REPRODUCTIVE BEHAVIOUR OF DIASTATOPS INTENSA MONTGOMERY (ANISOPTERA: LIBELLULIDAE)

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The reproductive behaviour of this neotropical dragonfly was studied at a farm pond in southern Brazil. The males are present at the oviposition site for ca 9 hrs daily, the maximum density being reached at midday. They are conspicuously territorial and behave as 'perchers'. Body posture and wing position of perching males vary greatly. Distinct positions of the black and red coloured wings may serve a thermoregulatory and visual function with respect to territorial behaviour. Females appear at water only at noon. Copulation lasts 3-7 s and oviposition takes place at hidden sites between emergent foliage of water plants. Oviposition is attended by the male (non-contact guarding) and multiple mating (up to 6 x consecutively) frequently occurs.

INTRODUCTION

Among the Anisoptera the libellulids excel in highly evolved behavioural patterns shown at the oviposition site. Many genera exhibit distinct territorial behaviour (PARR, 1983a, for review), and a few species even have a similarly complex courtship behaviour such as *Calopteryx* or *Platycypha* among the Zygoptera (JACOBS, 1955; MOORE, 1960; WILLIAMS, 1977; WILDERMUTH, 1991). The best known libellulids with respect to reproductive behaviour are some European, African and North American species (e.g. JACOBS, 1955; PAJU-NEN, 1962; CAMPANELLA & WOLF, 1974; KRÜNER, 1977; MILLER, 1982a, 1982b, 1991; HILTON, 1983, 1984; PARR, 1980, 1983b; KOENIG & ALBANO, 1985; ALCOCK, 1987, 1989; MOORE, 1987; UTZERI & DELL'ANNA, 1989), whereas the reproductive behaviour of neotropical species is extremely poorly known so far. Detailed information is available only about *Orthemis ferruginea* (NOVELO & GONZALEZ, 1984; HARVEY & HUBBARD, 1987) and *Perithemis mooma* (WILDERMUTH, 1991). Here I describe the behaviour of *Diastatops*

intensa, a previously unstudied species of South America, as a contribution to the body of information available for the Libellulidae. I shall consider perching and territorial behaviour, copulation and oviposition. Special attention will be paid to the variability in the posture of the conspicuously coloured wings which may serve a visual function in the context of intraspecific communication.

LOCALITY AND METHODS

The study site was a man-made farm pond near Guaiba, S of Porto Allegre, Rio Grande do Sul, Brazil (30°06'S, 51°18'W), ca 200 m in diameter, bordered by a dam 150 m long on one side and surrounded by pasture and woodland. The water was rather muddy and bare of vegetation except for some small scattered patches of *Eichhornia azurea* and some other water plants (for vegetation map of the pond see WILDERMUTH, 1991).

D. intensa was seen at the study site between 20 November 1990 and 12 January 1991. However, in November and December only very few individuals were about. Their number increased considerably in January. The observations on the behaviour of the species lasted from 9 to 12 January and were made by eye or with the aid of binoculars (Nikon Travelite II) which allowed a short working distance up to 2.8 m. During the investigation the animals were concentrated at two patches of *Eichhornia* plants along the dam. The larger of them (ca $3.5 \times 10 \text{ m}$) was chosen for the behavioural study.

APPEARANCE, PERCHING AND FLIGHT BEHAVIOUR

D. intensa is a rather small libellulid (male total body length 30-31 mm, fore wing length 26-27 mm) with relatively broad hind wings. The ratio of the maximum width of the hind wing to its length is about 1 : 2.6. The head and the thorax of the male are black, whereas the abdomen is blood red in colour. The wings are anthracite black with a violet gleam except for a large red basal spot on the hind wings. For the human observer the general appearance of the dragonfly has some similarity with that of a butterfly, especially when in flight. In the female the colour pattern is similar, however black is replaced by dark brown and the red parts are dirty yellow or ochre instead.

The males perched on *Typha* leaves 0.5 to 1.2 m above the water or on leaf tops of *Eichhornia* foliage. The position of the body and the wings varied greatly (Fig. 1). Depending on the support and the insolation, the body axis was held obliquely upwards, horizontally or slightly downwards. The most frequent perching posture seen was that with body axis horizontal and with wings lowered and twisted. However, the wings could also be spread completely flat, perpendicular to the body axis. Sometimes individuals lowered the wings of one side and raised those of the other side, or they lifted both fore wings while the hind wings were lowered. In each posture the males were conspicuous in appearance, however, besides thermoregulation no relation between wing positions and distinct behavioural elements could be recorded. Early in the morning males which had freshly arrived at the oviposition site perched with the body at right-angles to

