

SHORT COMMUNICATIONS

**THE AMAZONIAN CAMPINA DRAGONFLY ASSEMBLAGE:
PATTERNS IN MICROHABITAT USE AND BEHAVIOUR
IN A FORAGING HABITAT (ANISOPTERA)**

P. DE MARCO

Departimento de Biologia Geral, Universidade Federal de Viçosa,
BR-36571-000 Viçosa, Minas Gerais, Brazil
e-mail: pdemarco@mail.ufv.br

Received March 18, 1997 / Revised and Accepted October 4, 1997

The Amazonian Campina is a woodland, with emergent trees of about 10 m, found in patches in the Amazonian rain forest. It usually has open areas with a white sand soil directly exposed to sun, and shaded areas with a more dense vegetation. I sampled the dragonfly assemblage in this system counting every dragonfly at pre-determined points, at 5 min intervals, between 7:00 and 18:00 h. *Erythrodiplax lativittata*, *Miathyria marcella* and *Erythemis vesiculosa* were the most abundant spp. The frequency data by point revealed an association of *E. lativittata* (percher) with shaded habitats, and *M. marcella* and *E. vesiculosa* (fliers) with open habitats. The characteristics of thermoregulation of fliers and perchers seem to explain this microhabitat selection. Due to high productivity and density of small insects, the Campina is probably an excellent habitat for foraging. It is suggested that in these foraging habitats the spatial species arrangement is mostly determined by behavioural-physiological traits, which may help to explain the community faunal composition.

INTRODUCTION

Behaviour is an important component of fitness (SCHALL & PIANKA, 1980; WCISLO, 1989; ALCOCK, 1994) and can also influence the species distribution. Sexual behaviour (e.g. ALCOCK, 1982, 1987a, 1987b; PARR, 1983) and thermoregulatory behaviour (MAY, 1977, 1980) have been intensively studied in odonates. Based on thermoregulatory behaviour, CORBET (1962) classified odonate species into fliers, that stay on the wing a large proportion of the activity time, and perchers, that remain perched on many kinds of substrata. Percher males are commonly found defending territories near water bodies while females are away foraging and go to water only to mate and oviposit (CORBET, 1962).

Many recent works suggest that fliers are endothermic and can warm their bodies by wing muscle activity and cool by thorax-abdomen heat exchange and wing whirling (HEINRICH & CASEY, 1978; MAY, 1991, 1995). Otherwise, the ectothermic perchers, can control body temperature by posture adjustments, microhabitat selection and activity time shifts (MAY, 1979).

Adult odonate assemblages are poorly known, although several behavioural or community studies had been performed near aquatic habitats (e.g. MOORE, 1964; ALCOCK, 1987a; JOHNSON & CROWLEY, 1989; POLCYN, 1994). In these habitats, competition between species for territory patches and a direct competition between males for females are readily acknowledged. Otherwise, far away from the water, where odonate species are commonly observed foraging, there is no study to my knowledge at the community level.

In the foraging habitats, the differences in thermoregulatory mechanisms between fliers and perchers should determine the use of different microhabitats. If so, the spatial arrangement of these species will be mainly determined by their behavioural-physiological characteristics. As a consequence, if resource competition is important between adult dragonflies in foraging habitats, it must be higher between species belonging to the same behavioural group.

The Amazonian Campina is a forest vegetation found in patches inside the full-grown tropical rain forest in Brazil (ANDERSON et al., 1975; SANTOS & RIBEIRO, 1975). It has one stratum with canopy at about 7-10 m and a white sand soil. This interruption of the forest canopy creates an excellent opportunity to study the assemblage of forest-dwelling odonates. Many species observed there are also present in the canopy where ecological and behavioural studies are not easy to perform. In these areas the temperature can rise to 38° C (RIBEIRO & SANTOS, 1975) and possibly represent a threat to dragonfly activity.

