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# RESIDENCE AND TERRITORIAL CHARACTERISTICS OF LIBELLULIDAE SPECIES IN A NEOTROPICAL ASSEMBLAGE (ANISOPTERA)

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During territorial behaviour, aggressive attacks among heterospecific odon. ♂♂ are common and may cause a separation of niches, based on the preferred sites for territorial defence. Here, territorial behaviour and the characteristics of territories in ♂♂ of *Erythrodiplax media*, *Micrathyria catenata* and *M. hesperis* are described and their territorial fidelity, capturing and marking of ♂♂ are discussed. In all spp. studied, there was a clear distinction among the microhabitats defended as territories. In both *Micrathyria* spp., ♂♂ seem to defend territories with defined resources. In *E. media*, the defended resources are less evident. Its ♂♂ are highly aggressive and show high territorial fidelity but, apparently, they lose the territory if they stay away from water for at least one day.

## INTRODUCTION

During territorial defence, aggressive attacks among heterospecific odonate males are common (HASSAN, 1978; MAY, 1980) and competition and aggressive interactions could cause some species to change their habitat selection (MAY, 1980; RUSSELL et al., 1998). These aggressive interactions may cause a separation of niches among species. Thus the co-occurring species, *Ischnura elegans* (Vander L.), *Coenagrion pulchellum* (Vander L.), *Enallagma cyathigerum* (Charp.) and *Erythromma najas* (Hans.), for example, have enough differentiation in their oviposition sites (JOHANNSSON, 1978). *Sympetrum flaveolum* (L.) males use

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lower perches than those of *S. sanguineum* (Müll.) but both species perch lower when their neighbour is a male of the other species (REHFELDT & HADRYS, 1988).

Differences in territorial quality between odonate species are little evident. In some species, males defended territories selected by the female based on the quantity of oviposition resource available (TSUBAKI & ONO, 1986; ALCOCK, 1987a; ALCOCK, 1987b; KOENIG, 1991; MEEK & HERMAN, 1991; BATTIN, 1993), whereas in other species, territorial defence seems to be more related to the chance of males detecting females arriving at the pond (ALCOCK, 1987a, 1987b; VAN BUSKIRK, 1986; BATTIN, 1993; DE MARCO & RESENDE, 2004) and in this case, the size of the territory can determine reproductive success of some species, since it increases the chance of male visualizing females (VAN BUSKIRK, 1986). The perches or substrates for the male perching in a territory can also be diverse (PARR, 1983; OSBORN & SAMWAYS, 1996), and change mainly as a function of their availability.

The objective of this study was to determine the criteria for selection of territories by males of *Erythrodiplax media* Borror, *Micrathyria catenata* Calvert, and *M. hesperis* Ris, by observing their territorial behaviour, territorial fidelity, and the characteristics of the respective territories.

## METHODS

STUDY AREA – The work was carried out during February-April in the Centro de Estudos de Florestas Naturais of Universidade Federal de Viçosa, Minas Gerais (20°45'S, 42°51'W). The regional climate is Cwa (Köppen classification), moderately humid sub-tropical with a hidric deficit between May and September (GOLFARI, 1975). The average annual rainfall is 1450 mm, relative air humidity ca 80% and the temperature varying from a maximum of 26,1°C to a minimum of 14,0°C (VALVERDE, 1958).

Due to a local dam, *Nymphea* cf. *ampla* and *Eleocharis* are very abundant in the coastal region. At the shoreline there are sticks and grasses that are used as perches by some dragonfly species.

BEHAVIOUR AND TERRITORIAL CHARACTERISTICS – During the study period, all activities relative to territorial defence, mating ritual and oviposition were recorded. The emphasis was on descriptions of the behaviour, courtship ritual before mating, male defence behaviour during oviposition and on the oviposition sites.

To characterize the territories defended by *E. media, M. catenata* and *M. hesperis*, we walked around the shoreline of the pond and recorded, for each individual, the type and height of its perch, the distance from the perch to the shoreline, the vegetation surrounding the perch and the distance between perches of the conspecific territorial males. To determine interspecific differences in the territorial characteristics, we performed analyses of Chi-square for categorical variables and analyses of variance (Parametric ANOVA and Kruskal Wallis) for quantitative variables.

TERRITORIAL FIDELITY – For the sake of the enquire into the use of the territories by males of the three species, 12 adjacent sections of five meters length were marked in the littoral zone of the pond. Males were captured and marked on the wings with non-toxic paint. The date of capture and the section in which the male was encountered were recorded. During the subsequent days, between 10:00 and 14:00, the segments were checked, all marked individuals and any new ones marked.

