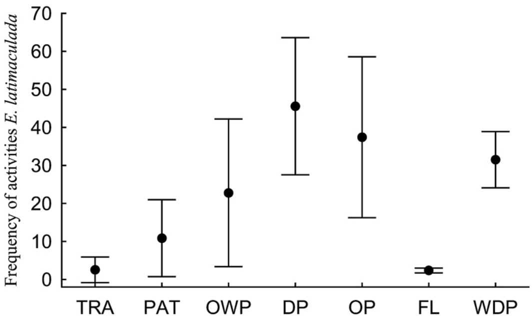

Fig. 1. *Erythrodiplax latimaculata*: frequency of activities in relation to the period of observation. – [Bars represent 95% CI] – TRA: transition flight; – PAT: patrolling; – OWP: open wings posture; – DP: dropping-wings perching; – OP: obelisk perching; – FL: flying; – WDP: wings in different positions.

treatments. This analysis and the rarefaction curve were implemented using the program EstimateS (COLWELL & CODDINGTON, 1994).

To test if time of day influenced the behaviour of individuals, we first tested the assumptions of normality and homoscedasticity (Levene test). If the assumptions were met, a one-way ANOVA (ZAR, 1999) was used, associated with a Tukey test, to identify which treatments had significantly different means. When they were not met, we used the nonparametric Kruskal-Wallis test (ZAR, 1999). The same routine was used to test if the three sections had differences in species abundance.

RESULTS

ETHOLOGICAL CATEGORIES AND TEMPORAL BUDGET

E. latimaculata remains in a dropping-wings posture while perching (DP) most of the time (41.448 ± 21.781; mean ± SD), followed by open wings posture (OWP) (7.107 ± 15.1571), transition flight (TRA) (0.535 ± 1.888), patrolling (PAT) (2.905 ± 7.296) and obelisk (OB) (2.23 ± 10.296; Figs 1, 2).

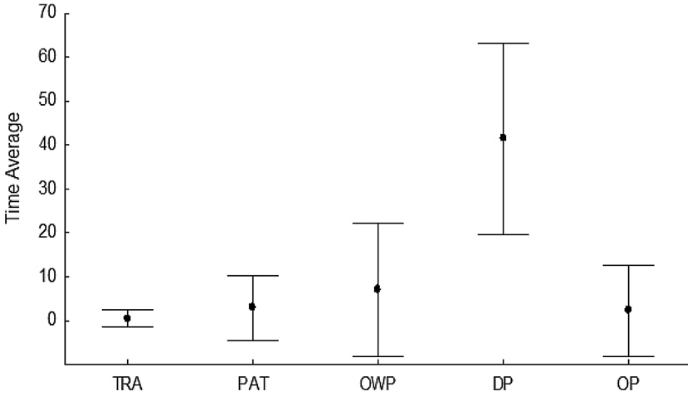

Fig. 2. *Erythrodiplax latimaculata*: mean proportion of time spent in each behavioural activity. – [Bars represent 95% CI] – TRA: transition flight; – PAT patrolling; – OWP: open wings posture; – DP: dropping-wings perching; – OP: obelisk perching.

During our observations, we found that *E. latimaculata* displayed two predominant flight types: the transition flight, associated with a change of perch usually last for 1 s, while the defense or patrolling flight around the territory lasted 4 to 10 s. These flights included agonistic interactions with direct contact and chasing when there was an intruder. However, this species spent most of the time in dropping-wings perching (DP; Fig. 2).

BREEDING BEHAVIOUR

Males displayed territorial behaviour in perches located in the vegetation extending towards the stream bank. When the male found a receptive female, he quickly held her in a tandem position. Generally, they remain perched after copulation for about two to three minutes, and then the female started ovipositing into the water. The male displayed guard behaviour, without physical contact. Immediately after oviposition, females perched on the vegetation while the male kept patrolling. Eventually the female moved away slowly while the male remained in his territory.

