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Cues for Territory Choice in Two Tropical Dragonflies

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CrITÉrios Para a Escolha de TerritÓrios em Duas LibÉlulas Tropicais

RESUMO - A classificação dos sistemas de acasalamento em Odonata geralmente baseia-se na habilidade dos machos em controlar o acesso das fêmeas aos recursos necessários à postura dos ovos. O objetivo deste artigo foi determinar os critérios de seleção de locais para a defesa de territórios para machos das espécies *Perithemis mooma* Kirby e *Orthemis discolor* (Burmeister) (Libellulidae), em Viçosa, controlando a disponibilidade de poleiros e de vegetação aquática. Machos de *P. mooma* defenderam territórios com vegetação e seus critérios de escolha devem estar relacionados com a oferta de recursos para a postura dos ovos para fêmeas. Machos de *O. discolor* defenderam territórios em locais com poleiros altos e essa escolha talvez esteja relacionada à possibilidade de visualizar rapidamente qualquer fêmea que se aproxime para copular. A interação com outra espécie de Libellulidae mais ativa e agressiva, *Planiplax phoenicura* (Ris), alterou a preferência dos machos de *O. discolor*, o que deixa clara a importância da composição da comunidade e das interações na seleção de microhabitats.

PALAVRAS-CHAVE: Odonata, comportamento, acasalamento, *Perithemis mooma*, *Orthemis discolor*

ABSTRACT - Classifications in mate systems of Odonata are generally based in the male ability to control the female access to oviposition resources. In this paper we discuss the criteria for male territory selection in the dragonflies *Perithemis mooma* Kirby and *Orthemis discolor* (Burmeister) (Libellulidae), in Viçosa, Brazil, controlling the availability of perches and aquatic vegetation. *P. mooma* males defended territories with vegetation and thus their choice was probably related to the oviposition resource of the females. *O. discolor* males preferred sites with tall perches, possibly because their choice was related to a mate-seeking resource. Interactions with another libellulid more active and aggressive, *Planiplax phoenicura* (Ris), changed the preference of *O. discolor* males to vegetated areas highlighting the influence of community composition and interactions on territorial site selection.

KEY WORDS: Odonata, behaviour, mating, *Perithemis mooma*, *Orthemis discolor*

General descriptions of odonate mating systems usually classify them as a resource defence polygyny (Emlen & Oring 1977, Thornhill & Alcock 1983). However, detailed studies have determined a more complex picture that classify their mating systems into: i) non-resource-based systems, subdivided into free female choice, female-control, and encounter-limited systems and ii) resource-based systems; subdivided into resource-control and resource-limitation systems (Conrad & Pritchard 1992, Battin 1993). As part of their classification, Conrad & Pritchard (1992) used the way that odonate males control female access to oviposition sites. For example, if oviposition sites are clumped it is economically possible to fight for control of female access to these sites (Sherman 1983, Buskirk & Sherman 1985, Alcock 1987).

Odonate females do not present any kind of parental care (Corbet 1962, 1999) and can only increase their reproductive success through two indirect ways (Michiels

& Dhondt 1990). First, through the selection of an oviposition site where egg survival and larval development could be higher, and second, through decreasing the costs associated with oviposition. These costs of oviposition arise through i) the energy spent during oviposition; ii) the time lost and energy spent avoiding male harassment (Robertson 1985, Michiels & Dhondt 1990, McMillan 1991, Cordero *et al.* 1995) and iii) predation by aquatic animal as frogs and fishes (Jacobs 1955, Michiels & Dhondt 1990).

There is little information that shows which characteristics determine the quality of a territory for odonates. Theoretically, the males could assess the quality of a territory by the presence of oviposition sites and by the presence or arrival rate of females. In some species, the females are capable to visualise the resources that represent the best microhabitat to larval development and the males defend the territories that will be selected by females based

on the abundance of these resources (Alcock 1987). In other species, the female is not capable to determine the oviposition resources before copulation, because they oviposit in submersed plants (Alcock 1982, 1987), so possibly they could not produce a strong inter-sexual selection over male's territories. As it is common to observe males defending the same territory day-by-day (Corbet 1999), a question arises about how this strategy could be linked to the access of females for mating.