In this paper, I searched for patterns in the odonate assemblage of the Amazonian Campina testing for the relation between behaviour and the microhabitat preferences. From this standing point, I also discuss how behavioural differences affect community organization in foraging habitats.

METHODS

The study area was the Suframa-INPA reserve at the Manaus Caracará road km 62. this area was studied by ANDERSON et al. (1975) who classified the vegetational type as open Campina, shaded Campina, and Campinarana. The open Campina has a low shrub vegetation (up to 2 m) and a sparse cover of trees, mainly *Sandemania hoehnei* (Cogn.) Wurdack (Melastomataceae) up to 5 m. There are large areas of white sand dominated by *Cladonia* lichens. The shaded Campina are clusters of trees, mainly *Aldina heterophylla* Spr. (Leguminosae) and *Glycoxylon inophyllum* (Mart.) Ducke (Sapotaceae), with a cover of litter on the sand floor. The trees have heights up to 10 m. The Campinarana has trees often higher than 10 m, is denser than the shaded Campina but with similar species composition.

All observations reported here were made in the shaded and open Campina and in the boundary between shaded Campina and Campinarana. A point-sample method was designed to determine the spatial variation in odonate species relative abundance and behaviour. I established points and counted

every dragonfly with a distance of 5 m from the observer, at 5 min intervals on 5 days. All observations were between 7:00 and 12:00 and between 14:00 and 18:00 sunlight in August 1993. There were a total of 36 hours of field observations, discounted the moments of heavy rains and movement from outside of the study area to capture individuals for species determinations. At each point I recorded each species, its abundance, the behaviour of each individual, and estimate height by comparison with a measured object near the observed dragonfly or dragonfly group. Some individuals were collected and I measured the distance from the base to the tip of the right anterior wing. In the study area I sampled a total of 57 points, 39 in open and 18 in shaded Campina. The points were scattered with no clear pattern in the area. I moved among the points in a systematic manner to distribute the sampling effort to each point equally at all times of the day.

I classified the species as fliers or perchers according to CORBET (1962). The behaviour was classified as follows:

- (1) normal perching;
- (2) droop-winged perching: the wing-tips are held below the body and/or the wings shade the thorax;
- (3) patrolling: flying back and forth through an area;
- (4) transition flight: passing through an area without patrolling;
- (5) agonistic interaction: chasing another individual.

RESULTS

I observed 16 odonate species (15 Libellulidae and 1 Corduliidae) in the Campina, with 14 in open and 9 in shaded microhabitats (Tab. I). *Erythrodiplax lativittata*, *Erythemis vesiculosa* and *Miathyria marcella* dominated both assemblages. I could not capture all observed individuals of *Zenithoptera*. As at least three species occur

Table I

Mean Anisoptera abundance in open and shaded Campina (standard deviations in brackets). – [The behavioural classification is according to CORBET (1962): F-fliers, – P-perchers]

Species	Behavioural classification	Open Campina	Shaded Campina
<i>Erythrodiplax lativittata</i> Borrer	P	0.259 (0.239)	0.557 (0.209)
<i>Erythemis vesiculosa</i> (Fabr.)	F	0.274 (0.268)	0.060 (0.104)
<i>Miathyria marcella</i> (Sel.)	F	0.223 (0.281)	0.088 (0.204)
<i>Tramea calverti</i> Muttkowski	F	0.033 (0.086)	0.012 (0.053)
<i>Idiataphe</i> sp.	P	0.031 (0.076)	0.000 (-)
<i>Brachymesia herbida</i> (Gundlach)	F	0.014 (0.049)	0.016 (0.068)
<i>Erythrodiplax umbrata</i> (L.)	P	0.009 (0.030)	0.019 (0.054)
<i>Erythemis haematogastra</i> (Burm.)	P	0.000 (0.000)	0.023 (0.072)
<i>Zenithoptera</i> spp.	P	0.015 (0.055)	0.000 (-)
<i>Tauriphila</i> sp.	F	0.000 (0.000)	0.012 (0.053)
<i>Micrathyria</i> sp.	P	0.008 (0.033)	0.000 (-)
<i>Aeschnosoma auripennis</i> Geijskes	F	0.007 (0.046)	0.000 (-)
<i>Miathyria simplex</i> (Ramb.)	F	0.006 (0.025)	0.000 (-)
<i>Erythrodiplax</i> sp.	P	0.002 (0.010)	0.004 (0.019)
<i>Pantala flavescens</i> (Fabr.)	F	0.005 (0.021)	0.000 (-)
Unidentified Libellulidae	?	0.004 (0.025)	0.000 (-)