EFFECT OF DAYTIME ON ABUNDANCE

The abundance of *E. latimaculata* did not vary with the time of day (Kruskal-Wallis =12.193; DF=4; N= 26; P =0.160; Fig. 3).

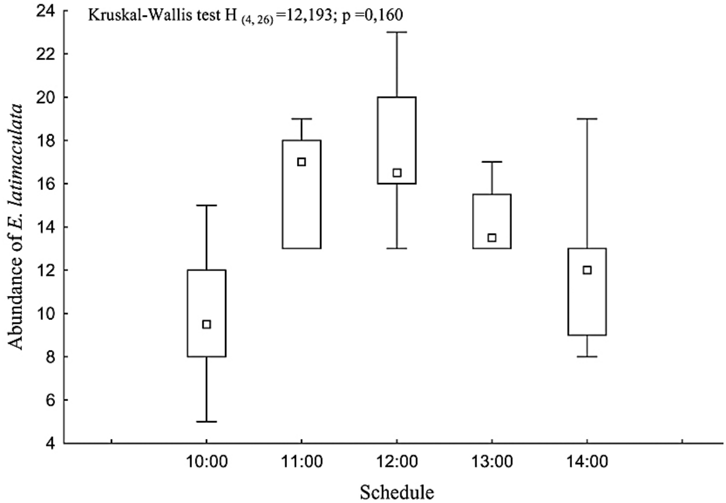

Fig. 3. *Erythrodiplax.latimaculata*: effect of daytime on the abundance. – [Bars represent the total ranges; – boxes represent 25 and 75% quartiles; – points represent the medians of the observed abundances].

ABUNDANCE PER AREA

E. latimaculata abundance was influenced by direct sunlight on their bodies. As a consequence, a higher abundance was found in open areas (Fig. 4), than in areas with dense vegetation (H = 19.231: df = 2; N = 40; P <0.001). Accordingly, a higher density of males defending territories was recorded in sunny areas. Dragonflies avoid shaded areas because it prevented heat gain to increase body temperature and hence the start of their activities. This influenced the distribution and abundance patterns of this species. For example, there was an increase in the abundance during periods of increased solar irradiation, possibly because they require direct sunlight on their bodies to become active.

ADULT ODONATA COMMUNITY

The following species were recorded at the farm dam, Aparecida de Goiânia (Goiás): *Acanthagrion lancea* Sel., *Neoneura sylvatica* Hag., *Telebasis limonco-cha* Bick & Bick, *Phyllogomphoides* sp., *Erythrodiplax basalis* (Kirby), *E. fusca* (Ramb.), *E. juliana* Ris, *E. latimaculata* Ris, *Erythrodiplax* sp., *Micrathyria artemis* Ris, *M. ocellata* Martin, *Orthemis discolor* (Burm.) and *Perithemis lais* (Perty).

Our sampling effort was adequate for determining the species richness in the area since the rarefaction curve and the estimated richness by the jackknife method reached an asymptote (Fig. 5).

A higher odonate richness was recorded in areas with higher sunlight but there

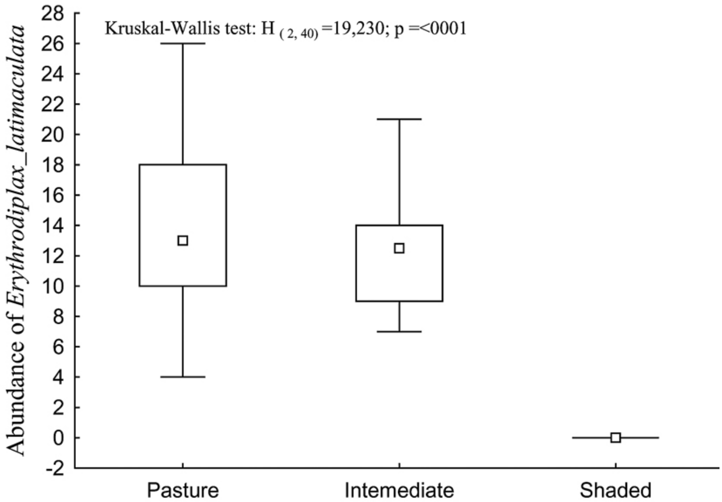

Fig. 4. *Erythrodiplax. latimaculata*: abundance in stream transects. – [Bars represent total range; – boxes represent 25 and 75% quartiles; – points represent the medians of the observed abundances].

