ACTIVITY PATTERNS AND THERMOREGULATION
IN A TROPICAL DRAGONFLY ASSEMBLAGE

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Solar exposure is a key factor determining odonate activity, particularly in tropical areas. Small sized perchers, classified as thermal conformers, can begin their activity when air temperature is sufficiently high, and larger species become active when direct exposure to the sun is possible. In this study, the activity patterns in a neotropical dragonfly assemblage present on the Federal University of Viçosa, SE Brazil, have been described and following predictions about their thermoregulatory behaviour tested: (a) a decrease in activity of the percher dragonflies in the warmest periods is expected due to high thoracic temperatures; (b) conformers species will be controlled by temperature, not luminosity, whereas in heliothermic species, the initiation and termination of their activity is only constrained by luminosity. In the dry season, low air temperatures represent a limiting factor to the beginning and the end of activity, resulting in a shorter total activity time. *Orthemis discolor* and *Micrathyria hesperis* showed a decrease in activity in the middle of the day in the rainy season. *Perithemis mooma* was the only sp. that had a higher abundance near midday. As this sp. had a light-coloured thorax compared to the others, it is suggested that it could minimize the effect of the high temperatures. There is a clear effect of season on activity time, and also large differences in the intensity of this effect among species. When clouds precluded direct exposure to sun, variations only in the temperature did not affect the activity of *Erythrodiplax fusca*, *M. hesperis* and *O. discolor*, but the activity of the small sized *P. mooma* remained dependent on temperature. These results highlighted that the minimum body size to be a heliotherm could be a complex function of behavioural and morphological characteristics, including body colour, preferred substrate and perch posture.

INTRODUCTION

According to MAY (1976), the odonates could be classified into three groups with respect to their ability to deal with variations in ambient temperature: (a) thermal

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conformers; (b) heliotherms or (c) endotherms. It is mainly the relationship between heat exchange and body size that determine this classification.

The processes of heat exchange with the environment are convection heat exchange (CHE) and irradiation heat exchange (IHE). CHE is dependent on the surface to volume ratio, but IHE is only dependent on the surface area directly exposed to the sun. From small to large species, there is a decrease in the surface to volume ratio, with a consequent decrease in CHE, and an increase in the importance of IHE for thermoregulation.

Thermal conformers show high conductance and their body temperature varies with environmental temperature, mainly due to convection heat exchange. These species are expected to be of a small size. The heliotherms have a larger size and consequently lower conductance. Their activity must be primarily determined by solar irradiation. The endothermic species escape from the previous scenario by producing endogenous heat and controlling their haemolymph circulation to enable them to thermoregulate (HEINRICH & CASEY, 1978; MAY, 1991; HEINRICH, 1993). MAY (1976) showed that, in heliotherms, the conductance coefficient and thermoregulatory ability decrease with body size. This suggests that, even within the same physiological group, a relationship is expected between thermoregulation and body size.

Odonate species are often behaviourally classified as perchers and fliers (CORBET, 1962, 1999; MAY, 1976, 1991; DE MARCO, 1998). This behavioural classification is directly related to thermoregulation. Percher species are usually thermal conformers or heliotherms. Small sized perchers, classified as thermal conformers, can begin their activity when the air temperature is sufficiently high. Larger species can be active as soon as direct exposure to the sun occur. Otherwise, it is possible that at dawn only thermal conformers could maintain their activity with lower luminosity but with air temperature exceeding the minimum critical temperature for flight.

Very larger odonates may rely on endothermy for body temperature to exceed the minimum critical temperature for flight, since convection heating or irradiation heating will be a time-consuming process. Following this argument, the fliers, which are recognised as endotherms, must be the larger species.

Males of percher species spend most of their time in active territorial disputes that include fast flights and intense thoracic muscle activity, increasing the thoracic temperatures (MAY, 1977; MARDEN, 1989). Other flight activities such as guarding females and mating also could increase thoracic temperatures (ISHIZAWA, 1998). Thoracic temperatures in some odonates is elevated to as much as 40–45°C (POLCYN, 1994; MARDEN et al., 1996), near to the lethal temperature for some species: 48,5°C (MARDEN, 1995).

