

**BEHAVIOURAL ECOLOGY OF *ERYTHEMIS PLEBEJA*
(BURMEISTER) AT A SMALL POND IN SOUTHEASTERN
BRAZIL (ANISOPTERA: LIBELLULIDAE)**

P. DE MARCO Jr¹, A.O. LATINI² and P.H.E. RIBEIRO³

¹Laboratório de Ecologia Quantitativa, Departamento de Biologia Geral, Universidade Federal de Viçosa, BR-36571-000 Viçosa, MG, Brazil; e-mail: pdemarco@ufv.br

²Graduate program in Ecology, Conservation and Wildlife Management, Federal University of Minas Gerais, Belo Horizonte, MG, Brazil; e-mail: aolatini@bol.com.br

³Graduate Program in Entomology, Federal University of Viçosa, Viçosa, MG, Brazil

Received May 15, 2001 / Revised and Accepted October 20, 2001

An analysis of the time-budget and a description of reproductive behaviour at a small pond in Viçosa, Minas Gerais, Brazil are presented. The observations support the classification of this sp. as a percher. It also conforms to the predictions of other studies that large perchers are usually more aggressive toward conspecifics. *E. plebeja* ♂♂ were usually observed simulating oviposition in the areas they previously defended, and evolutionary aspects of this behaviour are discussed.

INTRODUCTION

The evolutionary ecology of a species is often related to the adaptations that allow its persistence and success in its habitat. Two main components of the adaptation traits that ecologists frequently investigate are the morphology and behaviour (WOLF & WALTZ, 1993; WAINWRIGHT, 1994; McPEEK, 1997). Morphological traits have dominated the general adaptationist program (GOULD & LEWONTIN, 1979) since the sixties, because these traits are more reliably measured, and many theoreticians have produced testable models that instigate research (HUTCHINSON & MacARTHUR, 1959; MacARTHUR & LEVINS, 1964). Now is the time for behavioural ecology, mainly because many researchers have claimed that behavioural adaptations are more flexible and could be an important way to adapt to a changing environment (WAINWRIGHT, 1994; McPEEK, 1995).

Odonates are one of the best animal models for behavioural studies due to their size and to the complex reproductive behaviours that have been studied in the past years

(JACOBS, 1955; CAMPANELLA & WOLF, 1974; ALCOCK, 1987; MILLER, 1991; CONRAD & PRITCHARD, 1992). In general, odonate species are classified into fliers and perchers based on their thermoregulatory adaptations (CORBET, 1962; MAY, 1976). The flier species are also endothermic and can control their thoracic temperature by hovering and wing whirling, while percher species are exclusively exothermic but can minimise problems of high thoracic temperature by posture adjustment and activity time shifts (CORBET, 1999).

A general understanding of odonate behaviour and the ways that evolution has shaped the actual behavioural characteristics of this group could only be achieved by a careful comparative method (HARVEY & PAGEL, 1991). This approach needs the description of the most relevant aspects of the behaviour and general biology of the species in the group and a supported phylogenetic study. In spite of the intense study of odonates, there are only few phylogenetic trees at the species level (CHIPPINDALE et al., 1999; WESTMAN et al., 2000) and few genuine comparative studies (McPEEK, 1995).

Here we present the descriptive data on behaviour of a neotropical libellulid dragonfly, as part of a general program designed to allow for future comparative studies into the genus *Erythemis*. We describe the behaviour of male and female *E. plebeja* (Burm.) near a small pond in Viçosa, MG, southeastern Brazil, paying special attention to reproductive behaviour and trying to explain some uncommon behaviours we observed during this study.

METHODOLOGY

We studied a population of *Erythemis plebeja* at a small pond with a 70m perimeter, approximate 20 m², at the Federal University of Viçosa campus (20°45'S, 42°51'W), Viçosa, Brazil. The area is near an Atlantic Forest residual fragment, with a sub-tropical climate (Köppen CWA classification). The pond was covered by *Salvinia molesta* and *Nymphaea* spp. over approximately one third of its total area, and bordered by a strip of *Eleocharis* sp. It also had a dominant presence of the submersed macrophyte *Miriophyllum brasiliense*. The pond was inhabited by some possible dragonflies predators, in particular a dense population of *Rana catesbaeana* Shaw and black bass (*Micropterus salmoides*).

