

ECOLOGY OF *TIGRIAGRION AURANTINIGRUM* CALVERT IN RESPONSE TO VARIATIONS IN ENVIRONMENTAL CONDITIONS (ZYGOPTERA: COENAGRIONIDAE)

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Received August 1, 2006 / Revised and Accepted February 13, 2007

The daily activity patterns, behaviour and population dynamics in Zygoptera are thought to be affected by the physical conditions of the environment. How and why the sp. reacts to those conditions is determined mainly by its bionomic characteristics. Here, an auto-ecological study is performed of *T. aurantinigrum*, in an attempt to clarify its responses to physical conditions. It is suggested that *T. aurantinigrum* could fit, with a few assumptions, in the “female-control” classification of odon. mating system. Some interactions were observed between individuals, but it is assumed that these play a role in sex recognition, rather than in territorial contests. The results indicate that this sp. is affected by the following physical conditions: the monthly rain fall, which has a positive effect on the abundance (with the possible exception of the heavy rain months); the water flow velocity, which seems to define a limit of its occurrence; and the daily variation in temperature, which seems to induce the sp. to restrict its activity to the hottest period of the day, as expected from a “thermal conformer”. *T. aurantinigrum* appears to be affected by small scale variations of environmental variables, as observed by the differences of its abundance at the 3 different sites of this study. Under conditions of the current “forest-to-pasture” conversion that is common in the Brazilian Atlantic Forest region, the sp. is expected to increase its abundance and to broaden its geographical range, although water body alterations could limit this process.

INTRODUCTION

Serious pressure due to habitat destruction caused by, e.g. damming large and medium size rivers, sewerage waste in streams and deforestation, has resulted in serious threat to much of the aquatic fauna in many areas of southeastern Brazil (MITTERMEIER et al., 1999). Most of this area is considered as regionally outstanding in biological value and must be prioritized in conservation actions (BIODIVERSITY SUPPORT PROGRAM et al., 1995). Recent studies have demonstrated that some species, such as *Hetaerina rosea* (Calopterygidae), may be favoured by the conversion of gallery forest to pasture, although other species, e.g. *Heteragrion aurantiacum* (Megapodagrionidae), may become rarer or completely disappear (FERREIRA-PERUQUETTI & DE MARCO, 2002). The possible cause of these results may be understandable in terms of bionomic characteristics of the respective species. Thus, *H. rosea* is a 'sun-species' that could also occur in the forest but does not require any special substrate for oviposition (DE MARCO & PEIXOTO, 2004), whereas *H. aurantiacum* is a shadow-species whose habitat is closely related to forest and which oviposits in trunks or stems of trees in streams, as do some other species in this genus (GONZALEZ-SORIANO & VERDUGO, 1982). Unfortunately, there is a very limited amount of information on ecological traits in neotropical species that could be used to understand and also predict which species could be more threatened under the impact of deforestation.

The physical conditions of a given environment are important factors in determining the ecology and behaviour of the species present (CORBET, 1999), and the knowledge of how these species respond to these conditions may lead to predictions on their distribution, population size and dynamics. Conditions that might be important in the regulation of odonate populations and communities are air temperature and water current velocity (in lotic environments). Temperature seems to be a determinant of daily activity and behaviour (MAY, 1991; HEINRICH, 1993; POLCYN, 1994; DE MARCO & RESENDE, 2002) and of the rate of development of the larvae (BAKER & FELTMATE, 1987; PRITCHARD et al., 1996). The combined effect of growth and efficiency under different thermal regimes may also determine the range of distribution of a given species and explain the relationship between species richness and temperature in a large scale view (EVERSHAM & COOPER, 1998; CORBET, 1999). Water current velocity may also play an important role, especially in species with endophytic oviposition, that may show preferences for specific velocities (GIBBONS & PAIN, 1992).