In the analyses of male territorial fidelity, males with at least four recaptures were used for *E. media*

and those with three recaptures for *M catenata* and *M. hesperis*. This difference in criteria was due to the lower frequency of recaptured individuals of the latter two species. A period of five consecutive days was used to determine whether the individuals absent from the dam for at least one day could lose their defended territories. It was assumed that a male had changed its territory when it appeared in a different section, not contiguous to the originally defended segment. The relationship between territorial change and the absence of males was tested by a $Chi^2$ analysis.

## RESULTS

### BEHAVIOUR AND TERRITORIAL CHARACTERISTICS

*Erythrodiplax media* seems to be more aggressive than the *Micrathyria* species. The females were abundant at the pond and couples in copula were often seen, but no courtship ritual was ever observed. After copulation, the females remained for some seconds perched on branches near the male territory, generally guarded by the male. Finally, they oviposited near the shoreline of the pond, in locations with submerged vegetation. Oviposition was not restricted to the respective male territories, although the males guarded the females during the entire oviposition period, attacking other males that approached.

*Micrathyria catenata* is not a very aggressive species, though the largest of the three species studied. Males were observed, but no females and matings were ever seen.

*M. hesperis* is a small and likewise not very aggressive species. A single mating was observed and there was neither a courtship ritual nor a pause between mating and oviposition. The female oviposited in the male's territory and it was guarded by the male flying above. However, we observed another female ovipositing unguarded, perched on a leaf of *Nymphea* and submerging her abdomen.

The two *Micrathyria* species perched more frequently on aquatic macrophytes (73.6%; n = 53), when compared with *E. media* males, which perched on branches, grasses or even on the soil (78.9%; n = 19; $Chi^2 = 15.76$; df = 1; $p<0.001$; Fig. 1) in addition to using macrophytes. Comparing only *Micrathyria* species, *M. catenata* perched mainly on *Eleocharis*, whereas *M. hesperis* perched more commonly on the bud or on the leaf of *Nymphea* (74% and 48%, respectively; $Chi^2 = 15.34$; df = 1; $p<0,01$; Figs 1b, 1c).

The perch's height was also different among the three species (ANOVA; F = 12,85; df = 2; $p<0,01$). *M. catenata* perched higher than *M. hesperis* (Fig. 2; Tukey test; $p<0,01$). The perch's height for *E. media* males was intermediate, not differing significantly from that in either of the two *Micrathyria* species (Fig. 2; Tukey test; p = 0,13).

Furthermore, the vegetation around the territories of the three species was different ($Chi^2 = 50,90$; df = 8; $p<0,01$). *E. media* defended territories with *Eleocharis* and grasses (37% and 42%, respectively; $Chi^2 = 19,89$; df = 4; $p<0,01$), whereas *M. catenata* defended mostly those with *Eleocharis* (76%; $Chi^2 = 28,09$; df = 1; $p<0,01$),

and *M. hesperis* those with *Nymphea* (94%; $Chi^2 = 18,1$; df = 1; $p<0,01$).

*E. media* males defended territories along the shoreline and perched on branches, grasses, directly on the soil or on *Eleocharis* at an average height of 14 cm. The two *Micrathyria* species perched further over the pond than *E. media*, particularly in the case of *M. hesperis* ($Chi^2 = 18,83$; df = 1; $p<0,01$) for comparison with *M. catenata* (Kruskal-Wallis ANOVA; $Chi^2 = 21,62$; df = 1; $p<0,01$). In *M. catenata*, the centre of the territories averaged one meter from the shoreline; males perched higher than the other species, primarily on *Eleocharis*. The territories of *M. hesperis* extended even further out over the water than those of *M. catenata* (Kruskal-Wallis ANOVA; $Chi^2 = 5,37$; df = 1; $p = 0,021$; Fig. 3) and they mainly perched on the leaves or flowers of *Nymphea*. However, the distance of *M. hesperis* territory from the shoreline varied and there was no homogeneity of variance in the data (Fig. 3; Bartlett Test; $Chi^2 = 27,128$; df = 2; $p<0,001$).