Due to the general relationship between convection heat exchange, irradiation heat exchange and body size, some general predictions were made concerning the activity of the percher odonate species in a given assemblage: (a) a decrease in activity of the percher dragonflies in the warmest moments was expected due to high thorax temperatures (HEINRICH & CASEY, 1978; MAY, 1979); (b) thermal conformers species, usually with small size, will be controlled by temperature, not luminosity,

whereas larger percher species, usually heliothermic, initiate and terminate their activity only as constrained by luminosity. Very large species are fliers and principally endothermic. In this study we aimed to describe the general activity patterns in a neotropical dragonfly assemblage and relate these data to the predictions about their thermoregulatory abilities.

METHODS

Dragonfly activity patterns were studied in two adjacent ponds on the Federal University of Viçosa, Viçosa, Minas Gerais, Brazil (20°45'S, 42°51'W). The climate of the region is wet sub-tropical, with the dry season from May to September. (GOLFARI, 1975). Mean annual rainfall is between 1500 and 2000 mm, with relative humidity about 80%, and the mean annual temperature ranged from 14.0°C to 26.1°C (VALVERDE, 1958).

Quantitative observations were made during August 1994 and on at least one day each month from February 1996 to January 1997. These observations began at 0600h and finished at 1800h. Every 15min a walk was made at a constant velocity past the two ponds and every individual was counted in one minute intervals. Air temperature, measured in shadow, and weather conditions were recorded during each walk. Data were grouped according to dry (March to September) and wet (October to February) season and also grouped in intervals of one hour during the day.

To test the predictions about the effects of luminosity on activity of these dragonflies the relationship between the presence of active individuals and temperature was investigated using data from the rainy season, and carrying out a separate analysis for sunny and cloudy samples. A Logistic Regression approach was used to analyse this dependency, using χ^2 to test for significant results according to HOSMER & LEMESHOW (1989). We called Activity Time the difference between the final time that the species was observed to be active to the initial time that it was active. For analyses that concerned body size, the hind wing length was measured for at least five males in each species.

GENERAL BEHAVIOURAL OBSERVATIONS

The most abundant percher dragonfly species found in the ponds were: *Perithemis mooma* Kirby, *Orthemis discolor* (Burm.), *Erythrodiplax fusca* (Ramb.), *E. media* Borror and *Micrathyria hesperis* Ris.

P. mooma is an amber-winged dragonfly that usually perched on emergent macrophytes and at low heights (10 to 20 cm). They were aggressive against conspecifics. *M. hesperis* is a clear-winged dragonfly that usually perched on emergent and floating vegetation (10 to 20 cm). This species was not very aggressive and were observed usually interacting with *P. mooma*. Both *E. media* and *E. fusca* usually perched on the marginal vegetation and on the soil around the lakes. When perched inside the lakes, they chose perches similar to *P. mooma* and *M. hesperis*. *O. discolor* selected perches often higher than 50 cm. They were very aggressive against conspecifics. A single male appeared to defend the whole pond and they rarely interacted with the other percher species.