in Manaus (*Z. americana*, *Z. anceps*, *Z. lanei*). Since I was unable to distinguish between them during observational sampling, I treated the observed individuals as *Zenithoptera* spp.

Sex ratio estimated from captured individuals was biased toward females for *E. lativittata* ($\delta/\text{♀}=0.047$; $n=89$) and *E. umbrata* (only ♀ captured; $n=7$). I observed both androchromatic and normal females and gynochromatic and normal males of *E. lativittata*.

Aeschnosoma auripennis (Corduliidae) appeared only once in the open Campina during sampling, but I captured two individuals in the boundary between shaded Campina and Campinarana. These individuals flew at 2-3 m in patrolling activities, suggesting a flier behaviour.

The proportion of fliers and perchers was not different between open and shaded habitats (Fisher exact test, $p=1.000$) with 54.5% (95% confidence interval assuming binomial distribution: 28.1 to 77.0%) of flier species and 45.5% (20.7 to 69.4% of percher species).

The smallest species was *Z. americana* (21.6 mm front wing) and the largest, was *Tramea calverti* (45.6 mm). The four largest species were fliers but there was no clear size discrimination between fliers and perchers; the small *M. simplex* and *M. marcella* are fliers and the medium sized *E. haematogastra* is a percher (Fig. 1).

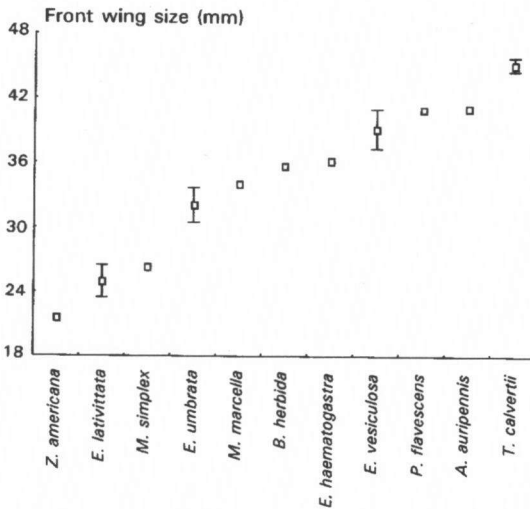


Fig. 1. Mean front wing size in the Anisoptera captured in Amazonian Campina (bars show standard deviations). The value for *Z. americana* is from a single individual captured near the Campina. *M. simplex* and *B. herbida* also represent individuals captured outside the study area. *Idiataphe* sp., *Tauriphila* sp., *Micrathyria* sp. and an unidentified Libellulidae were not measured.

To compare the patterns of habitat use I tested dragonfly frequency at points in open and shaded Campina only when I observed a species at least ten times. Three species showed a significant association with open sites: *M. marcella* (in 64.1% of the open sites and 27.8% of the shaded sites; $\chi^2=6.518$, $P=0.011$), *E. vesiculosa* (in 69.2% of the open sites and 27.8% in shaded sites; $\chi^2=8.595$, $P<0.001$) and *Idiataphe* sp. (in 20.5% of the open sites and absent in shaded sites; Fisher exact test, $p=0.046$). *T. calverti* was found in 20.5% of the open sites, to 5.6% of the shaded areas but this difference was not statistically significant

($\chi^2=2.072$, $P=0.150$). Only *E. lativittata* showed a significant association with shaded areas (100% in shaded and 79.6% in open Campina; Fisher exact test, $P<0.001$).