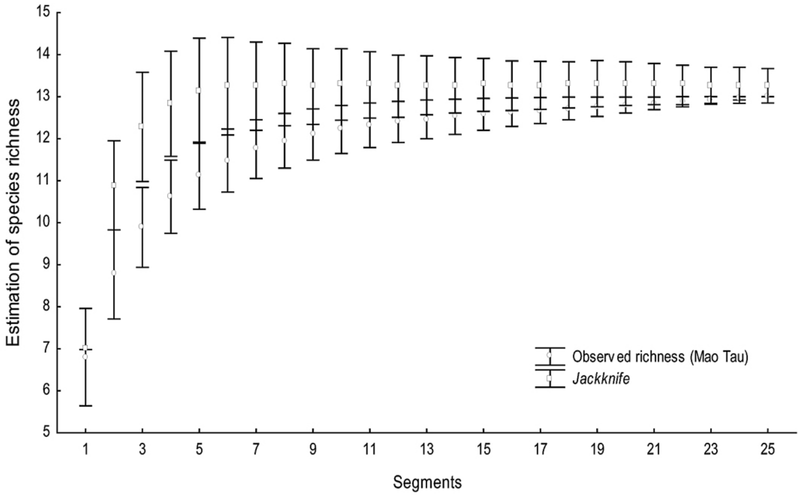

Fig. 5. Rarefaction curve of odonate species and richness estimate using the jackknife method.

was no difference between the pasture (14 ± 1.41, mean ± confidence interval) and the intermediate area (13 ± 1.00). The more shaded area showed the lowest richness, i.e. six species (7 ± 1.00) in mean (Fig. 6).

The larger proportion of large-bodied anisopteran species may be due to the availability of oviposition sites with constant sunlight, which may be related to their ecophysiological needs.

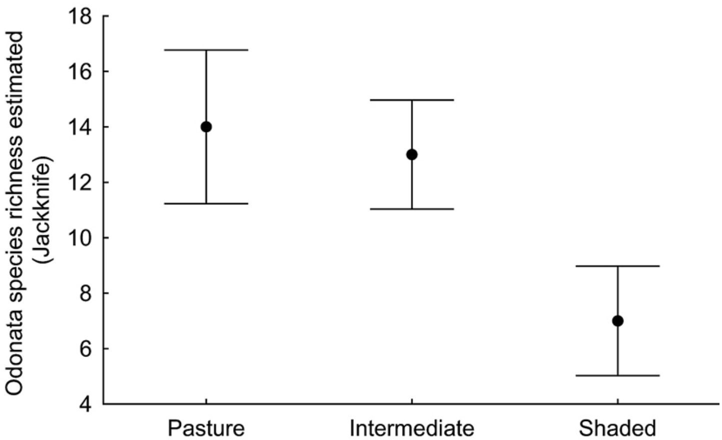

Fig. 6. Estimated richness of odonate species (jackknife) found in areas with different shade intensities. – [Bars represent 95% CI].

DISCUSSION

BEHAVIOUR

Individuals of *Erythrodiplax latimaculata* can be classified as heliothermic perchers, since they need direct sunlight incidence on their bodies to increase their body temperature and start their activities (CORBET & MAY, 2008; MAY, 1976; RESENDE, 2010). Males occur more frequently than females at the breeding site and defend territories on perches near water. On the other hand, females visit these sites only to mate and oviposit, selecting males that defend the best territories (e.g. MILLER, 1995; RESENDE, 2010; CORBET, 1999). In *E. latimaculata* the pattern of spatial distribution, habitat choice, territorial defense and time spent in activity were directly affected by direct solar incidence on their bodies and they concentrated most of their activity in periods of strong sunlight (RESENDE, 2010) as a consequence of their ecophysiological constraints.