ACTIVITY PATTERNS

In all species the females were rarely observed at the ponds. They usually appeared at 10:00 h, except for *O. discolor,* which had an additional peak density at 14:00 h in the rainy season (Fig. 1). In all species, females arrived at the pond and usually copulated for a few minutes. It is possible that some females stayed so briefly at the pond that they could not be detected during the observations but, with respect to thermoregulation, these events were of minor importance.
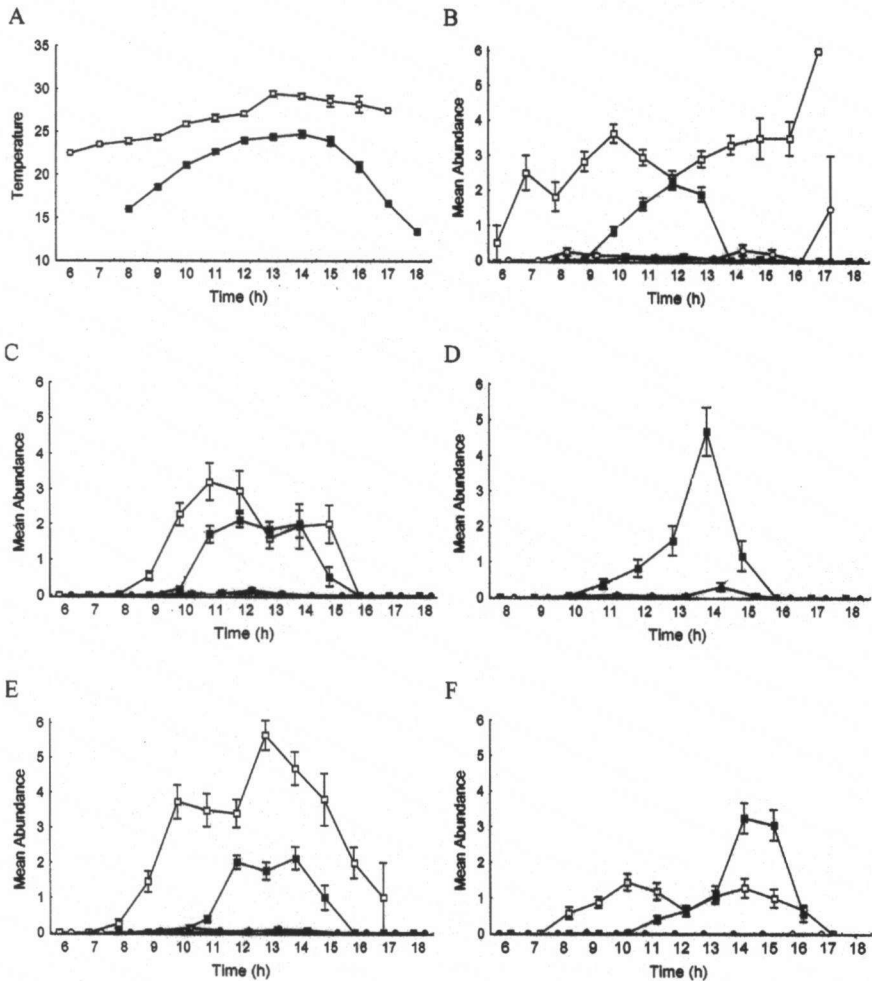

Fig. 1. Daily variation of air temperature (A); also male (squares) and female (circles) abundance of *O. discolor* (B), *E. fusca* (C), *E. media* (D), *P. mooma* (E), *M. hesperis* (F), in the rainy season (open symbols) and dry season (filled symbols) in two adjacent ponds in Viçosa, MG. Bars represent standard deviation.

Table I

Seasonal variation in total activity time and air temperatures in the initial (T_{in}) and final (T_{fi}) activity of dragonflies in a pond at Viçosa, MG

Species	Hind wing Size (mm)	Dry season			Wet season		
		T_{in} (°C)	T_{fi} (°C)	Activity time (h)	T_{in} (°C)	T_{fi} (°C)	Activity time (h)
P. mooma	20.6	26.5	22.0	5.00	24.0	27.5	8.75
M. hesperis	23.7	22.5	24.0	5.50	24.0	30.5	·8.75
E. media	25.0	20.0	26.0	5.50	—	—	—
E. fusca	25.7	18.0	28.0	5.25	25.0	31.0	7.50
O. discolor	40.5	18.0	22.0	5.75	22.5	27.5	10.25

In the dry season, males for all species showed an activity pattern restricted to a short period in the middle of the day (Fig. 1B-F). *O. discolor* and *E. fusca* were first observed, at about 10:00 h (Fig. 1B, C), while the other species were first observed somewhat later at 11:00 h. *O. discolor* was the first species to leave the pond (14:00 h) and *M. hesperis* only left the pond at 17:00 h (Fig. 1F).

