ECOLOGY, BEHAVIOR AND BIONOMICS

Thermoregulatory Constraints on Behavior: Patterns in a Neotropical Dragonfly Assemblage

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Restrições de Termoregulação sobre o Comportamento: Padrões em Uma Assembléia de Libélulas Tropicais

RESUMO - As libélulas são classificadas comportamentalmente em voadoras e pousadoras com relação a sua capacidade de termoregulação. Libélulas de grande tamanho corporal devem termoregular de forma mais eficiente em locais com elevada irradiação solar, ao passo que libélulas menores dependem da temperatura ambiente. Neste estudo, foram realizadas análises de orçamento temporal de uma assembléia de libélulas para determinar como o tamanho corporal pode restringir a defesa de territórios e outros comportamentos. Baseado no orçamento temporal, foram observados três grupos de espécies. O primeiro e o segundo grupos abrangem espécies que permaneceram pousadas grande parte do tempo de atividade, entretanto espécies do primeiro grupo realizaram vôos de transição mais freqüentemente. O terceiro grupo conteve as espécies que foram observadas freqüentemente patrulhando seus territórios ou executando atividades reprodutivas. As espécies maiores permaneceram mais tempo em atividades de patrulha e defesa de seus territórios enquanto as espécies menores ficaram mais tempo pousadas. Libélulas maiores com maior habilidade de termoregulação puderam gastar mais tempo em atividades reprodutivas. A classificação das libélulas em voadoras e pousadoras é considerada extremamente útil, mas simplifica os padrões comportamentais observados entre espécies que têm grande variação de tamanho corporal. É provável que o contínuo comportamental associado com a variação de tamanho corporal, nos pousadores, possa explicar os padrões de interações entre espécies em comunidades de libélulas.

PALAVRAS-CHAVE: Tamanho corporal, efeito densidade-dependente, neotropical, territorialidade, orçamento temporal

ABSTRACT - Odonate species are classified in terms of their thermoregulatory behavior into flier and percher categories. Larger perchers could be more efficient thermoregulators in sunny sites and smaller perchers depend more on air temperature. In this paper, an analysis of the behavioral temporal budget of an odonate neotropical assemblage was performed to determine the role of body size on territorial defense and general behavioral strategies. This analysis revealed three groups based on time budget. The first and second groups contained the species that remained perched for most of the activity time, but species of the first group differ from the second group by the larger proportion of transition flights. The third group contained species which were usually observed patrolling or in reproductive activities. The larger species spent more time in patrol and territorial defense activities, while smaller species remained perched. Larger dragonflies, with better thermoregulatory abilities could spend more time in reproductive activities. The behavioral classification of fliers and perchers is considered extremely useful but could oversimplify the behavioral patterns among species that have a wide body size variation. It is proposed that a behavioral continuum associated with the body size variation in perchers could explain some patterns of species interactions in odonate communities.

KEY WORDS: Body size, density-dependent effect, neotropical, territoriality, time budget

Corbet (1962) classified the adults of odonate species into fliers and perchers. The fliers spend most of their time on the wing and usually visit water bodies only to mate or oviposit, while the male perchers stay perched near the water defending territories that increase their chance to find females.

The fliers have a dorsal vessel that allows them to control the distribution of the haemolymph warmed by the thoracic muscle to the entire body. In low air temperatures these species can raise their thoracic temperature by increasing wing motion (wing whirring) and closing the dorsal vessel (Heinrich & Casey 1978), and so concentrating the warmed haemolymph in the thorax. In high air temperatures they open the dorsal vessel and hover, facilitating fast heat loss by convection, mainly from the abdomen (May 1977, Heinrich & Casey 1978). For the perchers, thermoregulation is mainly by body posture adjustments in relation to the sun (May 1976, 1977), microhabitat choice (Clausnitzer 1996, De Marco 1998) and activity time shifts (May 1980, De Marco & Resende 2002). These species are more dependent on air temperature to initiate their activities and are especially affected by higher air temperatures in the middle of the day, which could overheat their thoracic muscles (May 1991, De Marco & Resende 2002). May (1976) suggests that some postures, like droop-wing perching (that face the thorax to the sun) are related to heating the thoracic muscle, while the so-called "obelisk" posture (the wing-tips are held below the body and the abdomen with an angle near 90º to the substrate) could minimise overheating by reducing exposure to the sun.