Based on flight or perch height, there is a clear distinction between *Erythrodiplax* species (*E. lativittata* and *E. umbrata*), usually perched at about 1 m, and the other species (Fig. 2). *Idiataphe* sp. perched mainly at 5 m and was observed foraging making short vertical flights in open Campina. *T. calverti*, *M. marcella* and *E. vesiculosa* flew at about 3.5-4.5 m (Fig. 2).

Of the species recorded at least 6 times *E. lativittata*, *E. umbrata*, *Idiataphe* sp. and *Zenithoptera* spp. remain perched for the great majority of the time; *E. vesiculosa*, *M. marcella* and *T. calverti* patrolled more than they perched (Tab. II). Chasing was observed for the three most abundant species (*E. lativittata*, *E. vesiculosa* and *M. marcella*) and for *Micrathyria* sp. No behaviour that could be considered related to reproductive activities was observed.

I observed *M. marcella* and *T. calverti* in swarms of up to 10 individuals on two occasions. I also observed groups with *M. simplex*, *M. marcella* and *T. calverti*.

In many moments of the day some species take a perch posture described here as droop-winged perching, when wings are at an obtuse angle to the body line. I observed this behaviour in many species, but the Trameinae *Idiataphe* sp. and *T. calverti*, and also *E. umbrata*, do not seem to take this posture under the temperature profiles of Campina (Tab. II).

DISCUSSION

There is a clear partition between flier species using open habitats and percher species in the shaded areas. Air temperature in open Campina can rise to 38°C (RIBEIRO & SANTOS, 1975) and the thermoregulation is very important to increase net energy supply. MAY (1991) suggested that thermal adaptations might be reflected in the composition of entire faunas and hypothesized that in the warm and relatively equable tropics the Zygoptera and percher Anisoptera might be at a relative advantage. I found 7 perchers and 8 fliers in the whole assemblage. The

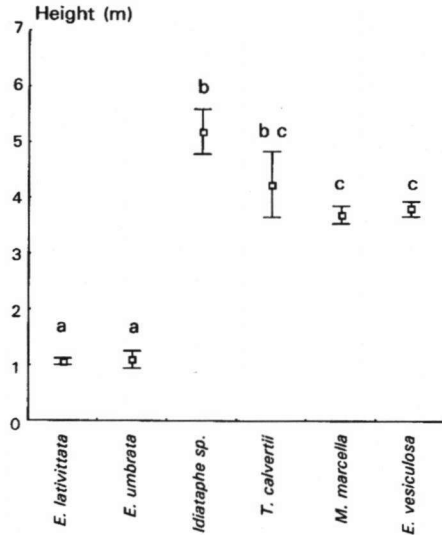


Fig. 2. Mean Anisoptera perch or flight height in Amazonian Campina (bars show standard deviations). Species with same letters were not statistically different at $p=0.05$ in a posteriori Tukey MSD test.

Table II

Frequency of behavioural categories (percents in brackets). At each point the behaviour of every dragonfly within 5m of the observer was recorded during 5 min period. – [Total sample represent 36 hours of field observations, n=576]