O. discolor had their highest abundance at 12:00 h with a temperature near 23°C. *E. media* and *M. hesperis* (Fig. 1D, F) showed a peak in activity at 14:00 h at 24°C. *E. fusca* and *P. mooma* had their period of maximum activity extended from 10:30-14:00 h and from 11:30-14:00 h, respectively (Fig. 1C, E), i.e. they became active when the temperature was only 22°C.

In the rainy season, *O. discolor* showed the longest activity time with a bimodal pattern (highest peaks at 10:00 h and 17:00 h; Fig. 1B). At the peak of activity at 17:00 h, the number of females exceeded the number observed at 14:00 h and they were almost all ovipositing without male guarding. We called this 'happy hour' behaviour.

M. hesperis had a bimodal activity pattern during the rainy season but was unimodal during the dry season (Fig. 1F). *P. mooma* and *E. fusca* both showed unimodal patterns with peaks at 13:00 h and 11:00 h, respectively, during the rainy season. During this

Table II

Results of the logistic regression analysis for the presence of active individuals in cloudy and sunny samples in the rainy season in relation to temperature. Statistically significant ($P \leqslant 0,05$) results indicate dependency on temperature

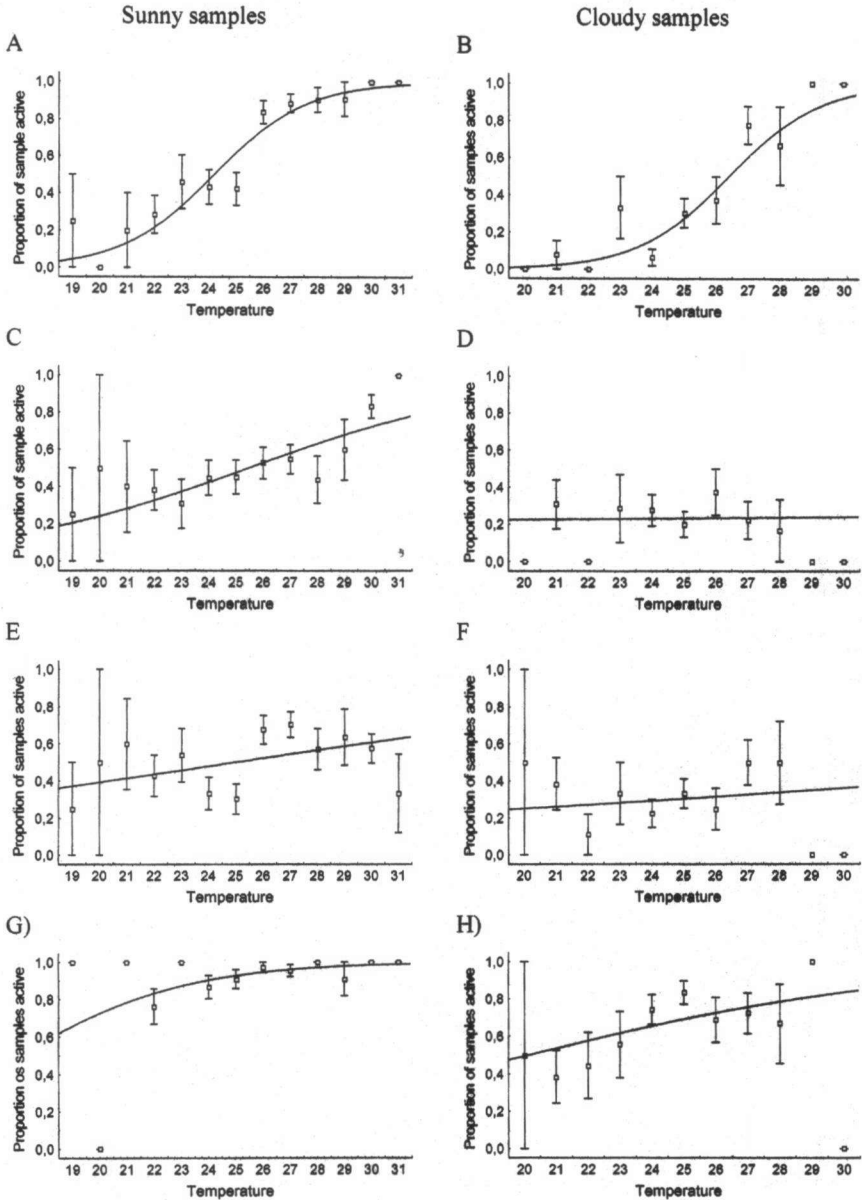| Species	Sunny samples			Cloudy samples		
	Proportion active	χ^2	P	Proportion active	χ^2	P
P. mooma	0,699	90,191	<0,001	0,308	39,190	<0,001
M. hesperis	0,534	19,384	<0,001	0,232	0,008	0,929
E. fusca	0,528	3,788	0,050	0,315	0,342	0,558
O. discolor	0,933	12,768	<0,001	0,678	3,350	0,060