The effects of temperature on perchers are not homogeneous over species. Theory predicts strong differences in the patterns of thermoregulatory responses in the perchers, mainly related to body size (May 1977, De Marco 1998). Larger insects could be more efficient basking in sunny sites at low air temperature, because the capacity to heat by irradiation increases with body size (May 1979, 1991; Bartholomew 1981). However, small perchers with a higher surface/volume ratio are more strongly dependent on air temperature for their activity.

It is possible that the restrictions imposed on these species by their thermoregulatory needs determine the range of their behavioral options. If higher temperatures are a potential danger for small perchers, the intensity of patrolling and territorial defense activities should be lower during high temperature periods than that for larger species.

The main activities of male Odonata near the water are the defense of territories and copulation. This is specially evident for perchers, and we only observed male individuals of flier species following females during oviposition [e.g. *Pantala flavescens* (Fabricius)], patrolling [e.g. many Aeshnidae in streams and *Tramea* species in lakes, (Sherman 1983)] or foraging. Although the Libellulidae have great behavioral flexibility in territoriality (Parr 1983), territory defense is mainly characterized by aggressive chasing of the intruders and they mate during complex courtship flights (Jacobs 1955; Wildermuth 1991, 1994). These activities involve a great metabolic effort that brings thoracic temperatures near the overheating limit. If a relationship

between body size and thermoregulatory efficiency exists, it is possible that larger species are more easily engaged in aggressive territorial defenses, spending a larger proportion of their temporal budget in these activities.

Here we perform a detailed analysis of the behavioral temporal budget of the odonate assemblage in a lake of the Parque Estadual do Rio Doce, MG, Southeast Brazil. We test the hypothesis that larger species spend more time in territorial defense activities and we thereby try to determine the role of body size on the territorial defense strategies.

Material and Methods

The behavioral observations were made in the Parque Estadual do Rio Doce (PERD), located in an Atlantic Forest region between 42o 38'W and 48o 28'W and 19o 41'S and 19o 30'S. This reserve has a total area of 35,000 ha with a mean altitude of 300 m, a hot tropical climate with the rainy season in the summer, and a dry season between May to September (Nimer 1989). Mean annual rainfall in the PERD is the 1480.3 mm, with mean annual temperature of 21.9°C.

Our study site was at Carioca Lake, which has a perimeter of 1.6 km and an area of 13.5 ha (Tundisi & Musarra 1986) with a near circular shape. Trunks and dead tree remnants of past fires remained in the littoral zone. The main microhabitats near the lake were the large areas where the forest reaches the lake bank and the areas where the bank is covered by grasses and logs (Fig. 1). In the forested areas, aquatic macrophytes were usually absent due to shading, but other areas were densely covered by macrophytes dominated by *Eleocharis* spp., with *Salvinia molesta* and some Nympheaceae. In the macrophyte areas, it was also possible to discriminate between the areas in the margins with bushes and some Gramineae and the macrophyte area in the lake.

The behavioral observations were made in June, September and October 1994 and May 1995. May and June are in the dry season and September-October in the rainy season. The sampling unit for these observations was the sequence of behaviors registered during 1 min of focal observation of an individual (Altmann 1974). The moment when each single behavior started was noted, allowing the calculation of the time spent in each activity. All observations were made between 10 a.m and 3 p.m, when territorial defense is usually more intense. Individuals were selected at different locations of the lake to avoid pseudoreplication due to repeated observation of the same individual. A similar method was used by May (1977) but with a sampling unit of 10 min. As the loss of individuals during observation was frequent, we chose to use a shorter time interval to minimise this effect as in De Marco *et al.* (2002). Indeed, this choice allowed us to sample a larger number of different individuals from each species, observed at different sites in the lake.