Taken together, the above observations suggest temporal restriction in the activities of this species that could also influence its spatial distribution. *E. latimaculata* seems to be restricted to open areas near water bodies, due to its dependence on direct sunlight, which influences choice of microhabitats. A prediction that can be put forward is that it may benefit from the disturbance of natural areas, due to its behavioural and eco-physiological aspects, as is the case in other species with heliothermal behaviour (FERREIRA-PERUQUETTI & DE MARCO, 2002; SILVA et al., 2010). This suggests that the geographical range of species such as *E. latimaculata* may be expanded as a consequence of current environmental changes, provided the availability of suitable aquatic environments.

CORBET (1999) pointed out that the behaviour of adult dragonflies is sensitive to several factors such as age, time of day and temperature. Ectothermic thermoregulation affects microhabitat selection and posture. Some body postures minimize the solar incidence, such as obelisk perching, with the body parallel to the sun, or maximize sun exposure, such as holding the wings raised and the abdomen horizontal while perching to increase or decrease body temperature. The dropping-wings perching may be related to balance in high winds. These dragonflies hold the wings open, preventing wing rotation. Possibly with dropping-wings perching, they decrease the contact surface. After the high winds, these species return to the initial dropping-wings position and remain on their perches (pers. obs.).

When clouds blocked the sun, we observed more individuals with dropped wings, probably to increase the body surface exposed to sunlight and thermoregulate. On other occasions, when an insect flew over *E. latimaculata*, it immediately opened its wings, showing the stains.

For a more intense defense, *E. latimaculata* males frequently displayed an agonistic defense, in which they flew in a spiral with physical contact, disputing perches or females (CORBET, 1999). These behavioural interactions directly influence the distribution of these animals (OSBORN & SAMWAYS, 1996). Many dragonflies defend territories attractive to females and can become involved in conflicts, chasings, expulsions and injuries. According to RESENDE (2010), males of *Erythrodiplax* species, such as *E. famula*, *E. media* and *E. fusca*, spend more time in territorial disputes than *E. latimaculata.* However, all species display an interspecific territorial dispute, i.e. agonistic behaviour. We recorded one of these disputes for a perch between *E. latimaculata, E. fusca* and *Acanthagrion lancea* males. *E. latimaculata* expelled *A. lancea* by physical contact in order to become the resident male. It is common to find *E. fusca* males perched on the same spots as *E. latimaculata.* This could have been influenced by *E. latimaculata* being larger than the others, since body size may determine the winner of a contest.

BREEDING BEHAVIOUR

The choice of the perch to be defended by a male is related to the arrangement of the vegetation and the availability of suitable sites for reproduction, particularly where females of *E. latimaculata* occur (RESENDE, 2010). Unlike *E. fusca* and *E. media* (DE MARCO & RESENDE, 2002), the frequency of females interacting with males in males' territories was very low. However, it is not clear whether this is a feature of this species, possibly related to the frequency females return to oviposition sites, or an environmental characteristic affecting the density of these insects.

After copulation, females of *E. latimaculata* lay eggs directly in the water while males remain nearby, protecting females against other males (CORBET, 1999; RESENDE, 2010). This guarding behaviour in mating is common in dragonflies, and happen in two ways: with or without physical contact. These behaviours are frequent in territorial species of the family Libellulidae (SILSBY, 2001).

During oviposition, *E. latimaculata* males guarded females by flying above them, without contact, preventing other males from approaching the female and extract the sperm, as occurs in some species of Odonata (CORBET, 1999). Since chasings between males are intense, it was common for the female to remain alone when ovipositing after copulation. This increases the chance of mating of other males with the female, similar to what was observed in *Libellula pulchella* (McMILLAN, 2000).