In this paper we aimed to determine the criteria for territorial site selection by males of *Perithemis mooma* Kirby and *Orthemis discolor* (Burmeister), two common libellulid dragonflies in southeastern Brazil. We tested specifically the effect of the presence of perches and floating aquatic vegetation on territorial selection in these species. We also investigated the effect of the interspecific interactions on territorial choice, comparing the site selection in a period of low and high species richness during the experiment.

Material and Methods

We conducted this work in a pond at the fruit-culture station on the Federal University of Viçosa campus, Viçosa, Minas Gerais (20° 45' S, 42° 51' W), Brazil. The climate of the region is Cwa (Köppen classification), a wet sub-tropical climate with the dry season from May to September. Mean annual precipitation is between 1500 mm and 2000 mm, and a mean annual temperature range from 14.0°C to 26.1°C (Valverde 1958).

We chose an area without aquatic vegetation and with little vegetation on the bank to install the experimental treatments. This area was not utilised by any dragonfly species before the experiment. The arena of this experiment was four squares with 1 m² total area built with PVC tubes. A 3 x 3 factorial design included the effects of the presence of aquatic vegetation and perch height. The aquatic vegetation used were mats of the floating-fern *Salvinia molesta*. The two levels of perch height were 0.2 m and 0.5 m. The combination of the treatments was: i) tall perch with vegetation, ii) tall perch without vegetation, iii) small perch with vegetation, and iv) small perch without vegetation. The replica for this experiment is the period of one minute of observation at each square, reporting the abundance of each species present. The procedure was repeated at 15 min intervals, between 1200h to 1400h, in five days in October and six days in December. Cloudy moments were omitted from the analysis. In October the community had lower species richness than in December, possibly due to low air temperatures. The comparison of these months allows testing the effect of the intensity of interspecific interactions on territorial choice.

We tested the effect of vegetation presence, perch height and the interaction between them by an Analysis of Variance (ANOVA). Species richness in treatments was estimated by the Jackknife procedure (Heltshe & Forrester 1983, Colwell & Coddington 1994). This method has the advantage of producing an unbiased estimation of species richness and allows the use of statistical tests using confidence interval estimates.

Results

In October, the first phase of the experiment, only *P. mooma*, *O. discolor* and *Micrathyria catenata* Calvert were observed in the experimental units. In December, the second phase, we also observed *Erythrodiplax fusca* (Rambur), *E. media* Borror, *Planiplax phoenicura* (Ris), *Micrathyria hesperis* Ris, *Miathyria simplex* (Rambur), *Miathyria marcella* (Selys) and *Pantala flavescens* (Fabricius). *O. discolor* and *P. mooma* were the most abundant species in both phases. Species richness was higher in the second phase for every treatment (Fig. 1). This increase in species richness occurred due to the presence of different species including the fliers *M. marcella*, *M. simplex* and *P. flavescens*.

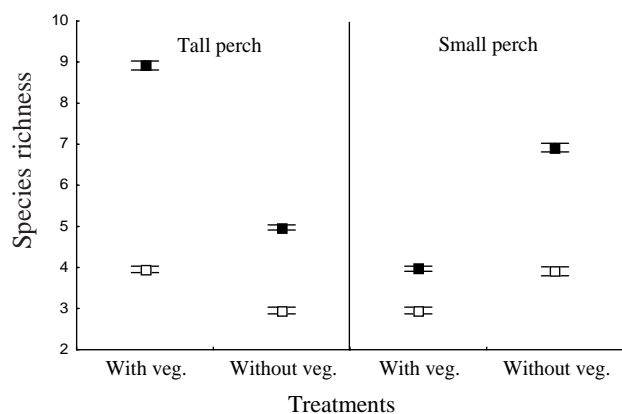


Figure 1. Species richness of Libellulidae estimated by the Jackknife procedure in the combination of treatments perch height and presence of vegetation, in the first (empty squares) and second phases (full squares), in the Fruticulture pond, Viçosa-MG. Bars represent confidence intervals of 95%.

P. mooma males defended territories in the treatments with vegetation (Table 1; Figs. 2a and 2b), but were not affected by perch height or by different phases (Table 1). They frequently perch directly on the aquatic vegetation and so this species was not influenced by the presence of perches in the experimental squares. However, we could not demonstrate the influence of perches on the female's choice due to low numbers.