We observed the behaviour of this species in the dry season from 4 to 12 August 1994, with the aid of binoculars (7×35) or by eye, from 7:00 a.m. to 6:00 p.m. The total observation effort was 77 hours. Due to the small dimensions of the pond we were able to count the abundance of each species in an area up to 2 m around the pond every 15 min. We also recorded the air temperature. To improve the measurements we used individual marks on the wings using a non-toxic black paint.

For the analysis of the temporal budget of this species we used the focal observation method (ALTMANN, 1974). The sampling unit of these observations is the sequence of behaviours reported during 1 min of focal observation of an individual. The moment when each behaviour starts was noted, and the time spent in each activity calculated. It is similar to the method used by MAY (1977) but we reduced the time spent following a single individual, due to the frequent loss of the individuals during observation. Indeed, a shorter interval also had statistical advantages because it allowed a larger number of different individuals to be sampled in each occasion.

The behavioural activities were classified following DE MARCO (1998), viz.:

- (1) normal perching (NP);
- (2) droop-winged perching: the wing tips are held below the body and/or the wings shade the thorax (DWP);

- (3) obelisk perching: the wing tips are held below the body and the abdomen with an angle close to 90° to the substrate (OB).
- (4) transition flight: passing through an area without patrolling (TRAN);
- (5) foraging flight: fast short-distance flights returning to the perches and interpreted as foraging (FO);
- (6) territorial defence: chasing another individual (TD);
- (7) copula (CP);
- (8) oviposition (DS).

RESULTS

The activity of male *Erythemis plebeja* was restricted to a small period of time between 10:00 and 16:00 h, with peak abundance at 14:00 at the time of the highest air temperatures (Fig. 1). However, the presence of territorial males is not explained by temperature alone because temperatures compatible with their activity occur earlier in the morning (09:00–10:00 h), but there were few or no individuals at the pond. After the period of intense territorial and reproductive activities (14:00–15:00) the abundance at the pond decreased sharply.

This species was always observed perched on bare soil near the pond bank. The most common posture observed was the droop-wing perch (Fig. 2). This species flies nearly 11% of the total time, usually in transition flights between perch sites. We observed almost 15% of the total time spent in reproductive activities, with a concentration of activities between 12:00 and 14:30 h.

In 63% of the territorial disputes observed ($n = 27$) male *E. plebeja* engaged in intra-specific disputes, with 90% of wins by the resident male. In the inter-specific disputes, 14,8% were against *Tramea binotata* and 22,2% against *Erythrodiplax fusca*. *T. binotata* always won against *E. plebeja*, but the latter always won the disputes against *E. fusca*.

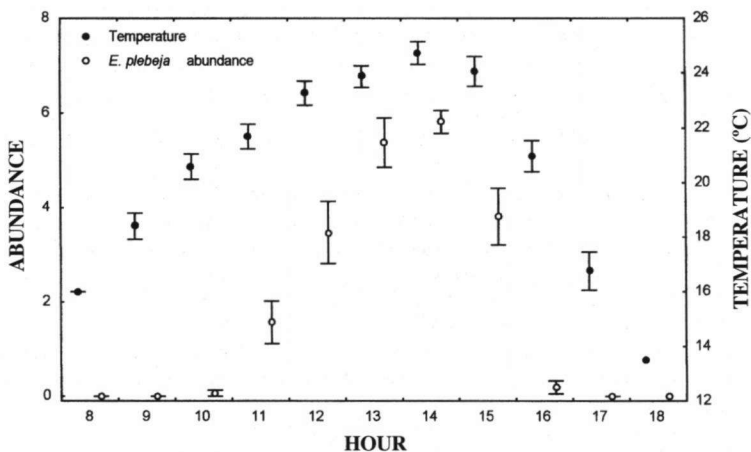


Fig. 1. Abundance of male *Erythemis plebeja* and air temperature at different times of the day at a small pond in Viçosa, MG, southeastern Brazil. — [Bars represent standard errors]