Fig. 2. Logistic regression fit of the relation between proportion of samples in which a species is active and air temperature, from the rainy season in two adjacent ponds in Viçosa, MG. The species studied are *P. mooma* (A, B), *M. hesperis* (C, D), *E. fusca* (E, F) and *O. discolor* (G, H). The data were grouped on 'sunny' and 'cloudy' samples.

study only one *M. hesperis* female was observed. In the other species, the peak of female activity was coincident with the peak of male activity.

In the wet season all species showed an increase in activity time (Tab. I, Friedman non-parametric $\chi^2 = 4.000$; $P = 0.045$). This analysis excluded *E. media* that were only observed in the dry season of 1994. Large dragonflies initiated their activity at the pond at lower air temperatures in the dry season (Spearman rank correlation -0,975; $P = 0,005$). However, this pattern was not observed among all species in the wet season (Spearman rank correlation -0,318; $P = 0,683$), but the largest dragonfly *O. discolor* did initiate its activity at lower temperature than the others (Tab. I).

The proportion of samples that have a species active increased in sunny relative to cloudy periods of the day (Tab. II). All species showed a significant dependency on temperature in terms of their activity in the rainy season in sunny samples (Tab. II, Fig. 2A, 2C, 2E and 2G). *P. mooma* had the lowest values for activity at low temperatures (18-19°C), and it clearly gave the best fit to the logistic regression and also the highest slope values. When the clouds preclude exposure to the sun only the activity of *P. mooma* continues to be dependent on temperature (Fig. 2B). For other species, logistic regressions of activity on temperature were not significant (Fig. 2D, 2F and 2H). As *P. mooma* is the smallest species in this assemblage, it gave support to the prediction that larger species are more constrained by luminosity, and smaller species on the air temperature, to develop their normal activities at the lake.

DISCUSSION

In many aspects time is an important resource for life. The opportunity to mate is directly related to the duration that territories are held in many dragonfly ˙species (JACOBS, 1955; JOHNSON, 1964; ALCOCK, 1987; McVEY, 1988). The dragonfly percher species studied here have their activity time strongly determined by ambient temperatures that generate a clear seasonal pattern. In the dry season, low air temperatures represents a limiting factor to the beginning and the end of the activity of these species. If mating opportunities are directly related to time at the reproductive areas, a male that emerged in the dry season would have a strong fitness constraint in tropical areas where many species have multivoltine populations (PRITCHARD, 1996; DE MARCO et al., 1999; SALMAH et al., 1999)

MAY (1979) suggested that diurnal species could show a bimodal activity pattern due to the high temperatures in the middle of the day, a prediction that is supported by our data. In *O. discolor*, it is expected that the effect of high air temperatures was compounded by the increase in thorax temperatures due to intense territorial defense activity. This cumulative effect may have resulted in a decrease in activity at the pond at 12:00 h. It is not clear how to extend this to *M. hesperis*, which has far less aggressive males that spend a great proportion of their time perched (P. De Marco Jr, pers. obs.). In this species the decrease in activity is also much less evident, despite the fact that it was statistically significant.