Table 1. Results of Analysis of Variance for mean abundance of *P. mooma* to test the effect of height of perch, presence of vegetation, and phase of experiment.

Source	F	P
Phase	2.054	0.154
Perch	0.467	0.495
Vegetation	43.109	<0.001*
Phase x perch	1.777	0.184
Phase x vegetation	0.022	0.881
Vegetation x perch	0.018	0.894
Phase x perch x vegetation	0.613	0.435

Residual mean square = 0.525; degrees of freedom of residual = 184

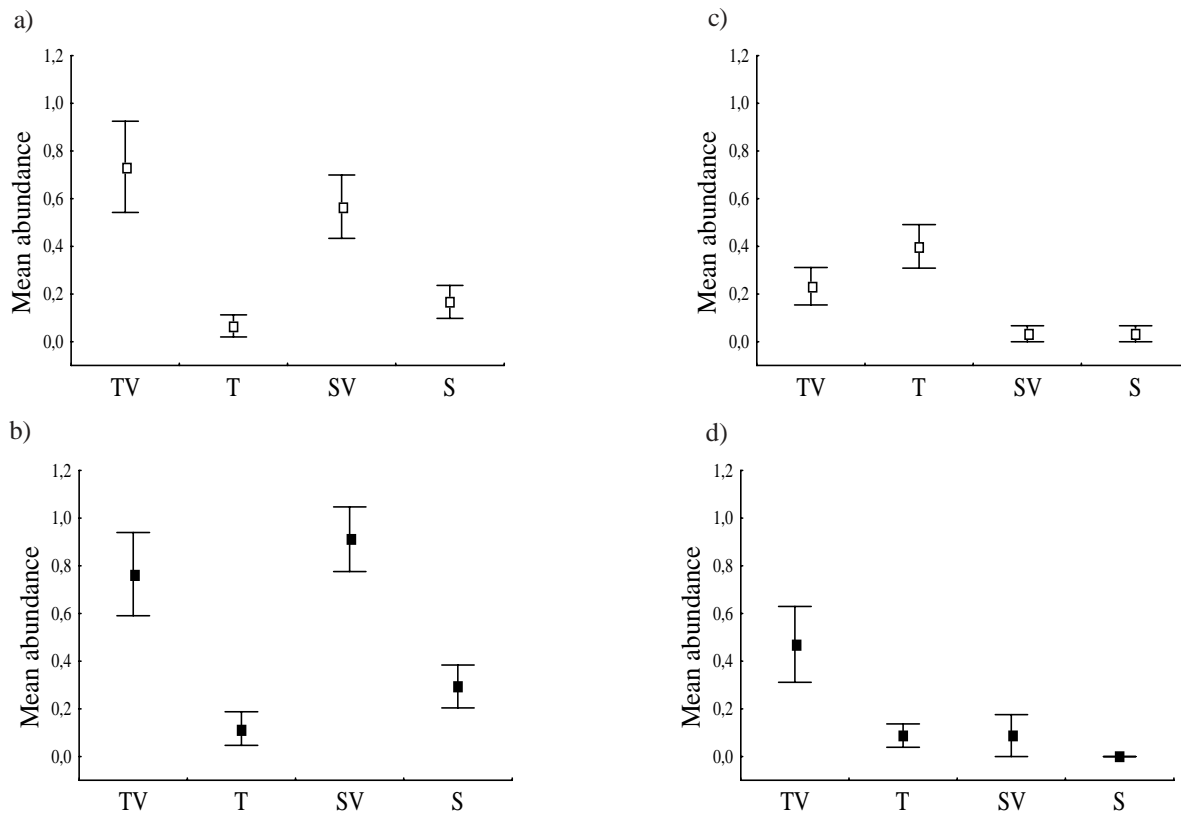


Figure 2. Mean abundance of *P. mooma* during the first (a) and second (b) experiment phase; and of *O. discolor* during the first (c) and second (d) phase at the combination of treatments: tall perch with vegetation (TV), tall perch without vegetation (T), small perch with vegetation (SV), small perch without vegetation (S), at the Fruticulture ponds in UFV, Viçosa-MG. Bars represent standard error.