We classified the species as fliers or perchers according to the characteristics determined by Corbet (1962). The behavioral activities were classified following De Marco (1998). The activites recorded were as follows:
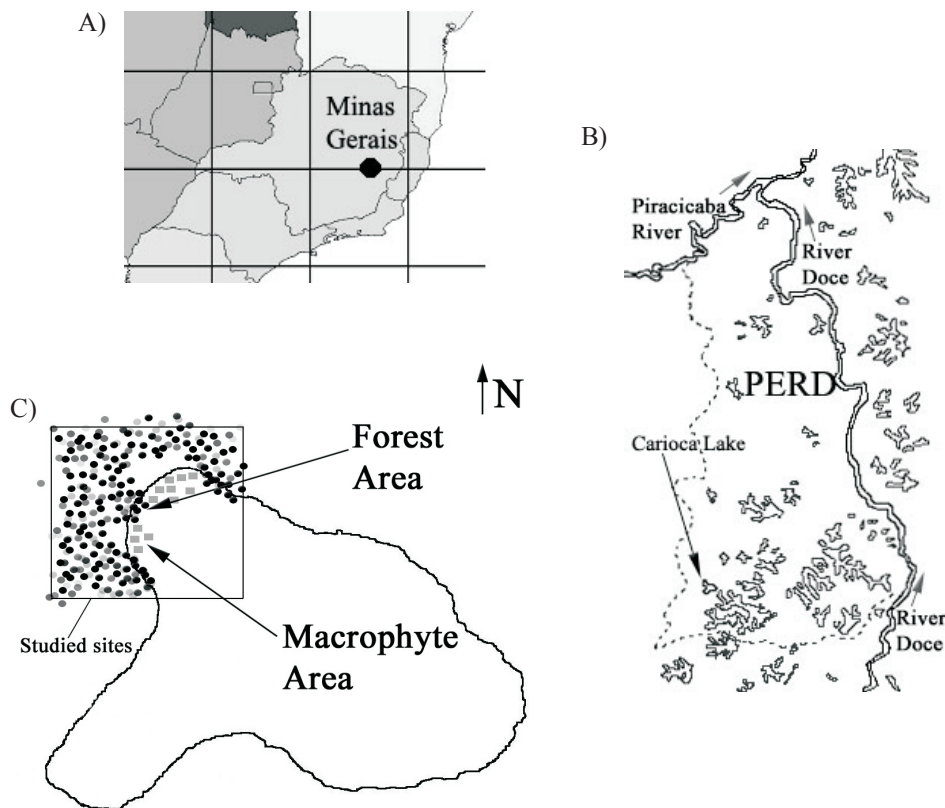
i) normal perching (NP);

Figure 1. (A) Location of Parque Estadual do Rio Doce (PERD), MG, Brazil; (B) Location of Carioca Lake in PERD; (C) Scheme of Carioca Lake, with the microhabitat where the forest reaches the lake bank (Forest Areas – without mats of aquatic plants) and where the bank is covered by grasses and logs (Macrophyte Areas – with banks of aquatic plants).

ii) droop-winged perching: the wing-tips are held below the body and/or the wings shade the thorax (DP);

iii) raised-wing perching: the wings are held above the body and close to each other (RP);

iv) obelisk perching: the wing-tips are held below the body and the abdomen with an angle near 90° to the substrate (OP);

v) patrolling: flying back and forth through an area (PAT);

vi) transition flight: passing through an area without patrolling (TRA);

vii) foraging flight: fast short-distance flights returning to the perches (FO);

viii) territorial defense: chasing another individual (TD);

ix) copulation (CO) and;

x) oviposition (OV).