Tigriagrion is a monotypic genus of small-sized damselflies whose biology and distribution are poorly known, and which appear to occur in streams in the South American continent. So far *T. aurantinigrum* is known from Paraguay, Bolivia and central and southern Brazil (COSTA & SANTOS, 2001). In this study we try to clarify some general aspects of its ecology based on an approach that rec-

ognizes the importance of scale (both spatial and temporal) to the knowledge of the natural history of a given species.

STUDY AREA

This work was conducted at three different sites (1, 2 and 3) of the São Bartolomeu stream, a small water body in the Viçosa region, Minas Gerais, Brazil. The region has a wet sub-tropical climate (Köppen CWb classification), with the dry season from May to September inclusive (GOLFARI, 1975). The mean annual rainfall ranges between 1500 and 2000 mm, the mean annual temperature between 14,0 and 26,1°C and the relative humidity is about 80% (VALVERDE, 1958). In all the three sites the stream width varies from one to three meters.

At site 1, the stream cuts through a pasture area, with minimum sewerage discharge and with the impact of some cattle grazing activity nearby. A few bushes are scattered along its margins, sometimes reaching more than one meter tall. The water flow velocity in the rainy season (which we measured with a current meter model 1210, Scientific Instruments, Inc.) was the highest from the three sites (mean = 0,596 m/s; s.d. = $\pm 0,292$). Site 2 is located approximately 50 m away, and is very similar, except for the lower velocity (0,261 m/s; s.d. = $\pm 0,147$). In addition to bushes, there are also some trees near the margins of the stream. Site 3, located ca 500 m from the other two, near a small urban concentration, therefore it is subject to some sewerage discharge. Like the other sites, it is located in a pasture area, with some bushes and small trees near the stream's margins. The water current velocity is very similar to that at site 2 (0,260 m/s; s.d. = $\pm 0,115$). Data on this site was collected a year before we started to work on sites 1 and 2.

METHODS

BEHAVIOUR ANALYSIS — The behavioural data was collected only at sites 1 and 2, always between 09:00 and 14:00. After having obtained an estimate of abundance (see below), we searched for individuals on which to perform an analysis of the species' temporal budget, using a focal observation method as described by DE MARCO et al. (2002). Each individual was observed for one minute and the time spent in each behaviour was recorded. For *T. aurantinigrum*, the only behavioural categories observed were flight activity, aggressive or territorial defense and perching. Additional data were collected in January 2004 with special emphasis on the observation of interactions.

ABUNDANCE ESTIMATION — A fixed-area scan method (FERREIRA-PERUQUETTI & DE MARCO, 2002) was used in order to estimate the monthly abundance of *Tigriagrion aurantinigrum* at each site. We divided the stream, at each study site, into two meter linear segments (50 segments at sites 1 and 2, and 49 at site 3). An estimate of abundance was obtained by counting the number of *T. aurantinigrum* individuals in each segment at sites 1 and 2 at least three days each month, always between 10:00 and 14:00. The counts took, on average, 15 minutes and no segment was scanned for more than two minutes. Sites 1 and 2 were investigated between September 2001 and August 2002. The monthly abundance of *T. aurantinigrum* was not investigated at site 3; this area was used in the estimation of daily variations of the species' abundance (see below).

DAILY ACTIVITY — In 30 minute intervals, between 8:00 and 17:00, the numbers of individuals were estimated with the same method as stated above, during three days in the rainy season (all sites) and during three days in the dry season (only sites 1 and 2). The air temperature in a shaded area was measured in 30 minute intervals.

STATISTICAL ANALYSIS — For analysis of the dependency of *T. aurantinigrum* occurrence in relation to stream velocity, a logistic regression according to HOSMER & LEMESHOW (1989) was applied using the quasi-Newton method. To examine the relationship between *Tigriagrion* abundance and rain fall, a linear regression analysis (SNEDECOR & COCHRAN, 1980) was used.