O. discolor males defended large territories and preferred the tall perch, but a significant interaction between experiment phase and vegetation was also observed (Table 2). In October, *O. discolor* mainly used the tall perch without vegetation (Fig. 2c), while in November it mainly occurred in the tall perch with vegetation (Fig. 2d). In this last phase, we often observed *O. discolor* being excluded from the tall perch without vegetation by *P. phoenicura*.

Table 2. Results of Analysis of Variance for mean abundance of *O. discolor* males testing the effect of height perch, presence of vegetation and phase of experiment.

Source	F	P
Phase	0.072	0.788
Perch	12.392	0.001*
Vegetation	0.614	0.434
Phase x perch	0.187	0.666
Phase x vegetation	5.308	0.022*
Vegetation x perch	0.001	0.991
Phase x perch x vegetation	2.347	0.127

Residues mean square = 0.266; degrees of freedom of residual = 184

Discussion

A mechanism to explain male preference for vegetated areas for territories should relate it to the oviposition site selection by females. In turn, females' choice could be affected by several factors including larval success (Buskirk & Sherman 1985), male harassment (Robertson 1985, Michiels & Dhondt 1990, McMillan 1991, Cordero *et al.* 1995) and oviposition resources (Alcock 1987, 1990). The importance of larval habitat to female oviposition selection must lie on the degree of vagility of the larval stage. If the larvae remain close to the oviposition site it must be expected that female selection affect strongly larval survival. However, it is common to observe a relative degree of larval dispersal within the complex aquatic environment where they live (Johannsson 1978).

P. mooma was associated with vegetated areas and is classified as a resource-control species. This species showed a characteristic behaviour of courtship before copula and the female always oviposit in the territory defended by the male (Johannsson 1978). Intermediary and later larval instars of *P. mooma* are bottom-dwellers and do not live on vegetation (De Marco *et al.* 1999). It is possible that the first instar of larval *P. mooma* gains protection against its predators in the macrophytes, explaining why female select vegetation sites to oviposit.

The large territories defended by individual male *O. discolor* - sometimes the entire pond as their closely related *O. ferruginea* (Harvey & Hubbard 1987) - could result from the poor discrimination of oviposition sites by the females, revealed by their behaviour at the pond. This species could be classified as female control mating mainly because the males grasp females almost immediately after they arrive in the territory, without courtship or any female choice (Conrad & Pritchard 1992). The necessary criteria suggested by Conrad and Pritchard (1992) for the female control mating systems are the impossibility of the male to control the female access to oviposition resource and the predictable co-occurrence of males and females in time and space. In their words "the encounters between individual males and females are likely to occur more-or-less at random and the oviposition sites are numerous and widely distributed within a limited area".

However, one characteristic of the *O. discolor* mating system differ from the Conrad-Pritchard model. They predicted that in female-control mating systems the intra-sexual competition favours individuals with traits that affect their mate-seeking ability, rather than the ability for direct contest. This argument arises because mate seeking is not localised around a defensible resource (Fincke 1987, Conrad & Pritchard 1990). Otherwise, *O. discolor* was very aggressive toward conspecifics and defended tall perches that could be important to control the females arriving in the pond. If points for female visualization could be defensible, it could become a mate-seeking resource for female-control insects. Intra-sexual competition between males for better perches could raise and the characteristics of their territorial defence would not be related to the female preferences. Therefore, we predict that strong intra-sexual selection may affect the ability for direct contest in female-control odonates that use perches as a mate-seeking resource.

The increase in use of the squares with vegetation by males of *O. discolor*, in the second phase of the experiment occurred due to the presence of *P. phoenicura*, that is more aggressive even toward other species. These species are similar in body size, but *P. phoenicura* was visibly dominant in the interactions. It is possible that males of *O. discolor* do not spent energy in interspecific fights because the resource defended (sites of visualization) is easily found. Despite, males of *O. discolor* are very aggressive intra-specifically, interespecific interactions are minimised perhaps because males that only interact with conspecific individuals might have a lower energetic cost and a possible reproductive advantage. So these characteristics appear to be a kind of evolutionary strategy stable.

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