Odonatologica 19(4): 375-380 *December 1, 1990*

PERCHING BEHAVIOUR IN *TRITHEMIS ANNULATA* (PAL. DE BEAUV.) (ANISOPTERA: LIBELLULIDAE)

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Received March 1, 1990 / Revised and Accepted August 2, 1990

T. annulata either increases or reduces the exposed surface of its body to the sun by orienting at various angles with respect to both the sun rays and the horizontal plane. Since the abdomen-raised position is observed in both sexes and is also adopted far from the reproductive habitat, it is probably not used as a territorial display but only as a means to warm up or cool the body temperature. The ability of thermoregulating by a wide variety of positions probably accounts for the long diurnal activity period in the population observed.

Several libellulid species regulate internal temperature by varying the postural angle of their bodies relative to the sun's rays. In the warmer period of the day, some point the abdomen toward the sun, and by so doing they expose to the sunlight a minimal surface, this position being known as the "obelisk position" (e.g. ANSELIN, 1986; CORBET, 1962; EDA, 1983; GONZALEZ SORIANO, 1987; HEINRICH & CASEY, 1978; JACOBS, 1955; KITAWAKI, 1973; MAY, 1977, 1978; MIYAKAWA, 1965; NEEDHAM & WESTFALL, 1955; TSUBAKI, 1986). The abdomen raised position may alternatively be adopted to increase the body surface exposed to the sun (ROWE & WINTERBOURN, 1981). Some other species apparently do not markedly raise their body above the horizontal, and they either increase or diminish the body surface exposed to the sun by varying the body angle below the horizontal (e.g. HEINRICH & CASEY, 1978). The abdomen raised position is also reported for some gomphids (CORBET, 1962; TESTARD, 1975; AIDA, 1974) and zygopterans (Calopterygidae, HEYMER, 1972; Euphaeidae, HEYMER, 1975). We have observed it in a number of species, including *Sympetrum meridionale, Celithemis eponina, Diplacodes trivialis, Brachymesia gravida* and *Erythrodiplax minuscula.* In *Aphylla williamsoni* and *Onychogomphus forcipatus unguiculatus,* the abdomen

may be also raised, but apparently not to the extent of the libellulid species (unpublished). The obelisk position is generally believed to have a thermoregulatory function, although JOHNSON (1962) has shown that by this position the males of *Pachydiplax longipennis* keep control of their territories and HEYMER (1975) and PRASAD & GHOSH (1982) for various species, including *Trithemis annulata,* maintain the same. HEYMER (1975) explicitly doubts that the obelisk position may have a thermoregulatory function. MAY (1977), with reference to *Micrathyria* suggests both functions.

In the present report we describe the perching behaviour of *Trithemis annulata,* which adopts both the raised and lowered abdomen positions either to reduce or to increase the body surface exposed to sunlight.

METHODS

Observations were carried out near an artificial pond of slightly brackish water at Marina di Ugento, Lecce, Italy. A place of about 30 square metres was selected about 20 m from the pond which was attended by numerous individuals throughout the day.

Twenty hourly censuses of all the male and females present were carried out in this area on 9 days between July 28 and August 26, 1986. The slope of the body relative to the horizontal, as estimated at intervals of roughly 30 degrees, and the orientation, with the sun in front, behind or to one side, were recorded for each individual. In the following, we shall refer to the lowered and raised positions of the abdomen as the "negative" and "positive" positions respectively. During each observation the air temperature was recorded by a bulb thermometer in the sun, at a height of about 1 m above the ground.

RESULTS

(1) Individuals of both sexes were present at the observation area, sometimes interacting with each other. In this area, male to female sex-ratio was 0.83:017 (N=276) and did not significantly vary at different times of the day. Dragonflies were somewhat active from 8:00 to after 18:00 hrs. Tandem formation was observed either over the water or adjacent to the pool between 10:30 and 16.30 hrs. Average temperature variation in the sun, as related to the observation times, is reported in Figure 1.

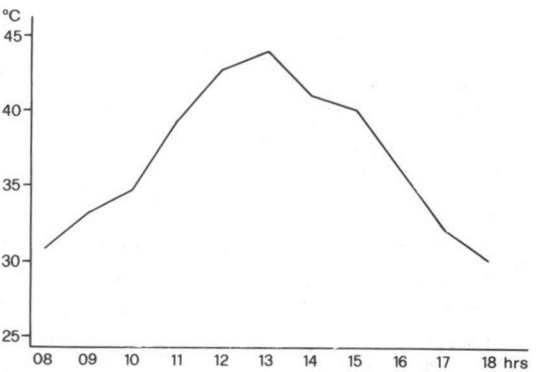

Fig. 1. Average air temperature variation during the day.

(2) Both males and females perched either on the ground or on the

surrounding vegetation, at heights between several centimetres to some metres. At any time of the day and at any temperature their bodies were kept at angles varying between about 90° below to above the horizontal. Generally, the horizontal position was maintained by dragonflies for not longer than a second after alighting, then it was adjusted as follows: at ambient temperatures between 28.5-34.5° C, individuals of both sexes exposed a greater surface to the sun by keeping their bodies either at positive angles, if facing the sun, or at negative angles, if the sun was behind. These were probably warming up. At temperatures 35.5-46.5° C, the dragonflies exposed a smaller body surface to the sun by keeping their bodies either at positive angles, if the sun was behind, or at negative angles, if facing the sun. These were probably cooling their internal temperature. The proportion of individuals exposing either a greater body surface to the sun at a temperature lower than 35° C or a smaller body surface at a temperature higher than 35° C, compared to those behaving the opposit way was significant (males: $\chi^2 = 103.9$; $P << 0.005$; females: $\chi^2 = 17.3$; $p < 0.005$) (Tab. I). Thus the ambient temperature value of 35° C in the sun appeared to be critical for the switch between the two behaviours.