RESULTS

Based on a sample size of 50 observations, it is clear that near its reproductive habitats, *T. aurantigrum* spends most of its time perched, and this seems to hold true for both dry and rainy seasons. During a single observation an indi-

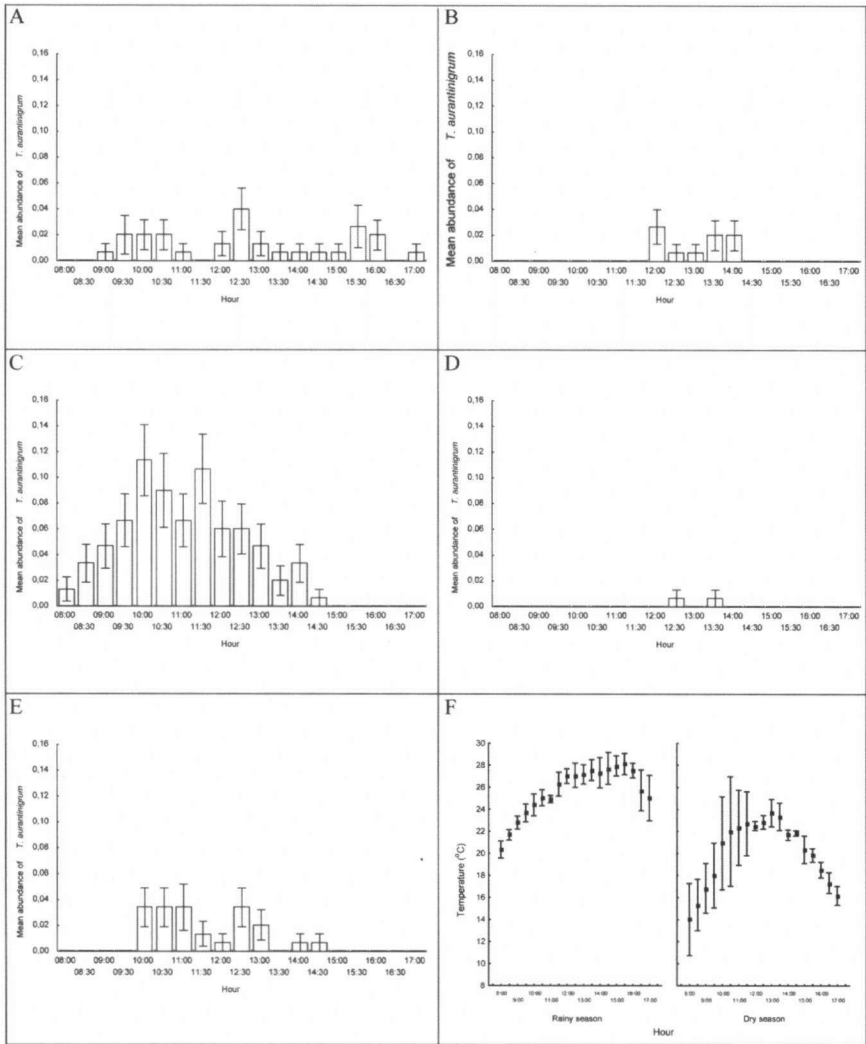


Fig. 1. Mean abundance of *Tigriagrion aurantigrum* between 8:00 and 17:30 at site 1 (A for rainy and B for dry season), site 2 (C for rainy and D for dry) and site 3 (E, rainy season only); the mean temperatures (°C) during the study are shown for both seasons (F). Mean abundance is measured by the mean number of individuals in the 2 meter segments. Bars show standard deviations.

vidual was seen pursuing another one that got close to it (but only for one second); this was recorded as defense behaviour. During another two observations, two individuals facing each other flying up and down were seen. This seems to be a territorial defense behaviour, although it could also be related to sex recognition. The same behaviour was noticed six more times, but outside the time-budget analysis. In two of these cases there was the impression one individual pursued the other one for a short distance (<1 m).