Where the density of females is high, it is expected that guarding behaviour without physical contact would occur after copulation (KNOX & SCOTT, 2005). This brings the advantage for males that they can continue to defend their territories and copulate with other females (ALCOCK, 1994). In this study, guarding behaviour without physical contact when there was a low female density suggests that there is a strong genetic component restricting behavioural plasticity. However, guarding a female without contact, even when there is a high male density, may be associated with energy saving, which increases longevity and fitness and reduces predation risk, as shown for *Tramea* (ALCOCK, 1994). Although air temperature is high in the tropics, factors such as higher wind velocity and increased detectability by predators in places without riparian vegetation are more pronounced, affecting survival and behavioural strategies.

We also observed that *E. latimaculata* males simulated oviposition, i.e., touched the water with the abdomen. This behaviour was interpreted as a test of oviposition sites against attacks by amphibians on females or mating pairs, as in *Erythemis plebeja* (DE MARCO et al., 2002), providing more chances for offspring survival.

HABITAT

Most odonate species display some kind of habitat selection (DE MARCO & RESENDE, 2004; CORDERO-RIVERA, 2006). According to ASSIS et al. (2004), the genus *Erythrodiplax* is typically associated with lentic environments with organic substrates, but can also invade lotic areas (FERREIRA-PERUQUETTI & DE MARCO, 2002). Microhabitat choice is related to ecophysiological requirements, such as maintenance of body temperature that requires places with high solar irradiation (MAY, 1976; DE MARCO, 1998). Our results corroborate these predictions, since we found that the abundance of *E. latimaculata* was directly influenced by the availability of sunlight (RESENDE, 2010).

RELATIONSHIP OF *ERYTHRODIPLAX LATIMACULATA* WITH OTHER ODONATE SPECIES

SAHLÉN (2006) points out that, in general, forest-dwelling species are specialists, while those found in open areas are generalists. Our results corroborate this assertion, since the majority of species recorded in this study belong to genera that are common and widely distributed in Brazil, such as *Erythrodiplax* and *Micrathyria* (COSTA et al., 2002). This suggests that environmental disturbances such as deforestation and dam construction may favour the establishment of populations of generalist species, at the expense of specialist ones (DE MARCO & VITAL, 2008; FERREIRA-PERUQUETTI & DE MARCO, 2002).

According to CORDERO-RIVERA (2006), habitat quality is a major factor dictating the success of colonization and establishment of biological communities. In this study, we found species that avoided open areas, more prone to environmental disturbances (DE MARCO & RESENDE, 2004; FULAN & HENRY, 2007), such as *Perithemis lais*, *Telebasis limoncocha* and *Acanthagrion lancea*.

Although *E. latimaculata* is a territorial species, it is common to find males on perches along with other odonate species, mainly *E. fusca*, which are more engaged in territorial contests than *E. latimaculata* (RESENDE, 2010). *Erythro-*

diplax fusca, *Micrathyria hesperis*, and *Orthemis discolor* are species with similar activity periods to *E. latimaculata*, suggesting that these species are also affected by sunlight (DE MARCO, 1998; DE MARCO & RESENDE, 2002).

CONCLUSION

Erythrodiplax latimaculata prefers environments with high solar irradiation. It can be classified as a heliothermal percher. Thus, the ability to maintain body temperature is influenced by climate and behaviour. Most of the time, individuals were found perched with dropped wings. The higher abundance in areas with constant solar incidence shows that shadow impairs thermoregulation in this species, preventing it from increasing the body temperature to start its activities or to keep it constant throughout the day. Males choose perches and defend them aggressively in suitable breeding sites, where encounters with females are more common. Although receptive females are not found generally in these sites, defending an oviposition site can increase a male's chances to be chosen by a female, thus increasing the probability of copulation.

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