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DIFFERENCES IN MALE AND FEMALE ACTIVITY PATTERNS IN THE DRAGONFLY *SYMPETRUM DANAE* (SULZER) AND THEIR RELATION TO MATE-FINDING (ANISOPTERA: LIBELLULIDAE)

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Flight activity patterns were studied under semi-natural conditions in a large outdoor field cage in which individuals were found to show normal behaviour. Sexual differences in usage of time and space and the influence of temperature were studied. Before solar noon males were mainly active away from the pond, where they searched for females if temperature was high enough. Most pair-formation was seen during this period. Around noon and in the early afternoon, acticity shifted towards the pond, where some more pairs were formed. Throughout the afternoon male activity decreased, and shorter, localized flights became relatively more important. Male maximal flight activity coincided with solar noon and peak reproductive activity. Females remained almost inactive throughout the morning. However, their activity increased rapidly from noon onwards and largely exceeded male activity in the late afternoon. Female activity at the pond was always low compared to that in the surroundings. Females preferred more overgrown parts of the cage than did males, and selected higher perches. Body-surface temperature had a positive exponential effect on flight activity within the interval 20°-40° C, the effect being stronger in males than in females. Higher temperature also had a positive effect on the selected perch height. The results demonstrate that observations made only at the waterside can give a misleading impression of total activity. The revealed sexual differences in activity patterns are discussed in relation to mate-finding strategies in both sexes.

INTRODUCTION

It is generally accepted that most matefinding in Odonata occurs at the waterside, where males space themselves out each day and wait for incoming receptive females (CORBET, 1980). As females develop clutches of eggs cyclically (FINCKE, 1982, 1986; SHERMAN, 1983; own observations), they visit the water only once every few days to mate and oviposit. As a result, the operational sex ratio at the waterside is male skewed, resulting in intense male-male competition. As most studies have focused on the waterside, this has led to two distinct problems:

(1) Male diurnal activity patterns (reproductive as well as non-reproductive) are well documented (see below), but restricted in space. Female activity patterns, on the other hand, are virtually unknown as existing knowledge mainly concerns observed matings and oviposition bouts. When observing *Sympetrum pedemontanum* in paddy fields, where roosting and oviposition sites overlap, TAGUCHI & WATANABE (1985) found that males searched for females throughout the morning and showed decreasing activity during the rest of the day, whereas females reached their maximum activity only after 12.00 hrs, demonstrating that male and female activity patterns can be quite different. As female recognition and capture by males occurs primarily in flight in most libellulids, the flight activity patterns of both sexes may yield information on the relative "availability" of both sexes in time and space, yielding insight in mate-finding tactics.

(2) If determined at the water, the operational sex ratio (EMLEN & ORING, 1977) may differ considerably from that of the population as a whole as only the mated individuals from the surroundings are counted at the waterside, and not the receptive, yet unmated individuals, which should be included as well. Outside-pond pair formation has been reported in *Nesciothemis nigeriensis* (PARR & PARR, 1974), *Sympetrum parvulum* (UEDA, 1979), *Enallagma hageni* (FINCKE, 1982) and *Orthetrum cancellatum* (SIVA-JOTHY, 1987) but its relative importance remains unknown.

We investigated male and female activity patterns in *Sympetrum danae* (Sulzer), a small (abdomen 20-23 mm), non-territorial, sexually dimorphic libellulid. By studying *S. danae* under semi-natural conditions in a large outdoor field cage, we were able to record the activity patterns of both sexes, before, during and after reproduction, at the water as well as away from the water.