The oviposition behaviour was noticed in a single female: it was perched on an aquatic plant close to the water surface, then submerged and stayed underwater for 90 s, bending the abdomen (while still holding the plant), with the tip touching the vegetation. In spite of the great amount of time spent at the reproductive habitats, we did not ob-

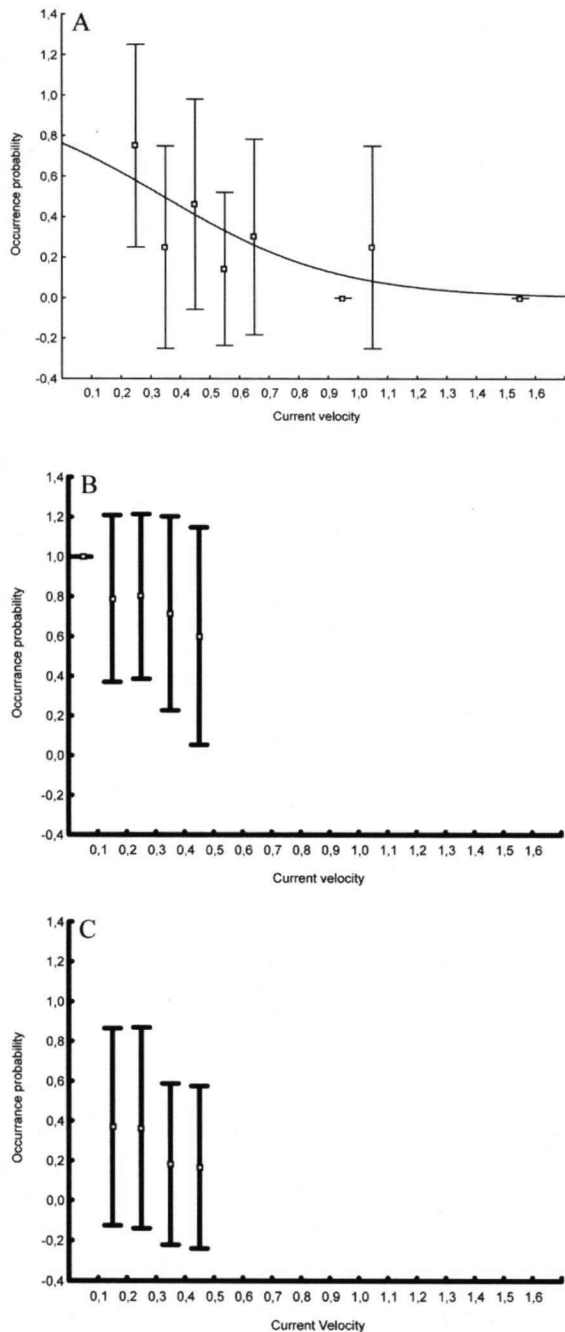


Fig. 2. Logistic regression of the presence of *Tigriagrion auranitigrum* on water current velocity (measured in m/s) for sites 1 (A), 2 (B) and 3 (C). Bars show standard deviations. Trend line shows a statistically significant relationship.

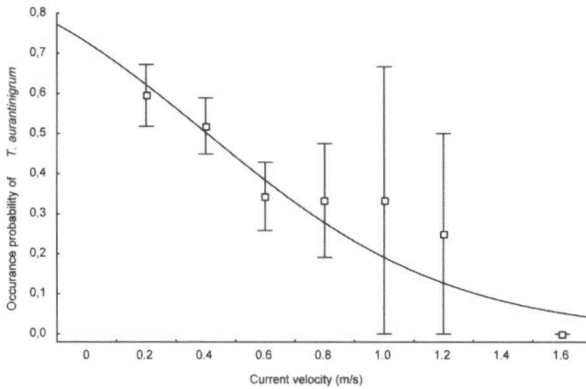


Fig. 3. Logistic regression of the presence of *Tigriagrion aurantigrum* on water current velocity (measured in m/s) for the data of all sites together. Bars show standard deviations. Trend line shows a statistically significant relationship.