Table I

Individuals adopting different postural slopes at different temperatures (° C). "+" and "—" indicate slopes above and below the horizontal respectively. The "warming up" and "cooling" columns include individuals exposing a greater and lesser body surface to the sun's rays respectively — [For further details see the text]

Temperature	Slope	Warming up		Cooling	
		♂	♀	♂	♀
28.5-34.5	+30	27	9	—	1
	+60	41	11	1	—
	+90	7	3	—	—
	−30	—	1	—	—
	−60	3	—	—	—
	−90	—	—	—	—
35.5-46.5	+30	4	1	4	3
	+60	—	—	15	—
	+90	1	—	18	3
	−30	—	—	6	—
	−60	—	—	3	—
	−90	—	—	1	—

Table II

Individuals perching with the sun to one side at various body slopes (both positive and negative) and at different temperatures (° C) — [The slope "0" means horizontal]

Temperature	Slope	♂	♀
28.5-34.5	0	16	2
	30	22	4
	60	9	3
	90	—	—
35.5-46.5	0	10	—
	30	19	1
	60	15	2
	90	7	3

(3) A significantly higher number of individuals adopted positive slopes either at lower temperatures than 35° C (males: $\chi^2 = 69.6$; $p << 0.005$; females: $\chi^2 = 19.4$; $p << 0.005$) or higher (males: $\chi^2 = 15.2$; $p < 0.005$; females: $\chi^2 = 5.1$, $p < 0.025$) (Tab. I). But, at higher temperatures, the males adopted negative slopes significantly more frequently, compared to positive ones, than at lower temperatures ($\chi^2 = 8.1$; $p < 0.005$), while in females there was no significant difference (Tab. I).

(4) At any time of the day and at any temperature, a number of individuals perched with the sun to one side and their bodies sloping at any angles, including horizontal. These were however less numerous than those facing or turning their back to the sun (Tab. II) (males: $\chi^2 = 4.5$; $p < 0.05$; females: $\chi^2 = 5.4$ $p < 0.025$).

DISCUSSION

In *Trithemis annulata,* the fact that at temperatures lower than 35° C, a significantly higher number of individuals of both sexes exposed a greater body surface to the sun, while at temperatures higher than 35° C, the reverse occurred, suggests that the slope of the body and the orientation with respect to the sun's rays varied in accordance with thermoregulatory constraints. Also, since within libellulids it is only the male that establishes a territory, this occurring over water surfaces where he mates (PARR, 1983), while in *T. annulata* the abdomen-raised position was adopted by both sexes in nearly equal proportions, and also far from the places and times where mating took place, it is improbable that this position was primarily connected with territorial defence.

In *T. annulata,* as probably in other libellulids, there is a continuous variation of the body posture with respect to the sun, both in the horizontal and vertical planes, each individual thus exposing to the sun's rays a surface related to its precise thermoregulatory needs. When, shortly after sunrise, the dragonfly is still chilled, it orients facing the sun while keeping its abdomen well above the horizontal; alternatively it keeps its body sloped downward with the sun behind; both positions increase the body surface exposed to the sunlight and allow it to warm up quickly. As the sun progresses higher in the sky, the dragonfly body is more lowered or raised, till the internal temperatures reaches the optimal value. Then the body is either lowered below the horizontal, if facing the sun or, more commonly the dragonfly, perching with the sun behind, raises its body, by both positions diminishing the exposed surface. With the sun at or near the zenith, which is generally connected with the highest temperatures in the day, the body is kept at the highest positive or negative slopes, according to the dragonfly's orientation with respect to the sun. Then, as the sun progresses from the zenith to the horizon, a reverse sequence of the same postural variation follows. Orientation with the sun to one side was probably less efficient, as suggested by a significantly lower number of individuals adopting it. Significantly, the hori-

zontal position was recorded only in individuals perching with the sun to one side, since in dragonflies perching with the sun in front or behind, it would have caused warming up with the sun near the zenith or cooling with the sun near the horizon.

Apparently, the ability of thermoregulating by adopting a variety of positions gave the dragonflies the possibility of lengthening their active period in the day. The present population was reproductively active during at least six hours of the day, and the dragonflies flew for about ten, which is considerably longer than for some other libellulids (e.g. *Libellula depressa,* UTZERI & DELL'ANNA, 1989). The time of the day in which reproductive activity was observed included temperatures higher than 35° C (Fig. 1), at which dragonflies kept body slopes such as to expose a lesser surface to the sun. This indicates they had reached their maximum voluntarily tolerated temperature (MVT) (May, 1978).

Although both negative and positive slopes were adopted by dragonflies, the latter were preferred to either warm up or cool the body, perhaps because the raised abdomen position is better for immediate flight. However, at least in males, negative slopes were more frequently adopted at higher than at lower temperatures. Since at higher temperatures, negative slopes involve orientation facing the sun, the vertical perch thus staying between the dragonfly and the sun, it is possible that dragonflies exploited the shade of vertical perches to some extent.

ACKNOWLEDGEMENT

Programma "Studio della fauna del Mediterraneo occidentale"; stanziamenti Min.P.I., quota Facoltá 60%; contratto C.N.R. n. 0989790, gruppo Biologia Naturalistica".

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