As dragonfly activity is related to temperature and light intensity (LUTZ & PITTMAN, 1970; TESTARD, 1972; SHELLY, 1982; WARINGER, 1982), activity patterns depend on the species' thermoregulatory capacities, especially in temperate-zone dragonflies (MAY, 1976, 1978). Small species thermoregulate mainly by controlling exogenous energy input, via microhabitat selection or postural adjustments relative to the sun while perched (heliothermy). In Anisoptera, such species are called "perchers" in contrast to the often larger "fliers" (CORBET, 1962; MAY, 1976; HEINRICH & CASEY, 1978). Small Anisoptera and Zygoptera, therefore, usually show an activity pattern — at the waterside — parallel with the diurnal course of temperature and radiation (e.g. JACOBS, 1955; AGUESSE, 1959; BICK & BICK, 1963; TESTARD, 1972, 1975; CAMPANELLA & WOLF, 1974; GREEN, 1974; KAISER, 1974; HIGASHI, 1976; CAMPANELLA, 1977; MAY, 1977, 1980; DREYER, 1978; HASSAN, 1978;

PEZALLA, 1979; FRIED & MAY, 1983; PARR, 1983; NOVELO & GONZALEZ, 1984; WATANABE & OHSAWA, 1984; MILLER & MILLER, 1985a; KOENIG & ALBANO, 1985; ROBINSON & FRYE, 1986; TSUBAKI & ONO, 1986; VAN BUSKIRK, 1986; ALCOCK, 1988). We previously demonstrated that male activity and reproduction at the waterside in *S. danae* peaks around solar noon as well (MICHIELS & DHONDT, 1987). LUTZ & PITTMAN (1970) argued that, in addition to the effect of temperature, time of the day can be a major determinant of odonate activity patterns.

Most activity patterns described in literature are based upon the number of individuals present per time interval. This, however, gives no direct information on the activity itself, but rather expresses diurnal movements to and away from the waterside. In *Nannophya pygmaea*, for example, the pattern of the number of individuals present at the pond is of the "plateau" type, whereas the number of aggressive interactions shows a distinct peak around 10.00 hrs, the period of greatest reproductive activity (NAKAMUTA et al. 1983). The number of flights or territorial disputes, as used by e.g. PARR (1983), MILLER & MILLER (1985b), HARVEY & HUBBARD (1987), is a better measure of activity, especially in percher type species, where virtually every agonistic behaviour follows a movement of the antagonist.

METHODS

The study was carried out in a large outdoor field cage in the nature reserve "De Tikkebroeken", near Turnhout, Belgium (5° 00'E, 51° 16'N). Libellulids were previously held in a cage by HASSAN (1977) and McVEY (1985), but for different purposes and in cages too small or not equipped for normal reproductive behaviour. Our field cage (10x20x5 m) was constructed on a plot with a natural, semi-open vegetation of *Betula pendula*, *Molinia caerulea*, *Rubus* sp., *Quercus robur* and *Alnus glutinosa* (Fig. 1). The borders of the artificial pond were sloped gently and were covered with natural shore vegetation, mainly consisting of *Sphagnum* spp., the favourite oviposition substrate of *S. danae*, and *Juncus* spp. Although the pond and its surroundings were subdivided in detail by markers, in this paper we refer only to the pond as a whole and to 8 main surrounding sectors. Data were collected from 6 August to 1 October 1986 and from 25 July to 21 August 1987.

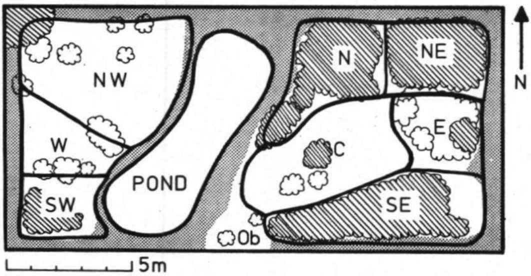

Fig. 1. Schematic ground plan of the field cage with location of the eight main sectors around the pond (C = center, Ob = location of observation post). — [Hatched: tree taller than 2 m; — dotted: vegetation lower than 5 cm or bare ground; — white (outside pond): grasses (*Molinia*) and trees below 2 m].