serve any other behaviour associated with reproduction. The daily activity patterns varied dramatically between sites 1 and 2 (Fig. 1, A-E). During the rainy season, the abundance of *T. aurantigrum* was much higher at site 2, although individuals left site 1 later in the day. Also, there was a period in the middle of the day when the abundances decreased at all three sites. The timing varied little between the sites: 11.00-12.30 at site 1, 10.30-11.30 at site 2 and 11.30-12.30 at site 3. During the dry season, the abundance decreased at site 1 (between 12.30 and 13.30) and there is some indication that it did so also at site 2. In this season individuals were active only during the hottest part of the day (Fig. 1F). At site 1, the activity started when the temperature reached ca 22°C in both seasons, i.e. at 9.00 in the rainy season and at 12.00 in the dry season and ceased, in the dry season at least, when it fell below ca 21.5°C.

A logistic regression was performed between the stream velocity and the abundance (using the daily activity data) of *T. aurantigrum* in the rainy season for each site. The relationship was not significant for site 2 ($\chi^2 = 0,027$, $df = 1$, $p = 0,870$) nor for site 3 ($\chi^2 = 1,932$, $df = 1$, $p = 0,164$), but it was so for site 1 ($\chi^2 = 5,819$, $df = 1$, $p = 0,016$). In the last case, the probability of *Tigriagrion* occurrence in a 2m-segment of the stream decreases with the increased water flow velocity (Fig. 2). It is important that site 1 was the one with the greatest standard deviation in velocity, suggesting that the relationship was not significant at the other sites only because they did not have a broad enough variation for this variable. A significant relationship was also found when pooling together the *Tigriagrion* abundance across all sample sites ($\chi^2 = 10,234$, $df = 1$, $p = 0,001$). As at site 1, the probability of occurrence decreased as the water current velocity increased (Fig. 3).

The changes in monthly abundance of *T. aurantigrum* seem to be similar between sites 1 and 2, although it was almost always higher at site 2 (Fig. 4). A significant relationship was found by the linear regression of the mean monthly abundance on the mean monthly rain fall for both sites ($p = 0,047$ and $R^2 = 0,30$ for site 1, and $p = 0,028$ and $R^2 = 0,37$ for site 2), showing that the abundance rises when

the rain fall is higher (Fig. 5). However, the abundance at the two sites decreased when the mean monthly precipitation exceeded ca 8 mm; this occurred during the heavy rains of January and February.

DISCUSSION

CONRAD & PRITCHARD (1992) presented a comprehensive review of odonate mating systems, describing a series of strategies that result from the predictability of male-female encounters and the ability of males to control the female access to oviposition resources. One of the simplest strategies, known as “female-control”, occurs when the females’ presence is predictable, but the males are not able to control oviposition resources. This can occur when ovi-

position sites are numerous and widely distributed within a limited area, hence males have little chance to control female access to them. The authors suggest that two main strategies are thought to evolve in such situation: the control of the female by grasping it, and the submerged oviposition. *Tigriagrion* appears to fit in this category, as females are predictably encountered near water and the oviposition resources are far more abundant than the males. However, CONRAD & PRITCHARD (1992) also predicted that the copula should occur far from the water, which does not seem to be the case in *Tigriagrion* (since males and females are predictably found in the margin of the stream). We think that female control may also occur near water bodies with the only assumption that the availability of resources should be much larger than the number of males in the area. This is reinforced because CONRAD & PRITCHARD (1992) suggest that males under this strategy may actively seek for mates or maintain a position that increase their ability to intercept females approaching the water. The probably most efficient