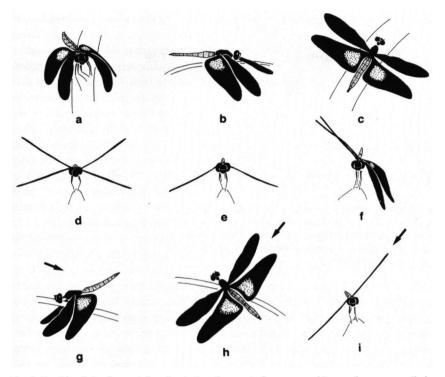


Fig. 1. Perching behaviour, (a) female, (b-i) males; - (a-f) postures without reference to radiation: (a) female at waiting room near oviposition site; body axis slightly inclined and wings lowered; - (b) body axis horizontal and wings lowered; - (c) all wings spread in one plane; - (d) fore wings lifted and hind wings lowered; - (e) all wings lowered, as in (b); - (f) wings of right side lifted and those of left side lowered. - (g-i) postures with thermoregulatory function: (g) basking posture in the morning; - (h, i) position at high irradiation. Arrow shows direction of sun rays. [The drawings are based on photographs and field sketches].

the sun's rays, and during periods of intense heat the animals could be seen holding the wings exactly parallel to the radiation. The obelisk posture was never observed.

Males cruising along the shoreline or pursuing a contestant on a horizontal course showed a rapid flight with relatively low wingstroke frequencies. The active flight was interrupted time and again by gliding phases. During wild chases on a vertical course the wing stroke frequency was raised.

TERRITORIAL BEHAVIOUR

The first males arrived at the oviposition site in the morning at 08.15 h Brazilian Summer Time (Fig. 2). Male density increased in the course of the forenoon,

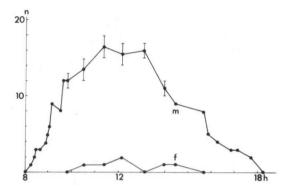


Fig. 2. Presence of males (m) and females (f) at the oviposition site (*Eichhornia* and *Typha* vegetation, area 3.5×15 m) on 11 January 1991. Between 10.00 and 14.00 h exact counts were impossible because of intense flight activity of males (indicated by bars).

peaked around midday and decreased continuously during the afternoon. The last individuals left the site just before 18.00 h. In periods of low density the males held territories of two to three metres in diameter at Eichhornia patches. They perched approximately in the centre of the defended area. No preferred direction of the body axis was recorded. The residents made periodic short patrol flights (Fig. 3). Returning to the centre of the territory they frequently used different perches. At periods

of high density the males were restless and changed their perching site every two to three seconds. While patrolling they flew either low over the water vegetation or within the *Eichhornia* foliage, possibly searching for females.

Residents pursued every intruder, including flying or perching pairs in wheel position. The pursuits frequently followed a horizontal course two to three metres above the water surface and led far beyond the territory over the pond. Besides horizontal pursuits I also observed fast vertical chases. The contestants rose in parallel lines holding a distance of 10 to 30 centimetres between each other. They climbed up to 15 metres and returned in separate wide loops to the starting point.

COPULATION AND OVIPOSITION

The first females arrived at the oviposition site in the late forenoon and the last ones left the place early in the afternoon (Fig. 2). After 15.00 h they had completely disappeared. Before visiting the oviposition site they waited on the dam near the water (up to five individuals), usually perched on the same shrub, together with some males (Fig. 1a). No special wing postures as observed in the males were noted. They approached the water in two different ways. Either they flew directly from the waiting room at a height of three to four metres, or they reached the *Eichhornia* patches stepwise in a leaping manner, presumably trying to sneak into the foliage and thus avoiding male attention. In general one of the males succeeded in intercepting an arriving female in the air (Fig. 4). Tandem formation and copulation followed immediately. Copulation lasted three to seven seconds and was usually completed after perching. No courtship display was

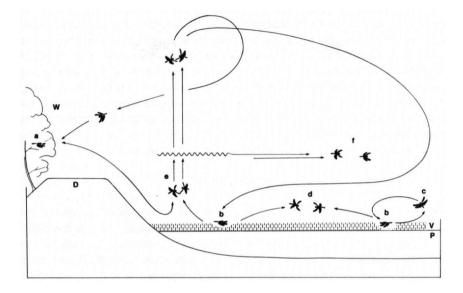


Fig. 3. Territorial behaviour of males. (D) dam; - (P) pond; - (V) emerged vegetation; - (W) waiting room. (a) male at waiting room; - (b) territorial male on perch; - (c) patrol flight; - (d) fight between neighbouring territorial males; - (e) ascending fight; - (f) pursuit on horizontal course with fluttering and gliding phase.