The behavioral dissimilarity among species was estimated by the Euclidean distance calculated from a matrix of mean proportion of time spent perched (NP, DP, RP, OP), in transit (TRA), foraging (FO) and in reproductive activities (PAT, TD, CO, OV). We use the unweighted pair-group average linkage (UPGMA) as the cluster algorithm, according to Manly (1994). The analysis, excluding individuals that were lost during the 1min sampling period, did not show differences in the groups produced, so we used all individuals in the analysis.

To test for the existence of differences in the proportion of time spent in different behavioral categories between microhabitat and season, we used the Mann-Whitney U non-parametric test, because the dependent variable had consistent departures from normality even after arcsin transformations.

To determine the relationship between behavioral patterns and species abundance, we estimated the abundance of all dragonfly species by a scan procedure with a fixed area (De Marco 1998). During 1 min every dragonfly that passed or was perched in a 5m segment of the lake bank within 5 m of the lake margin was counted. The area inside the lake was chosen to cover an aggregation of *Eleocharis* spp. This procedure allowed testing for differences between these two microhabitats by means of a standard Student's t-test. The mean right front wing size was used as a measure of body size. A minimum of five mature individuals of each species were measured from our voucher individuals captured at PERD and deposited in the Quantitative Ecology Lab, at the Universidade Federal de Viçosa.

Results

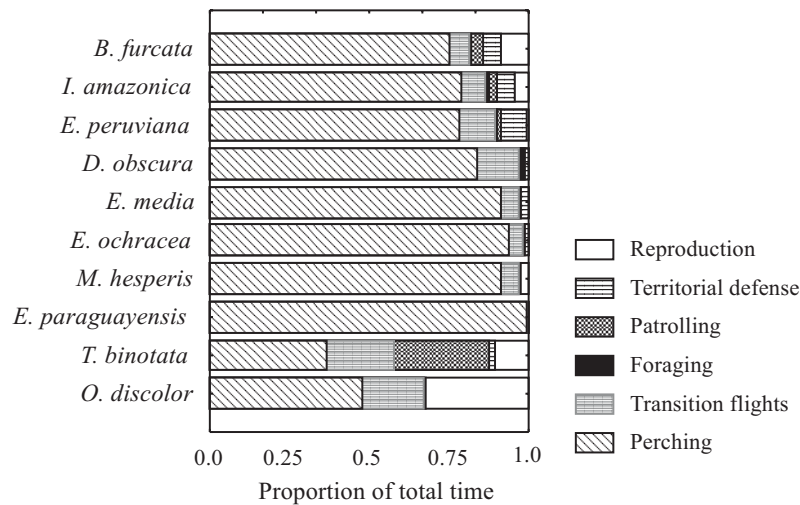**Behavioral Patterns.** From the total dragonfly assemblage

Figure 2. Mean proportion of time spent in different behavioral activities by members of the dragonfly assemblage of Carioca Lake, MG, Brazil. The proportion of time spent in oviposition and copulation is summed in the reproduction category.

that is usually observed in the Carioca Lake, only *Orthemis discolor* (Burmeister) (n = 8), *Erythrodiplax paraguayensis* (Föster) (n = 5) and *Diastatops obscura* (Fabricius) (n = 5) were observed less than 10 times. The most abundant species were *Brachymesia furcata* (Hagen) (n = 91) and *Idiataphe amazonica* (Kirby) (n = 67).

Tramea binotata (Rambur) and *O. discolor* showed a distinct behavioral pattern; both spent most of their time in reproductive activities and transition flights (Fig. 2). All other species spent most of the time perched, usually a larger portion of time than all of the other behavioral categories combined (Fig. 2). Only *Microthyria hesperis* Ris and *D. obscura* spent a large proportion of time in transition flights

but with a minor proportion of time spent in activities related to reproduction.