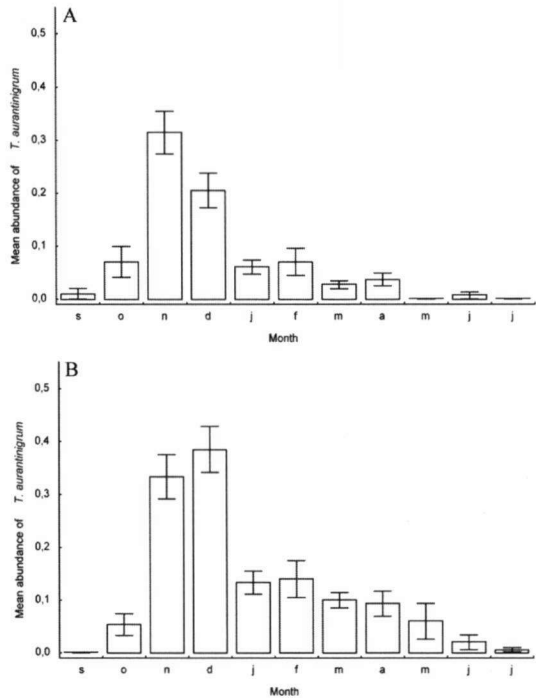


Fig. 4. Mean monthly abundance of *Tigriagrion aurantigrum* in 2 meter segments at sites 1 (A) and 2 (B). Mean abundance is measured by the mean number of individuals in the 2 meter segments. Bars show standard deviations. Letters on x-axis indicate months from September to July.

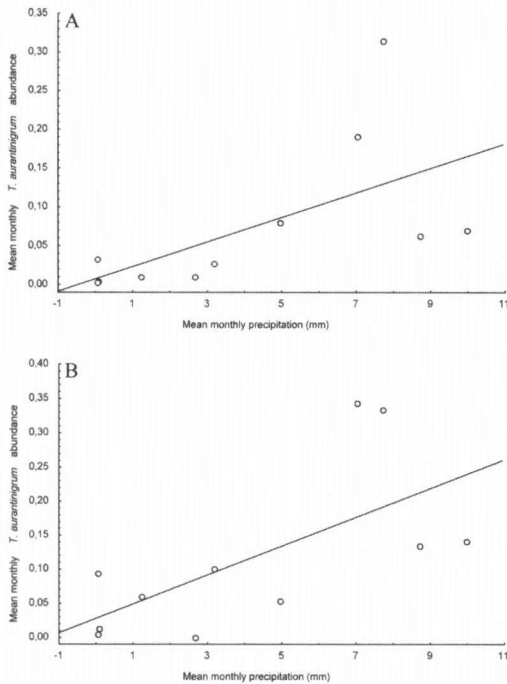


Fig. 5. Linear regression of the mean abundance of *Tigrigrion aurantinigrum* on mean rain fall for each month of the study for sites 1 (A) and 2 (B). Mean abundance is measured by the mean number of individuals in the 2 meter segments.

T. aurantinigrum activity seems to depend on the air temperature, allowing to classify it as a “thermal conformer”, sensu MAY (1976; 1991). However, it should be emphasized that there is a continuum between the thermal conformer and the heliotherm classes, with body size playing a significant role in determining the position of a given species in this scale. The concept is most powerful if we consider it comparatively. As an example, *Hetaerina rosea* (Calopterygidae), which has both greater body size and broader period of activity at site 3 (DE MARCO & PEIXOTO, 2004), could be placed further in the heliotherm direction than *T. aurantinigrum*.

Small-sized species are probably affected by small-scale variations in conditions and resources (ZIV, 2000). In these species, a small gradient in temperature or water flow may represent the entire scale from worst, sub-optimal and optimal habitats. This distinction may be very important here as some of the studied areas may represent sub-optimal habitats for *T. aurantinigrum*, as measured by the mean abundances. This is also a warning about the need of replication on behav-

place to intercept females approaching oviposition sites are the margins of the water body and this seems to be an incipient phase in the evolution of territoriality.

In Zygoptera, the male recognition of their conspecific females is thought to occur mainly by visual cues (CORBET, 1999), so sexual dimorphism should be important in male-female encounters. *T. aurantinigrum*, however, does not show any degree of sexual dimorphism, and it is suggested that the interactions observed during this study are a mechanism of behavioural sex recognition. Further observations are still needed in order to clarify this subject, since these interactions could be associated with the territoriality in this species.