Species	Perch			Flight			Total
	Normal	Droop-winged	Patrolling	Chasing	Transition		
<i>Erythrodiplax lativittata</i>	126 (84.0)	10 (6.7)	2 (1.3)	6 (4.0)	6 (4.0)	150	
<i>Erythemis vesiculosa</i>	4 (4.0)	3 (3.0)	76 (75.2)	1 (1.0)	17 (16.8)	101	
<i>Miathyria marcella</i>	3 (4.9)	1 (1.6)	56 (91.8)	1 (1.6)	0 (0.0)	61	
<i>Idiataphe</i> sp.	12 (85.7)	0 (0.0)	0 (0.0)	0 (0.0)	2 (14.3)	14	
<i>Tramea calverti</i>	3 (25.0)	0 (0.0)	8 (66.7)	0 (0.0)	1 (8.3)	12	
<i>Zenithoptera</i> spp.	6 (75.0)	2 (25.0)	0 (0.0)	0 (0.0)	0 (0.0)	8	
<i>Erythrodiplax umbrata</i>	7 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	7	
<i>Brachymesia herbida</i>	0 (0.0)	0 (0.0)	5 (83.3)	0 (0.0)	1 (16.7)	6	
<i>Micrathyria</i> sp.	2 (50.0)	0 (0.0)	1 (25.0)	1 (25.0)	0 (0.0)	4	
<i>Pantala flavescens</i>	2 (66.7)	0 (0.0)	0 (0.0)	0 (0.0)	1 (33.3)	3	
<i>Miathyria simplex</i>	3 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	3	
<i>Erythrodiplax</i> sp.	2 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	2	
<i>Erythemis haematogastra</i>	2 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	2	
<i>Aeschnosoma auripennis</i>	0 (0.0)	0 (0.0)	0 (0.0)	0 (0.0)	1 (100.0)	1	
<i>Tauriphila</i> sp.	0 (0.0)	0 (0.0)	1 (100.0)	0 (0.0)	0 (0.0)	1	
Unidentified Libellulidae	0 (0.0)	1 (100.0)	0 (0.0)	0 (0.0)	0 (0.0)	1	

most abundant species in this habitat was the percher *E. lativittata*, but the other three species that followed it in abundance were fliers. It seems that even if they suffer a relative disadvantage, fliers can cope with these problems and efficiently use the Campina habitat.

POLCYN (1994), studying another extreme habitat with respect to air temperatures, the Mojave desert, did not observe any difference in activity periods or thermoregulation abilities between fliers and perchers. Possibly both fliers and perchers face potential problems at higher air temperatures that constrain their activity (POLCYN, 1994). Due to the observed microhabitat selection, fliers foraged under higher air temperatures than the perchers in Campina. Although I did not regularly measure the temperatures, some observations during normal activities of dragonflies in open Campina show values ranging from 25-35°C. Polcyn's study was done in a breeding pool where only reproductive activities were observed while my observations only refer to foraging activities. Further studies are needed to understand how different activities influence thermal adaptation in dragonflies.

It is expected that percher species that inhabit shaded tropical forests will come to the tree tops for basking (e.g. CLAUSNITZER, 1996). This was not the case for the species that preferred the shaded Campina. Due to the particular structure of this habitat, it is possible that the air temperature here is near the optima for the activity for these species and sun basking is not needed.

I did not observe dragonflies in the obelisk position, which is common when the temperature is high (MAY, 1977; WILDERMUTH, 1991), presumably because the percher species I observed were generally not directly exposed to sun. *Idiataphe* sp. was the only percher species exposed for long periods to sun because it used 5 m trees in open areas. This species differs from the other Trameinae that are fliers, and from the perchers that usually used lower strata. It is possible that the percher behaviour in this species is a derived trait and physiological characteristics shared with other Trameinae lead to an intermediary status with high success.

B. herbida was classified as a flier in this study despite a percher behaviour in the reproductive habitats (pers. observ.). In the foraging habitat here studied I never observed it perched. In the same way, this species can use urban areas (as it is common to *P. flavescens*) and I observed many individuals foraging inside the city of Santarém, Pará, Brazil, usually exhibiting a patrolling behaviour. Further studies are needed to establish to what extent its behavioural classification is a function of the habitat under consideration.

Which factors determine the species composition in a dragonfly assemblage? Dragonflies are generalist predators as adults and larvae and resource preferences do not seem to be an important factor determining species composition. However, in the larval stage, substrata preferences (including macrophyte association: WELLBORN & ROBINSON, 1987; LOUNIBOS et al., 1990), predation by other dragonflies (BENKE et al., 1982; ROBINSON & WELLBORN, 1987; WISSINGER, 1989) and fish predation (MORIN, 1984a, 1984b) may determine if a species is present or not in a given assemblage.