B. furcata, I. amazonica and *Erythemis peruviana* (Rambur) spent more time in reproductive activities (territorial defense, copulation and oviposition). The *Erythrodiplax* spp. (*E. media* Borror, *E. ochracea* (Burmeister) and *E. paraguayensis*) and *D. obscura* showed a small proportion of reproductive activities. *I. amazonica* showed a perched position unique among the observed species. This species perched with the wings raised, and was found mainly in the internal boundary of macrophyte vegetation in the lake.

The cluster analysis revealed a clear distinction in three
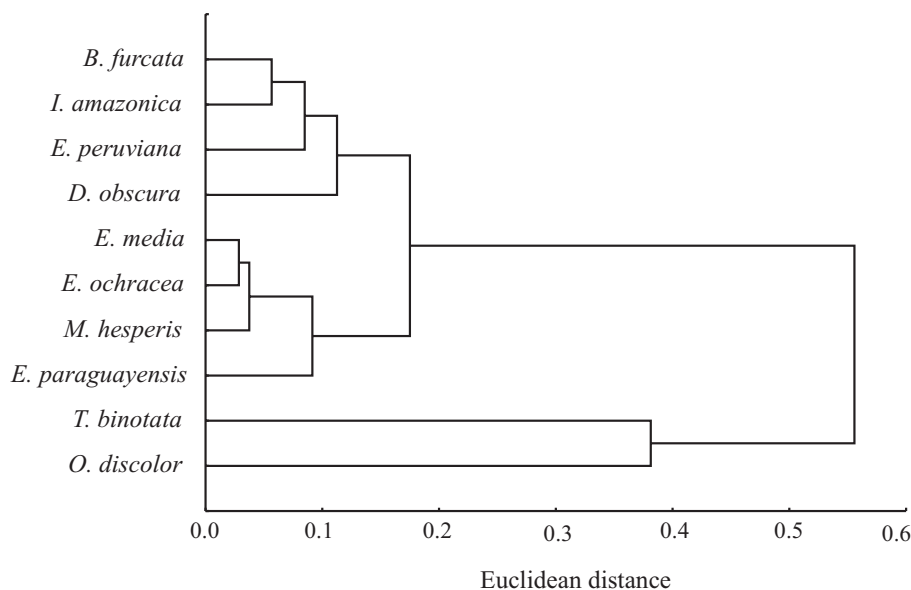

Figure 3. Cluster analysis for the proportion of time spent in different behavioral categories by members of the dragonfly assemblage of Carioca Lake, MG, Brazil.

Table 1. Mean abundance of odonate species (±SD) observed in the Parque Estadual do Rio Doce, Marliéria, MG.

	Eleocharis	Lake bank	t-test	P
B. furcata	4.6* ± 4.55	1.5 ± 1.93	6.206	>0.001
E. peruviana	1.7* ± 2.46	0.3 ± 0.73	5.302	>0.001
I. amazonica	1.1* ± 1.36	0.5 ± 0.96	4.072	>0.001
E. media	0.5 ± 0.97	1.6*± 1.59	5.497	>0.001
E. ochracea	0.8 ± 1.46	1.0 ± 1.56	1.099	0.273
M. hesperis	1.0* ± 1.40	0.01 ± 0.38	6.872	>0.001
O. discolor	0.6* ± 1.08	0.3 ± 0.71	2.125	0.035
T. binotata	0.3* ± 0.59	0.1 ± 0.31	4.193	>0.001
D. obscura	0.01 ± 0.13	0.02 ± 0.20	0.056	0.955
E. paraguayensis	0.01 ± 0.09	0.1* ± 0.39	2.990	0.003

groups (Fig. 3):
- *B. furcata*, *I. amazonica*, *E. peruviana* and *D. obscura*
- *Erythrodiplax* spp. (*media, ochracea, paraguayensis*) and *M. hesperis*
- *T. binotata* and *O. discolor*