As expected from such a small-sized damselfly, *T. au-*

joural and activity pattern studies to avoid conclusions drawn from analysis of a sub-optimal habitat.

The great variation in the activity pattern of *T. aurantinigrum* that was found between the three sites, despite the proximity of sites 1 and 2, suggests that its abundance is strongly affected by local conditions, such as the water current velocity. In fact, this variable can easily explain the differences between sites 1 and 2, since the first one has a higher current velocity and lower *T. aurantinigrum* abundance. However, site 3 has a flow velocity similar to site 2, but holds the smallest population abundance. Thus, other local conditions or resources we were unable to measure (e.g. some reproductive resource, like an aquatic plant) are probably important to the species. Of course, the lower abundance in site 3 could also be caused, directly or indirectly, by the higher sewer discharge in the stream at this point.

Although we observed only one reproductive event, we believe that the underwater oviposition could be common in *T. aurantinigrum*, also explaining the difficulty to observe such behaviour. This oviposition habit could be important to protect the eggs from desiccation, since the water level of the small streams that are usually the habitat of this species often fall drastically during the dry season. However, if *T. aurantinigrum* is really restricted to underwater endophytic oviposition, it would be reasonable to expect to avoid the fast currents (as it is shown in our results), since they could be harmful given its small size. The underwater oviposition is known to be potentially harmful mainly due to water current (CORBET, 1999), although it seems that no one suggested that the body size could limit the maximum current velocity that a given species could endure. On the other hand, some species, as *Calopteryx splendens xanthostoma* (Calopterygidae), may seek for faster current at oviposition sites, as this may prevent the growth of algae on the eggs that decreases its survival (SIVA-JOTHY et al., 1995).

The population dynamics of *T. aurantinigrum* appears to follow a pattern common in other species found in this area with higher abundances in the rainy season (DE MARCO & PEIXOTO, 2004). In *H. rosea* it is suggested that the dynamics is adjusted to have higher adult abundance in months with longer photoperiod duration and lower evapotranspiration, which may provide the opportunity to increase the total time spent in reproduction. However, *T. aurantinigrum* abundance peak occurs earlier in the rainy season than in *H. rosea* and other species that we have observed in the region. It is possible that the heavy rains that are common in January and February could cause a great mortality in those months that, otherwise, show climatic conditions similar to those during the population peaks. These heavy rains could play an important role in synchronizing the populations where the larval period lasts about one year.

A special feature of population dynamics in this and other species found in the Atlantic Forest (cf. DE MARCO & FURIERI, 2000; DE MARCO & PEIXOTO, 2004) is the apparent general trend towards univoltinism. This is believed to be

due to seasonal constraints that would overcome the potential of these species for a faster larval development (CORBET, 1999). CORBET (1999) also notes that tropical-centered species that reproduce in upland streams usually are univoltine and their emergence commonly takes place just before heavy rains, that could make the water course hazardous to the larvae. If this is so, the heavy rains, aside of increasing the *Tigriagrion* mortality (as suggested above), would actually controlling its population dynamics.

T. aurantinigrum appears well adapted to areas where the forest cover is withdrawn, and we predict that this species, as *H. rosea*, should increase its abundance, and possibly its geographical range, under the conversion of forest to pasture that is the dominant landscape change in the Brazilian Atlantic Forest. On the other hand, *T. aurantinigrum* requirement of intermediate water flow velocities could be a restriction, since the regulation of the streams, by canalization into more straight and fast water systems or by changing them into a complete lentic environment, is a common feature in a pasture dominated landscape.

ACKNOWLEDGEMENTS

We are greatly indebted to P.E.C. PEIXOTO for the massive help in the field work and for suggestions on the manuscript. We are also very thankful to D.C. RESENDE for valuable comments and suggestions on the manuscript. This work was partially supported by the Instituto de Pesquisas da Mata Atlântica (IPEMA).

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