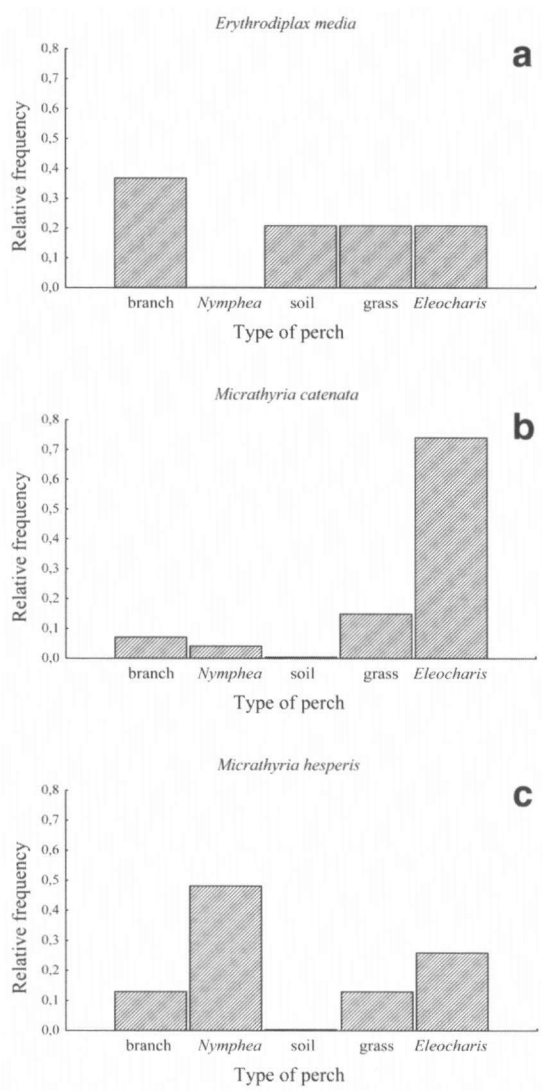


Fig. 1. Relative frequency of the type of perches in Viçosa, MG, Brazil, used by males of: (a) *E. media*, – (b) *M. catenata*, – and (c) *M. hesperis*.

There was some difference in the distance between perches used by males of the three species ($F = 11,06$; df = 2; $p<0,01$; Fig. 4). The distance between the perches used by *E. media* males ($\bar{x}$ = 229 cm) was similar to the distance between these in *M. hesperis* ($\bar{x}$ = 338 cm; Tukey test; $p = 0,87$). However, *M. catenata* males perched near-

er their neighbours ($\bar{x}$ = 103 cm) than the other two species (Tukey test; p<0,001).

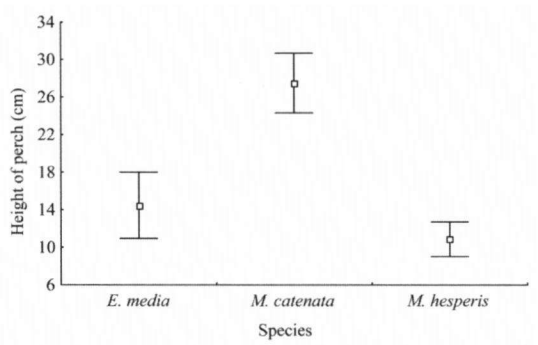


Fig. 2. Mean height of perches used for males of *E. media*, *M. catenata* and *M. hesperis* in Viçosa, MG, Brazil. Bars indicate the standard deviation.

## TERRITORIAL FIDELITY

The displacement of males of the three species between sections of the pond was similar (F = 2,24; df = 2; p = 0,13; Fig. 5). However, the recapture rate was very low, especially, for the *Micrathyria* species. Of the 151 marked *E. media* males only 35 were recaptured at least four times, whereas of the 114 marked *M. catenata* and 24 *M. hesperis* males, only seven and four, respectively, were recaptured at least three times. Thus only the *E. media* data were considered further. The frequency distribution of displacement in this species showed that most males defended territories in the same place, moving about 10 to 20 meters, with only a few individuals moving more than 35 meters (Fig. 6). Furthermore, in 77% of the occasions when *E. media* males stayed away from the pond for at least one day they lost their section of territorial defence, whereas this occurred in only 34% of the cases when males remained at the pond ($Chi^2$ = 9,19; n = 38; df = 1; p<0,05).

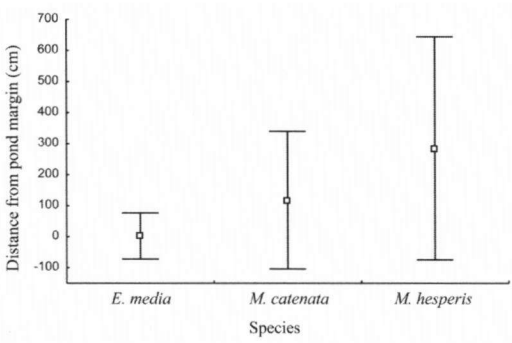


Fig. 3. Distance of perches to the pond margin in males of *E. media*, *M. catenata* and *M. hesperis*, in Viçosa, MG, Brazil. Positive values, in the pond; – negative values, away from the pond. Bars indicate the standard deviation.