The first group contained the abundant species (Table 1) and the less abundant *D. obscura*. This species is rare in the Carioca Lake, but it is one of the most abundant in the Dom Helvécio Lake nearby. The species in the first group remained perched for long time and differed from the second group by the larger proportion of transition flights. Except for *D. obscura*, these species are also very aggressive, spending a high proportion of time in territorial defense. The second group was composed of the species that remain perched but rarely defend or patrol territories. They are also the four smallest species of the assemblage. The third group spent a low proportion of time perched. However, *T. binotata* showed strong flight behavior with a high proportion of patrolling flights. *O. discolor* was rarely observed in the lakes, but when it occurred the individuals were usually in copula or were ovipositing females. These groups were considered consistent because other dissimilarity measures (Manhattan distance and percent dissimilarity) produced the same results.

Microhabitat, Abundance and Behavior. *B. furcata* showed a microhabitat-context determination of their behavior, with reproductive activities in the *Eleocharis* area, and perching at the bank (Fig. 4A). *I. amazonica, E. peruviana* and *E. media* showed similar distributions of behavioral activities between the areas (Fig. 4B, C and D, respectively). In all cases the behavioral observations were concentrated on the *Eleocharis* area where the odonates, except *E. media*, were more abundant (Table 1). Members of this species, as with other *Erythrodiplax* spp. that were observed, were often perched in the bank area, in low height grasses or on bare soil.

The proportion of time spent in reproduction during the rainy season was twice as high (0.16) as during the dry season (0.08) for *B. furcata* (Mann Whitney U test: U = 466.5, N1 = 28, N2 = 63, P = 0.033). For *I. amazonica* the proportion of time spent in reproduction was not affected by season (Mann Whitney U test: U = 471.5, N1 = 26, N2 = 41, P = 0.377).

Except for two *Erythrodiplax* spp., the dragonflies that showed statistical differences in abundance between microhabitats were more abundant in *Eleocharis* areas (Table 1). *E. media* and *E. paraguayensis* were more abundant on the lake bank and *E. ochracea* and *D. obscura* did not show any differences. The *Erythrodiplax* species appear to stay perched on the lake bank most of the time, where no defendable resource could be observed.

I. amazonica defend territories mainly in the macrophyte aggregations distant to the lake bank, where the abundance of *B. furcata* is lower. Their reproductive activities occur in the open areas, without macrophytes, where harassment of *B. furcata* and *I. amazonica* males decreases. The *Erythrodiplax* and *Erythemis* spent most of their time at the lake banks where *B. furcata* did not defend territory. They only invaded the macrophyte area for female guarding during oviposition.

Ecological Determinants of Behavior: Abundance and Body Size. There was a strong effect of body size on behavior (Table 2). The variations of size explained 90.8% of the variation in perching time among species. The values for patrol (60.5%) and territorial defense (55.8%) were lower but remained statistically significant. Larger species spent more time in patrol and territorial defense, while smaller species remained perched.

An effect of abundance was only observed for the time spent patrolling (Table 2). However, it is difficult to determine the real importance of this relationship because there is some colinearity between body size and abundance (Regression Analysis: R^2 = 0.482, t = 2.362, df = 6, P = 0.056; Table 2).