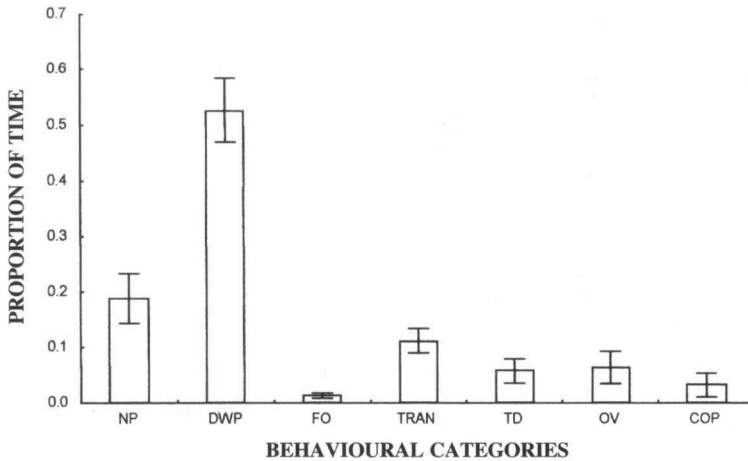


Fig. 2. Time-budget analysis for *Eritthemis plebeja* at a small pond in Viçosa, MG, southeastern Brazil. — [Bars represent standard errors; — NP = normal perching; — DWP = droop-winged perching; — FO = foraging; — TRAN = transition flight; — TD = territorial defence; — OV = oviposition; — COP = copula]

This dominance order reflects the differences in body size of these species. The territorial defences occurred mainly between 12:00 h and 14:00 h (Fig. 3), but were more dispersed during the day.

We followed long sequences of reproductive behaviours, including copula and oviposition six times during that season. Table I shows a complete enumeration of the largest sequence observed. The general sequence included: (a) the male found the female while she flew nearby; (b) they initiated the copula while in flight; (c) they perched in copula; (d) the male went to a region of the pond while the female stays at the pond bank or patrols near the male; (e) the male initiated a sequence that resembled the oviposition behaviour of the female ('simulated oviposition movement'); (f) the male went to the female and initiated oviposition in the region where the male was earlier.

In 50% ($n = 18$) of the cases, the male followed a female that entered its territory, accompanying it to the margin. They coupled, usually perched on the marginal vegetation or on the soil from 48 to 99 seconds. When disturbed, they sometimes flew away for a few seconds and perched again. After sperm transfer, the male flies to the oviposition site while the female remains perched. The male then "simulated" oviposition movements in the area, sometimes touching the water. After about 40 seconds the male returned to the female, touched it, and they flew together to the oviposition site where the female began oviposition. The male executed non-contact guarding movements around the female with rapid linear moves.

In the other oviposition events observed, the female was alone and they occurred when there are few individuals in the pond, mainly in the evening. The ovipositing

behaviour was very distinct from when the male was together with the female. She deposited eggs without a defined area, exploring with short pauses a large area of the pond.

We observed on one occasion that, while the male was doing its simulation of oviposition movements, a *Rana catesbeiana* individual attacked him but failed.

DISCUSSION

Erythemis plebeja presents a clear behavioural pattern which agrees to its classification as a percher species. P. De Marco Jr et al. (unpublished) discussed body-size variation and behavioural variations in neotropical percher species. The general pattern that emerged from this analysis was that larger perchers are usually more aggressive, with a larger proportion of their time budget spent in territorial defence activities. The data on *E. plebeja* support this claim. It is one of the larger perches in this pond and was generally observed involved in territorial contests.

One problem of such generalisation is that the behavioural environment could be a confounding factor for the determination of the degree of aggressiveness of a given species. In different communities, where they suffer competition from different species, their behaviour would be expected to change if the species choose optimal territorial defence strategies. There are only a few studies that describe the behavioural characteristics, especially their time budgets (DE MARCO, 1998). Of course, replicated studies of the same species in different behavioural environments are much rarer. These studies were generally neglected due to a relatively typological view of behaviour (e.g. percher vs flier) that hid the real evolutionary nature of this discipline.