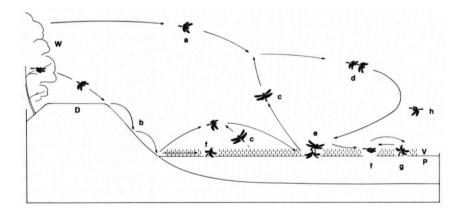


Fig. 4. Copulation and oviposition. (a) female directly approaching the oviposition site; - (b) female approaching the oviposition site stepwise; - (c) male on the way to intercept female; - (d) tandem flight; - (e) copulation; - (f) perching after copulation or between oviposition bouts; - (g) oviposition; - (h) male guarding ovipositing female. (D), (P), (V) and (W) as in Fig. 3.

observed. When flying in tandem or wheel position, active wing movements were seen only in the male. Multiple mating frequently occurred. One female was observed mating six times consecutively before she left the site. Oviposition was possible only for short periods in this case. At least two males were involved. After disconnection the females rested on a perch for 10 to 15 seconds. During oviposition they fluttered nervously between *Eichhornia* leaves immediately above the water, periodically touching the surface with the abdominal tip. Oviposition bouts were regularly interrupted by short rests if otherwise undisturbed by males. Resting and oviposition the females were circled over and again by their guarding mates. After oviposition the females left the place.

DISCUSSION

Males of D. intensa behave as typical 'perchers' at the viposition site (HEIN-RICH & CASEY, 1978). Although they may leave their perch every few seconds in situations of high male density, on average they spend far more time at rest than on the wing. The black and red coloured males perching on the tips of green leaves are conspicuous to the human eye and presumably also to the conspecifics. Although in many cases no clear relationships between the various wing positions and distinct behavioural elements could be found, I suggest that the coloured wings may serve a visual function with respect to territorial behaviour, as in Calopteryx. In this genus postures and movements of the wings are used as signals for intraspecific communication (e.g. HEYMER, 1973; RÜPPELL et al., 1984; CONRAD & HERMAN, 1987). Mutual aggressive display in flight as described in some libellulids (e.g. JACOBS, 1955) could not be recorded in D. intensa. However, in this species the mere presence of a male displaying his conspicuous wings might signal to a possible intruder that a territory is occupied. Unlike in Perithemis mooma which occurred at the same locality (WILDER-MUTH, 1991), the body axis and the wing posture of the perched D. intensa resident changed frequently. Together with short leaping patrol flights such perching behaviour may attract attention to the conspecifics all around. In some cases the perching posture was clearly related to thermoregulation. It is known from other libellulids that thermal adaptations may be achieved behaviourally by posture adjustments (MAY, 1978). Wings have also a striking appearance in flight. According to the length-width ratio of the hind wings, D. intensa may be classified as a glider, like members of the genus Paltothemis, Pantala and Tramea (DUNKLE, 1978). The flight behaviour of a male chasing a rival (alternatively fluttering and gliding) may involve - unlike in Pantala which has completely colourless wings - an aggressive display element.

The reproductive behaviour of D. *intensa* is similar to that of other members of the family. Male adults are conspicuously territorial. Residents attack any intruder and try to copulate with every female which arrives at the oviposition

site. The duration of the copulation is as short as in *Libellula quadrimaculata* (MOORE, 1960) or *Crocothemis erythraea* SIVA-JOTHY, 1988). After separating from the copulation wheel the female remains perched before she starts to oviposit, as was also observed in *Orthetrum* spp. (HEYMER, 1969; MILLER & MILLER, 1989; REHFELDT, 1989). Oviposition occurs at hidden places and is regularly interrupted by perching bouts. This behaviour suggests that the non-receptive females try to avoid any (additional) male interference. Similar male avoiding behaviour was observed in some aeshnids and corduliids (KAISER, 1976; UBU-KATA, 1984).

Non-contact guarding of ovipositing females as observed in D. intensa is known from many other libellulids (e.g. JACOBS, 1955; CAMPANELLA & WOLF, 1974; UTZERI & DELL'ANNA, 1989). This behaviour may allow a male to maintain his territory while guarding his mate. Simultaneously he may take an opportunity of additional mating (ALCOCK, 1979; UÉDA, 1979; SHER-MAN, 1983; HARVEY & HUBBARD, 1987). On the other hand this system involves the risk of surprise attacks by neighbouring males before the end of an oviposition bout, thus resulting in female multiple mating. This was frequently observed in D. intensa. It is suggested that at high male densities situations females are forced to pay for access to the oviposition site by multiple mating. As copulation lasts only a few seconds the loss of time is negligible for a female.

The daily activity pattern of *D. intensa* males is similar to that of other libellulids such as *Libellula lydia* and *Micrathyria aequalis* (CAMPANELLA & WOLF, 1974; MAY, 1980). Males are present at the oviposition site for almost the whole day, the maximum activity period falling between 11.00 and 13.00 h. As the females are reproductively active only for ca 3 hours during midday, they have no chance of avoiding male interference temporally at the oviposition site. The only possibility for them to avoid from aggressive males is to oviposit at hidden places in the foliage of emergent water plants.

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