Discussion

The behavioral groups generated from the analysis of the temporal budget are compatible with the distinction between fliers and perchers and a subdivision of perchers
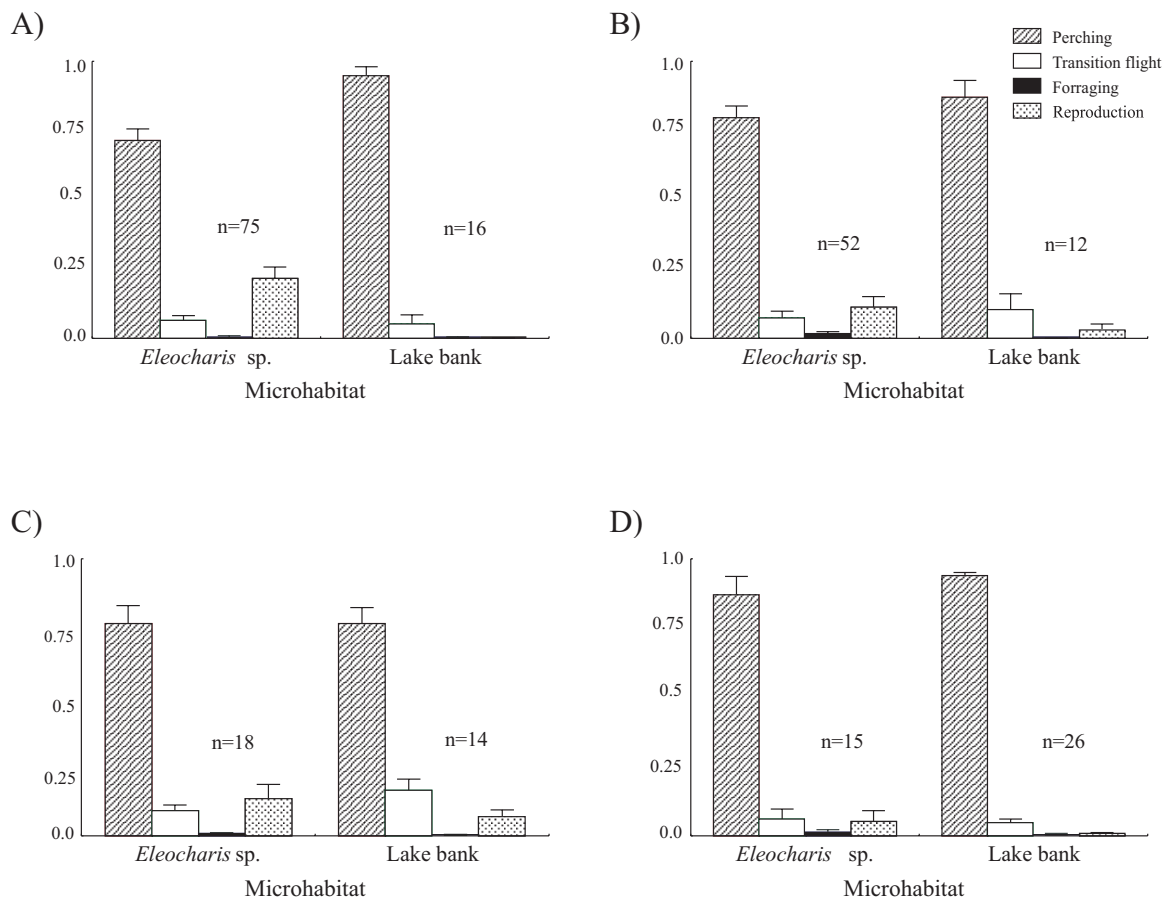
Figura 4. Proportion of time spent in different behaviors in relation to each microhabitat type for *B. furcata* (A), *I. amazonica* (B), *E. peruviana* (C) and *E. media* (D) in Carioca Lake at Parque Estadual do Rio Doce, MG, Brazil.

due to aggressiveness related to body size. Large perchers were more aggressive than their small heterospecific relatives.

Ecological variables strongly affect the behavioral characteristics of these species. The abundant species were more aggressive, but it is not clear whether aggressiveness is a simple predictor or a factor responsible for the abundance of the species. It is possible that species that aggressively defend their territories are able to affect the local density of other species, preventing their females from ovipositing in the area. Many authors have found an intraspecific relationship between male abundance and behavioral characteristics. In *Paltothemis lineatipes* Karsch the increase in abundance was associated with small territories and higher interaction frequency (Alcock 1989). However, both increases (Hassan 1978, Moore 1987) and decreases (DeBano 1993, Reinhardt 1998) of territoriality have been observed with the increase of abundance.