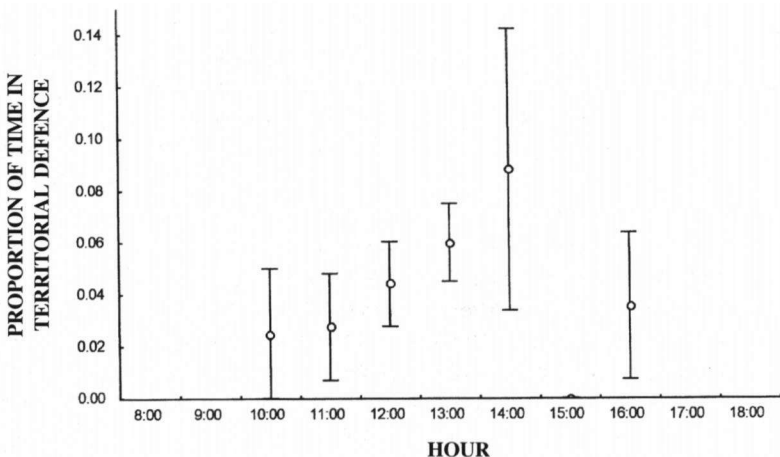


Fig. 3. Proportion of time spent in territorial defence by male *Erythemis plebeja* at different times of the day at a small pond in Viçosa, MG, southeastern Brazil. — [Bars represent standard errors]

Table I

Behavioural sequence of a male *Eritthemis plebeja* at small pond in Viçosa, MG, southeastern Brazil. The observation started at a 14:00 h with an air temperature of 26,0 °C

Posture observed on specimens	Seconds elapsed	Cumulative time
Starting observation: ♂ in oviposition procedure	10	10
♀ and ♂ in copulation flight	14	24
♀ and ♂ in copulation perched	54	78
♂ starts the "oviposition simulation posture" and the ♀ is perched	46	124
After the "oviposition simulation" of ♂ is finished, restarts the oviposition procedure with the ♂ patrolling at turn	10	134
♂ chases a <i>E. fusca</i> and wins, ♀ ovipositioning	2	136
♀ ovipositioning and ♂ patrolling at turn	59	195
♀ and ♂ in copulation flight	4	199
♂ perched and ♀ ovipositioning	11	210
♂ chases an <i>E. fusca</i> again and wins, ♀ ovipositioning	9	219
♂ perched and ♀ ovipositioning	74	293
♀ and ♂ in copulation flight	4	297
♀ and ♂ in copulation perched	67	364
♂ is patrolling and the ♀ is perched	14	378
♂ starts the "oviposition simulation" and the ♀ is perched	43	421
After the "oviposition simulation" is finished, the ♂ is perched near and like the ♀	21	442
♂ chases another <i>E. fusca</i> and wins, the ♀ restarts the oviposition procedure	2	444
♀ in oviposition procedure, with the ♂ patrolling at turn	39	483
A specimen of <i>Rana catesbeiana</i> invests over the ♂; the ♂ flight into the edge of trees and the ♀ is not observed near the pond	1	484

Actually, we have only general behavioural information from *E. peruviana* (P. De Marco et al., unpublished), *E. vesiculosa* (DE MARCO, 1998) and *E. simplicicollis* (McVEY, 1988). The first two of these studies produced a time-budget that could allow us to tentatively compare these species. *E. plebeja* is more similar to *E. peruviana*, that also spent nearly 10% of their time in territorial disputes. Both species appear very different from *E. vesiculosa*, that spends a large proportion of time in patrol activities. The latter comparison is subject to criticism because the data for *E. vesiculosa* came from a foraging area while the other species were observed near reproductive sites.

As a large libellulid, *E. plebeja* is also more efficient at thermoregulating in sunny sites at low air temperature, due to its capacity to heat by irradiation (MAY, 1979, 1991). Compared to other dragonfly species, we observed a much larger part of the day with territorial defence of sites, probably as a consequence of its thermoregulatory capabilities.

JACOBS (1955) reported male examination of oviposition sites before the female's proper oviposition in *Perithemis tenera*. He noted that predators, including frogs, sometimes kill males examining sites. As the pond during this study was inhabited by

a dense population of *Rana catesbeiana*, that were often observed attacking this species, this behaviour clearly increase the risk of males being predated. It is very difficult to propose an explanation for this apparent altruistic behaviour. We consider that this behaviour could only be evolved if the decrease in male fitness was accompanied by an increased survival of females and, consequently, their offspring. In all cases, the male first copulates and then initiates the exploration of the oviposition site. This behaviour probably secures its fitness, even if he is killed during the examination of the site. We do not observe this behaviour in the other species of the genera, and it clearly deserves further studies to understand the possible impact on male fitness and also its spread among odonates.

ACKNOWLEDGEMENT

This work is partly supported by FAPEMIG, CNPq and IPEMA.