Males and females were caught

at an oligotrophic pond 1 km away. Before release in the insectarium they were individually marked with a number and a unique combination of coloured bands using a felt-tipped pen (TOMBO Paint Marker). In captivity, the individuals showed normal behaviour and had a high survival rate (MICHIELS & DHONDT, 1989). In 1986, mean daily density in the cage was 14.3 males/20.4 females and the mean male proportion 0.40. In 1987 this was respectively 9.3 males/15.1 females and 0.39. Under natural conditions, the male proportion at emergence was 0.42. In 1986 14 males and 17 females were teneral when released (4-5 August), while this was 19 resp. 27 in 1987 (most on 10-16 July). All other individuals were sexually mature. The overall number of individuals released in the cage throughout the season (upto end September in 1986), was 55 males/51 females in 1986 and 20 males/28 females in 1987. As most observations were held when all individuals had matured, only 2.3% of all observations concerned immatures, and, hence, were not considered separately.

On sunny days observations were made continuously from ± 9.00 Mid European Summer Time until ± 16.00. Usually, however, the onset and end varied in relation to cloudiness and temperature. Time was later transformed to Mean Solar Time (MST). Mean Solar Noon at 5°00'E is at ± 13.40 hrs Mid European Summer Time.

Flight activity was recorded by noting any flight that could be seen throughout the day from a 2-m high seat, located in the middle of the southern side of the cage (Fig. 1). Differences in vertical distribution were assessed by noting perch height. Six classes were used: 0 m, 0.01-0.05 m, 0.06-0.50 m, 0.51-1.50 m, 1.51-4.50 m, 4.51-5.00 m. Individuals were recognized by sight, or with a pair of binoculars (8x40). Data were either written down or tape-recorded. In 1987, more than 75% of the observations were directly entered into a pre-programmed pocket computer (PSION ORGANISER II, model XP), allowing immediate processing on a personal computer.

The combined effect of air temperature, convection and radiation was recorded with a needle probe, inserted through the abdomen into the thorax of a freshly killed and subsequently dried *S. danae* male. The temperature thus obtained resembles the effective environmental temperature (T_e), defined by BAKKEN & GATES (1975) as "the temperature of an inanimate object of zero heat capacity with the same size, shape, and radiative properties as the animal, and exposed to the same microclimate". We will call our estimation of T_e body surface temperature (T_{bs}) and use it as a global descriptor of the energetic environment a dragonfly experiences, before it makes any thermoregulatory adjustments. The probe was mounted on a pole 1.5 m high, parallel with the soil and perpendicular to the sun's rays. A probe for air temperature T_a) measurements, inserted in an aluminum-covered and aerated plastic vial was mounted identically. The pole was placed in the sun at the north side of the pond. Recordings were made with an electronic data-recorder storing one measurement per minute (GRANT SQUIRREL MODEL Q8). We will only use T_{bs} in further analyses, but for comparison with T_a, we give the relation between T_{bs} and T_a, based on all temperature measurements (N=10790): $T_{bs}=1.27+1.12\ T_a$; $R^2=0.82$; $P << 0.001$; 95% conf. int. for slope: 1.11-1.13, for intercept: 1.03-1.51.

Means and standard deviation are given, unless specified otherwise.

RESULTS

Data were collected on 47 different days (1986: 32; 1987: 15) during 191.2 hours of observation (1986: 127.5; 1987: 63.7). In total, we noted 12210 flights (1986: 7765; 1987: 4445). 6.1% of these were made by pairs in tandem or copula. 4035 times a flying individual was recognized as a female (1986: 2362; 1987: 1673) and 7374 times as a male (1986: 4747; 1987: 2627). 11 flight types could be distinguished. In this paper, only the six most common types, amounting to 96.5% of all available data, will be used.