It is possible that increase abundance causes an increase in time spent in territorial defense up to a limit where many mate opportunities are lost. In these conditions territoriality is inefficient and the time spent in this activity is expected

to decrease (Wickman & Wiklund 1983, Alcock & O'Neill 1986). Interspecific comparisons of this kind of phenomena are complicated because they include many other variables including body size and phylogeny.

It is generally thought that the adult abundance of dragonflies should be strongly determined by the success of their larval stage (Harvey & Corbet 1985; Van Buskirk 1987, 1993; Banks 1987; Thompson 1987; Moore 1987). It is also possible that adult behavior (e.g. the higher proportion of patrolling in a given species) could also determine its long-term mean abundance. Two conditions must exist to give rise to such a phenomenon: i) the aggressive species should be dominant over the other species and defend territories even interspecifically; ii) their activity periods and their territorial defense areas should overlap largely with the observed in other species.

B. furcata is the dominant species that fulfils these requirements. It was aggressive toward other species in this assemblage, largely overlapped its defense areas in *Eleocharis* and was present in the lake throughout the day, with higher abundance at mid-day. For the less aggressive species the main alternatives are the changing in activity time, and/or the area of defense and oviposition. It is less probable that

Table 2. Effect of body size (anterior wing length) and mean abundance on the proportion of time spent in some behaviors of odonate species in the Parque Estadual do Rio Doce, Marliéria, MG. R2= coefficient of determination, t = Student's t-test statistic and P = p-value

Variables						
Independent	Dependent	R^2	Slope	SE	t(df=6)	P
Body size	Abundance	0.482	0.1196	0.05	2.362	0.056
Body size	Perching	0.908	-0.0145	0.001	7.719	<0.001
Body size	Patrolling	0.605	0.0019	0.0006	3.031	0.023
Body size	Territ. defense	0.558	0.0038	0.001	2.750	0.033
Abundance	Perching	0.356	-0.0526	0.02	1.822	0.118
Abundance	Patrolling	0.645	0.0114	0.003	3.306	0.016
Abundance	Territ. defense	0.297	0.0161	0.01	1.591	0.163

the time of territorial defense shifts because the female usually arrives at the lake at mid-day. However**,** there are evident microhabitat differences among these species.

The *Erythrodiplax* species were very similar in behavior. Their position in the behavioral groups suggests a phylogenetic effect in this classification. Body size, that strongly affects these behavioral patterns, also appears to be similar in this congeneric species.

May (1976, 1977, 1980, 1991) carefully demonstrated differences in thermoregulatory abilities among perchers related to body size. Because thermoregulation could restrict the activity time and the local where territorial defense could occur, it also determines an evolutionary landscape where other characteristics, as reproductive behaviors, could vary.

O. discolor is a generalist species that could occur in lakes, temporary ponds or aquaculture ponds (De Marco *et al.* 1999). In general, it is observed actively patrolling these locales and defending territories. However, it is possible that in the lakes, with an intense competition with *B. furcata*, this species could change its behavior. Because *O. discolor* was the largest percher in this assemblage, it shows a heliothermic thermoregulatory adaptation (May 1976, De Marco & Resende 2002) that allows more similar behavior to the fliers.

The behavioral classification in fliers and perchers is extremely useful but it could oversimplify the behavioral patterns among the species because it is common to find a great body size and behavioral variation between the species usually classified into flier or percher categories. In this study, we found a body size relationship where larger dragonflies, with better thermoregulatory abilities, could spend more time in reproductive activities. We propose the existence of a behavioral continuum associated with the body size variation in perchers, because larger perchers, like the fliers, spend a great proportion of their behavioral time budget in flight activities, including patrolling. It is also important to note that this dependency on body size of some reproductive activities (e.g. territorial defense) could affect the patterns of species interactions in odonate adult communities.

Acknowledgments

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