A decrease in activity at the pond could be a result of the departure to forage on insects, and should be considered as an alternative explanation. Usually, dragonflies forage at field margins and succesional areas (DE MARCO, 1998), but some individuals were also observed foranging at the lake. It is possible that different sized dragonflies have distinct times for departure to forage due to differences in their insect prey activity time. Nevertheless, our observations suggests that most of these dragonfly species forage near dusk when the activity of mosquitoes (Culicidae) increase (NAYAR & SAUERMAN, 1971; GUIMARÃES et al., 1997). Unfortunately, a detailed account of movements from ponds to forage areas are not known from the literature and in this study.

Light-coloured individuals have less heat gain by solar exposure than dark ones (HENWOOD, 1975; HILFERT-RÜPPELL, 1998). *P. mooma* has an amber wing colour and a brighter thorax compared to the other species. These characteristics could diminish the heat absorbed by the body and allow it to remain for a longer period of time in the direct sun compared to the other small species. Another possibility, which could work in conjunctions with these characteristics, is their higher thermoregulatory capabilities due to body posture adjustments. Some postures, as the obelisk position (MAY, 1976, 1977; DE MARCO, 1998), may minimise heating and, qualitative observations suggest that *P. mooma* is more often observed in this postures than other similar sized species (including the *Erythrodiplax*).

A second prediction of this study is that small-size species could be constrained by temperature and suffer a time restriction between the dry and wet seasons. There is a clear effect of season on activity time, but there are also large differences in the intensity of this effect on the total activity time between species. *E. fusca* was the least affected, with a loss of 2.25 h of their activity time, while *O. discolor* had a loss of 4.5 h. More comparative data must be collected for a complete understanding of this phenomenon, but the current data suggest that larger species are more affected.

Some of the species in the current study were observed in the dry and wet seasons (*O. discolor*, *P. mooma*, *E. fusca*, *M. hesperis*). A male *O. discolor* that emerges at the beginning of the dry season has less time to find mates during its adult period (possibly between 30 to 60 days) than another male that emerges at the beginning of the wet season. If there exists a link between activity time and reproductive opportunities, strong selection on thermoregulatory capabilities that minimise the effect of the dry season would be expected. Possible adaptations are the increased efficiency to initiate activity at low air temperatures and activity time shifts (HILFERT-RÜPPELL, 1998).

It is also expected that larger species are more dependent on luminosity for their normal activities. On cloudy periods the temperature did not affect the activity of *E. fusca*, *M. hesperis* and *O. discolor*, but the activity of *P. mooma* remained dependent on temperature. Due to the differences in body size among these species it is in part an unexpected result, because heliothermic behaviour occurs in the medium sized *E. fusca* and *M. hesperis* and it was expected only in the large *O. discolor*. *P. mooma* behaviour continues to support the suggestions that small species should be thermal conformers.

Comparing *M. hesperis* to the slightly smaller *P. mooma*, the latter species had a light-coloured thorax that could be an advantage in the high exposure to sun at midday but preclude heat gain from direct exposure to sun when temperature is lower. These indicate that the minimum body size to be a heliotherm could be a complex function of other behavioural and morphological characteristics, including body colour, preferred substrate and perch posture.

The 'happy hour' behaviour of *O. discolor*, with many ovipositing unguarded females after 17:00 h, could be explained by two main hypotheses: (i) it could be a compensation for the decrease of reproductive activity around midday and (ii) females that copulate earlier escape from their mates and return to oviposit further without the disturbing effect of males. Disturbance by males is a factor that could affect female oviposition in a variety of dragonfly species (ROBERTSON, 1985; McMILLAN, 1991; CORDERO et al., 1995; HILFERT & RÜPPELL, 1997). PAULSON (1998) observed that the main adaptations to avoid severe harassment by males are "(i) male closely attends female, guarding her against other males...; (ii) male and female remain in tandem for the duration of egg-laying; (iii) female oviposits only at times when or in places where males are not present (a relatively uncommon strategy)". In *O. discolor* male non-contact guarding is observed while the female oviposits, but the shift of the activity time for ovipositing females could be more common than reported (see also HILFERT & RÜPPELL, 1997). Whatever the cause, these observations highlight the importance of following the activities of species thorough the day to obtain a more detailed description and understanding of their behaviour.

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