Here, I discuss whether adult behaviour is also important in determining species composition using the patterns shown in the Amazonian Campina.

This dragonfly assemblage was composed mainly of open-habitat long-distant dispersers such as *E. vesiculosa*, *M. marcella*, *B. herbida*, *P. flavescens*. These species have wide distribution in the Neotropical region or are pantropical (DAVIES & TOBIN, 1985). They are observed in plantations, roads and open habitats near the study area, and their abundances are high in the Campina. *T. calverti* is the most widespread species from the 'cophysa-group' of *Tramea*, ranging from southern United States to Rio de Janeiro, Brazil. It is considered a migratory species in Central America and Venezuela (DE MARMELS & RACENIS, 1982).

It has long been considered that species with wide distributions also have large mean abundances (e.g. DARWIN, 1859). BROWN (1984) suggested that species with broad niches will be widespread and abundant. The species of fliers found seem to be abundant and widespread but they are dependent on the existence of open habitats. These species forage in open Campina but are less frequent in shaded Campina where they use the emergent trees with direct exposure to sun. Open habitats like grasslands, successional patches or forest edges may also be important habitats for these flier species. They can be viewed not as habitat generalists, to conform to Brown's theory, but foragers that use a widespread habitat. In these

systems it is common to observe fliers such as Trameinae species in foraging swarms like those observed among *M. marcella*, *M. simplex* and *T. calverti* in Campina. On the other hand, *E. lativittata* was the most abundant species in Campina and was not observed in other nearby habitats. Females of this percher species, and also *E. umbrata*, have a cryptic and somewhat disruptive coloration in shaded habitats. Both species were commonly observed on shrubs at about 1 m in shaded Campina but *E. lativittata* was more of a habitat specialist having a close association with shaded areas. Its coloration and behaviour seems to lead to a higher success in these habitats.

Usually odonate females spend most of their time in foraging habitats (CORBET, 1957; ANHOLT, 1992). The excess of females of *E. lativittata* and *E. umbrata* suggest that the shaded habitat is used for foraging by females and possibly by recently emerged males that stay there before they search for a breeding territory near water bodies. The gynochromatic coloration in recently emerged males would increase the success of these individuals here as suggested by CORBET (1962).

Foraging habitats are usually neglected in community and population studies of dragonflies, in spite of their obvious importance in persistence and composition of communities. In theory, a female that uses a highly productive habitat will produce more eggs, mature faster and visit the reproductive habitat more frequently. In the same way, it is assumed that after emergence many dragonfly males go to foraging habitats for a few days (CORBET, 1957, 1980). A more productive habitat should increase the rate of male weight gain and then increase their ability to maintain a territory or go more quickly to the reproductive habitats. With higher solar incidence, the Campina could be more productive, maintain a rich shrub flora attractive to insects, and then an excellent foraging habitat for these dragonflies.

The argument above suggests that natural selection on adult dragonflies will favor better foraging habitat selection and mechanisms that increase efficiency in these habitats. The coloration of the *Erythrodiplax* females from Campina suggests that predation could be an important selective factor in these foraging habitats. But, in a more general view, behavioural adaptations associated with microhabitat selection are the more impressive characteristic of this assemblage.

PIMM (1991) writes: "A community is considered to have structure or to be patterned if the species it contains are a nonrandom subset of those that could occur in it". Ecological communities are commonly viewed as a set of "compatible" species sampled from a species pool by their competitive abilities (DIAMOND, 1975; CASE, 1990; DRAKE, 1990) or a set of species that co-occur by their nested spatial distribution determined by the tolerances and efficiency to a given abiotic gradient (GLEASON, 1926; ANDREWARTHA & BIRCH, 1954). The 'sampling' process that produced the Amazonian Campina dragonfly assemblage seems to be conveniently described by behavioural-physiological characteristics that are associated with microhabitat preferences. In this generalist predator assemblage one might expect that resource-partitioning should be achieved by spatial organization

due to territorial disputes or microhabitat selection. Disputes for foraging space were a rare event among the fliers (*E. vesiculosa* and *M. marcella*) and the percher *E. lativittata*. These observations suggest that this assemblage of foraging organisms should be considered a non-interactive system without resource monopolization or strong competitive interactions.