## DISCUSSION

The partition of microhabitat among the species of a community is a common phenomenon and can occur due to interspecific competition. Females of many *Micrathyria* species oviposit on aquatic plants, such as *Nymphea* (PAULSON, 1969), hence it is hard to say whether the microhabitats selected by *Micrathyria* species as described in this study are a consequence of competition with *E. media* or a characteristic of the genus. Libellulidae mostly oviposit directly on the surface of the water or on the surface of wet floating objects, including plant material – exophytic oviposition – (COR-

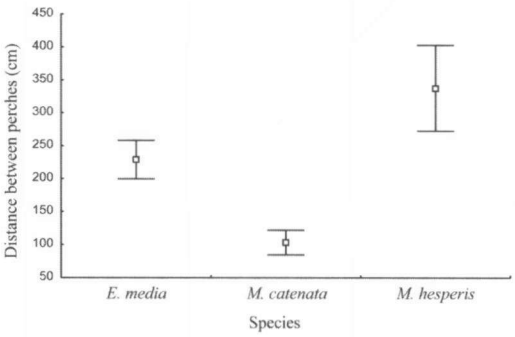


Fig. 4. Distance between perches used by males of *E. media*, *M. catenata* and *M. hesperis* in Viçosa, MG, Brazil. Bars indicate the standard deviation.

BET, 1999). The oviposition on plant material can possibly result in (1) an increase in the parental care survival as the eggs would be less exposed to predators such as fish and other aquatic organisms, or (2) a decrease in harassment of the ovipositing female by males trying to copulate.

Males with a high degree of residence should be displaced less often than males that continually lose territorial disputes (PARR, 1983; HARVEY & CORBET, 1985; CONVEY, 1989). The time of absence of a territorial male from water can be related to the energy restoration or the period of foraging (FRIED & MAY, 1983; ANHOLT et al., 1991; MARDEN & ROLLINS, 1994; DE MARCO, 1998). This can cause confusion in the residence of a territory (GRIBBIN & THOMPSON, 1991), resulting in a greater displacement of resident males. DUNHAM (1994) has already emphasized that the departure for foraging can make it difficult to maintain good territories and, consequently, males can lose mating opportunities. Nevertheless, if territorial defence demands a high energetic cost (FRIED & MAY, 1983), larger males, with larger energetic reserves, are supposed to show a higher reproductive success, since they stay for a longer time in the territories without foraging (HARVEY & CORBET, 1985).

The distance between individuals of a species can be directly related to the degree of aggressiveness of territorial males (VAN BUSKIRK, 1986). Differences in the resource abundance can also affect male distribution (MEEK & HERMAN, 1991). At our locality *Nymphea* covers a large area of the dam, therefore *M. hesperis* males are in the position to establish territories rather distant from each other, per-

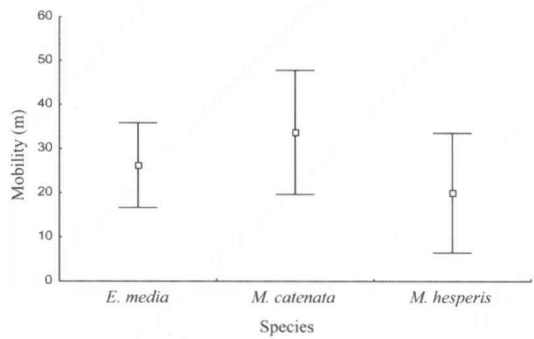


Fig. 5. Mean mobility of males of *E. media*, *M. catenata* and *M. hesperis* in Viçosa, MG, Brazil. Bars indicate the standard deviation.

haps minimising therewith the intraspecific competition. Nevertheless, no difference in the resource availability was evident in *E. media* and *M. catenata* at the pond, the greater distance between perches in *E. media* territorial males was probably due to the fact that this species performs more aggressive interactions than does *M. catenata*.

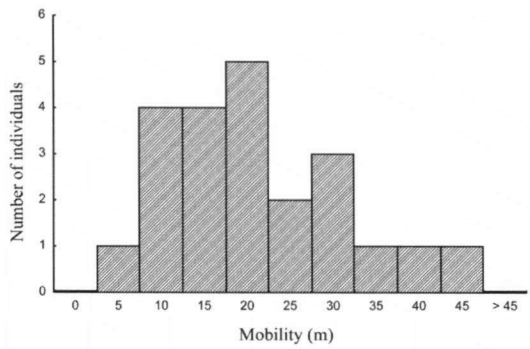


Fig. 6. Frequency distribution of mobility of marked *E. media* males in Viçosa-MG, Brazil.

The spatial arrangement of species into habitat units is a complex result of bionomic characteristics, including oviposition resources and perch choice, and interactions with other species in the community. The bionomic features are probably the most important force driving the choice of habitat used by a species at a locality, despite the fact that the co-occurring species can affect, at least within certain limits, the choice of microhabitat.

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