REFERENCES

- ALCOCK, J., 1987. The effects of experimental manipulation of resources on the behavior of two calopterygid damselflies that exhibit resource-defense polygyny. *Can. J. Zool.* 65: 2475-2482.
- ALTMANN, J., 1974. Observational study of behavior: sampling methods. *Behaviour* 49: 227-267.
- CAMPANELLA, P.J. & L.L. WOLF, 1974. Temporal leks as a mating systems in a temperate zone dragonfly (Odonata: Anisoptera). I. *Plathemis lydia* (Drury). *Behaviour* 51: 49-87.
- CHIPPINDALE, P.T., V.K. DAVE, D.H. WHITMORE & J.V. ROBINSON, 1999. Phylogenetic relationships of North American damselflies of the genus *Ischnura* (Odonata: Zygoptera: Coenagrionidae) based on sequences of three mitochondrial genes. *Molec. Phylogenet. Evol.* 11: 110-121.
- CONRAD, K.F. & G. PRITCHARD, 1992. An ecological classification of odonate mating systems: the relative influence of natural, inter- and intra-sexual selection on males. *Biol. J. Linn. Soc.* 45: 255-269.
- CORBET, P.S., 1962. *A biology of dragonflies*. Witherby, London.
- CORBET, P.S., 1999. *Dragonflies: behavior and ecology of Odonata*. Comstock Publ. Assoc., Ithaca/NY.
- DE MARCO, P., 1998. The Amazonian Campina dragonfly assemblage: patterns in microhabitat use and behavior in a foraging habitat. *Odonatologica* 27: 239-248.
- GOULD, S.J. & R.C. LEWONTIN, 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. *Proc. R. Soc. Lond. (B)* 205: 581-598.
- HARVEY, P.H. & M.D. PAGEL, 1991. *The comparative method in evolutionary biology*. Oxford Univ. Press, Oxford.
- HUTCHINSON, G.E. & R.H. MacARTHUR, 1959. A theoretical ecological model of size distributions among species of animals. *Am. Nat.* 93: 117-125.
- JACOBS, M.E., 1955. Studies on territorialism and sexual selection in dragonflies. *Ecology* 36: 566-586.
- MacARTHUR, R. & R. LEVINS, 1964. Competition, habitat selection and character displacement in a patchy environment. *Proc. natn. Acad. Sci. USA* 51: 1207-1210.
- MAY, M.L., 1976. Thermoregulation in adaptation to temperature in dragonflies (Odonata: Anisoptera). *Ecol. Monogr.* 46: 1-32.
- MAY, M.L., 1977. Thermoregulation and reproductive activity in tropical dragonflies of the genus *Micrathyria*. *Ecology* 58: 787-798.
- MAY, M.L., 1979. Insect thermoregulation. *Annu. Rev. Ent.* 24: 313-349.

- MAY, M.L., 1991. Thermal adaptations of dragonflies, revisited. *Adv. Odonatol.* 5: 71-88.
- McPEEK, M.A., 1995. Morphological evolution mediated by behavior in the damselflies of two communities. *Evolution* 49: 749-769.
- McPEEK, M.A., 1997. Measuring phenotypic selection on an adaptation: lamellae of damselflies experiencing dragonfly predation. *Evolution* 51: 459-466.
- McVEY, M.E., 1988. The opportunity for sexual selection in a territorial dragonfly, *Erythemis simplicicollis*. In: T.H. Clutton-Brock, [Ed.], *Reproductive success*, pp. 44-58, Univ. Chicago Press, Chicago-London.
- MILLER, P.L., 1991. Pre-tandem and in-tandem courtship in Libellulidae (Anisoptera). *Adv. Odonatol.* 5: 89-101.
- WAINWRIGHT, P.C., 1994. Functional morphology as a tool in ecological research. In: P.C. Wainwright & S.M. Reilly, [Eds], *Ecological morphology: integrative organismal biology*, pp. 42-59, Univ. Chicago Press, Chicago-London.
- WESTMAN, A., F. JOHANSSON & A.N. NILSSON, 2000. The phylogeny of the genus *Leucorrhinia* and the evolution of larval spines (Anisoptera: Libellulidae). *Odonatologica* 29: 129-136.
- WOLF, L.L. & E.C. WALTZ, 1993. Alternative mating tactics in male white-faced dragonflies: experimental evidence for a behavioural assessment ESS. *Anim. Behav.* 46: 325-334.