ACKNOWLEDGEMENTS

This work was done during the first course of the "Ecology of Amazonian Forest" organized by Universidade Estadual de Campinas (UNICAMP), Instituto de Pesquisas da Amazonia (INPA-MANAUS), Organization for Tropical Studies (OTS) and the Smithsonian Institute. I am grateful to WOODY BENSON and BRUCE WILLIAMSON, who encouraged me to develop this work. I am also greatly indebted to A.B.M. MACHADO, J.H. SCHOEREDER, E.F. MORATO and M.A. MELO, who read an early draft of the manuscript.

REFERENCES

- ALCOCK, J., 1982. Post-copulatory guarding by males of the damselfly *Hetaerina vulnerata* Selys (Odonata: Calopterygidae). *Anim. Behav.* 30: 99-107.
- ALCOCK, J., 1987a. The effects of experimental manipulation of resources on the behavior of two calopterygid damselflies that exhibit resource-defence polygyny. *Can. J. Zool.* 65: 2475-2482.
- ALCOCK, J., 1987b. Male reproductive tactics in the libellulid dragonfly *Paltothemis lineatipes*: temporal partitioning of territories. *Behaviour* 103: 157-173.
- ALCOCK, J., 1994. Postinsemination associations between males and females in insects: the mate-guarding hypothesis. *Annu. Rev. Ent.* 39: 1-21.
- ANDERSON, A.B., G.T. PRANCE & B.W.P. ALBUQUERQUE, 1975. Estudos sobre a vegetação das Campinas Amazônicas: 3. A vegetação lehosa da Campina da Reserva Biológica INPA-SUFRAMA (Manaus - Caracaraí, km 62). *Acta amazôn.* 5: 225-246.
- ANDREWARTHA, H.G. & L.C. BIRCH, 1954. *The distribution and abundance of animals*. Univ. Chicago Press, Chicago.
- ANHOLT, B.R., 1992. Sex and habitat differences in feeding by an adult damselfly. *Oikos* 65: 428-432.
- BENKE, A.C., P.H. CROWLEY & D.M. JOHNSON, 1982. Interactions among coexisting larval Odonata: an in situ experiment using small enclosures. *Hydrobiologia* 94: 121-130.
- BROWN, J.H., 1984. On the relationship between abundance and distribution of species. *Am. Nat.* 124: 255-279.
- CASE, T.J., 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proc. natn. Acad. Sci.* 87: 9610-9614.
- CLAUSNITZER, V., 1996. Territoriality in *Notiothemis robertsi* Fraser (Anisoptera: Libellulidae). *Odonatologica* 25: 335-345.
- CORBET, P.S., 1957. The life-history of the emperor dragonfly *Anax imperator* Leach (Odonata: Aeshnidae). *J. Anim. Ecol.* 26: 1-69.
- CORBET, P.S., 1962. *A biology of dragonflies*. Witherby, London.
- CORBET, P.S., 1980. Biology of Odonata. *Annu. Rev. Ent.* 25: 189-217.
- DARWIN, C.R., 1859. *On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life*. Murray, London.
- DAVIES, D.A.L. & P. TOBIN, 1985. The dragonflies of the world: a systematic list of the extant species of Odonata. Anisoptera. *Soc. int. odonatol. rapid Comm.* (Suppl.) 5: 1-151.

- DE MARMELS, J. & J. RACENIS, 1982. An analysis of the cophysa-group of Tramea Hagen, with descriptions of two new species (Anisoptera: Libellulidae). *Odonatologica* 11: 109-128.
- DIAMOND, J.M., 1975. Assembly of species communities. In: M.L. Cody & J.M. Diamond, [Eds], *Ecology and evolution in communities*, pp. 342-444, Harvard Univ. Press, Cambridge/MA.
- DRAKE, J.A., 1990. Communities as assembled structures: Do rules govern pattern? *Trends Ecol. Evol.* 5: 159-164.
- GLEASON, H.A., 1926. The individualistic concept of the plant association. *Bull. Torrey bot. Club* 53: 7-26.
- HEINRICH, B. & T.M. CASEY, 1978. Heat transfer in dragonflies: 'fliers' and 'perchers'. *J. exp. Biol.* 74: 17-36.
- JOHNSON, D.M. & P.H. CROWLEY, 1989. A ten year study of the odonate assemblage of Bays Mountain Lake, Tennessee. *Adv. Odonatol.* 4: 27-43.
- LOUNIBOS, L.P., R.L. ESCHER, L.B. DEWALD, N. NISHIMURA & V.L. LARSON, 1990. Odonata associated with water lettuce (*Pistia stratiotes* L.) in south Florida. *Odonatologica* 19: 359-366.
- 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., 1980. Temporal activity patterns of *Micrathyria* in Central America (Anisoptera: Libellulidae). *Odonatologica* 9: 57-74.
- MAY, M.L., 1991. Thermal adaptations of dragonflies, revisited. *Adv. Odonatol.* 5: 71-88.
- MAY, M.L., 1995. Simultaneous control of head and thoracic temperature by the green darner dragonfly *Anax junius* (Odonata: Aeshnidae). *J. exp. Biol.* 198: 2373-2384.
- MOORE, N.W., 1964. Intra- and inter-specific competition among dragonflies (Odonata). *J. Anim. Ecol.* 33: 49-71.
- MORIN, P.J., 1984a. The impact of fish exclusion on the abundance and species composition of larval odonates: results of short-term experiments in a North Carolina farm pond. *Ecology* 65: 53-60.
- MORIN, P.J., 1984b. Odonate guild composition: experiments with colonization history and fish predation. *Ecology* 65: 1866-1873.
- PARR, M.J., 1983. An analysis of territoriality in libellulid dragonflies (Anisoptera: Libellulidae). *Odonatologica* 12: 39-57.
- PIMM, S.L., 1991. *The balance of nature: ecological issues in the conservation of species and communities*. Univ. Chicago Press, Chicago/IL.
- POLCYN, D.M., 1994. Thermoregulation during summer activity in Mojave Desert dragonfly (Odonata: Anisoptera). *Funct. Ecol.* 8: 441-449.
- RIBEIRO, M.N.G. & A. SANTOS, 1975. Observações microclimáticas no ecossistema Campina amazônica. *Acta amazôn.* 5: 183-189.
- ROBINSON, J.V. & G.A. WELLBORN, 1987. Mutual predation in assembled communities of odonate species. *Ecology* 68: 921-927.
- SANTOS, A. & M.N.G. RIBEIRO, 1975. Nitrogênio na água do solo do ecossistema Campina Amazônica. *Acta amazôn.* 5: 173-182.
- SCHALL, J.J. & E.R. PIANKA, 1980. Evolution of scape behaviour diversity. *Am. Nat.* 115: 551-566.
- WCISLO, W.T., 1989. Behavioral environments and evolutionary change. *Annu. Rev. Ecol. Syst.* 20: 137-169.
- WELLBORN, G.A. & J.V. ROBINSON, 1987. Microhabitat selection as an antipredator strategy in the aquatic insect *Pachydiplax longipennis* Burmeister (Odonata: Libellulidae). *Oecologia* 71: 185-189.
- WILDERMUTH, H., 1991. Behaviour of *Perithemis mooma* Kirby at the oviposition site (Anisoptera: Libellulidae). *Odonatologica* 20: 471-478.
- WISSINGER, S.A., 1989. Seasonal variation in the intensity of competition and predation among dragonfly larvae. *Ecology* 70: 1017-1027.