Four "general" flight types were seen in both males and females:

- SHORT FLIGHT: 1-2 seconds, starting and end point are close (⩽ 1. m) or identical, take-off angle more or less horizontal; possible function: improvement of position relative to the sun or cooling by convection.
- FEEDING FLIGHT: 1-2 seconds, starting and end point close (⩽ 1 m) or identical, take-off angle between 45° and 90°, clearly quicker than short flight. The successful capture of prey, presumably Diptera, was witnessed only occasionally due to the distance and because this information was not of major importance in this study.
- NORMAL FLIGHT: longer than the previous type, starting and end point are usually different, take-off angle horizontal, usually below 1.5 m, used for moving around (arg. duration $\bar{x}=12.8 \pm 6.0$ sec, min=3, max=27, N=40).
- LONG FLIGHT: duration several tens of seconds, without clear destination, typically at a height of 2-5 m; function unknown ($\bar{x}=44.6 \pm 21.1$ sec, min 15, max 131, N=59)).

Two flight types, seen in males only, were associated with mate finding:

- SEARCH FLIGHT: non-directional, fluttering flight during which the male moves slowly up and down, back and forth, between stems of the vegetation, always away from the oviposition sites; any encounter with a female leads to a sexual interaction ($\bar{x}=46.4 \pm 34.4$ sec, min 4, max 180, N=88). Searching was previously described in *S. depressiusculum* by MILLER et al. (1984) and in *S. pedemontanum* by TAGUCHI & WATANABE (1985).
- PATROL FLIGHT: slow, investigating directional flight, always low above the oviposition sites, usually from and back to the same perch ($\bar{x}=19.2 \pm 15.6$ sec, min 6, max 90, N=31).

This subdivision is arbitrary and flights of uncertain nature inevitably occurred. If doubt arose between a short or a feeding flight, a short flight was chosen. If the same happened with one of the other types, the observation was noted as a normal flight.

All observations were pooled irrespective of weather conditions.

REPRODUCTIVE ACTIVITY

The formation of a new pre-copula tandem pair was recorded 239 times. Tandem formation was observed as early as 08.37 MST, but usually did not start before 10.00 MST (Fig. 2). A clear peak occurred between 11.00 and 12.00 MST,

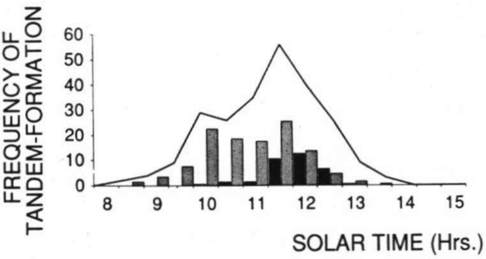

Fig. 2. Frequency of pre-copula tandem formation of *S. danae* per 30 min in the field cage. — [Black bars: at pond (N=37); — grey bars: in surroundings of pond (N=122); — black line: total, including pair formations for which the exact location was not noted (N=239)].

followed by a rapid decrease after solar noon. The latest formation was observed at 13.40 MST. Of those pairs of which the exact location of formation was observed (N=159), the vast majority (N=122; 77%) were formed in the surroundings, while only 37 (23%) at the shores or above the water. Tandem formation occurred significantly earlier in the surroundings ($\bar{x}$=11h06′ ± 58′ MST) than at the pond ($\bar{x}$=11h59′ ±37′ MST): M-W U-test: z = -5.10; $P \ll 0.001$). After tandem formation and copulation, oviposition always started in tandem, often followed by non-contact guarding and finally abandonment of the female by the male. Seventeen % of all oviposition bouts were by females that had not mated yet on that particular day.

DIURNAL FLIGHT ACTIVITY

The four general flight types of males and females were observed throughout the investigated time interval (Fig. 3). The first flights were often preceded by wing-whirring, seemingly used to remove dew from the wings and to warm-up endothermically, and were directed to sunny, east oriented perches. In males the pattern of localized flight types (short, feeding) differed from that in non-localized types (normal, long). Short flights increased throughout the day and were most commonly seen in the early afternoon. Feeding flights seemed to increase towards 14.00-14.30 MST. Normal flights reached their maximum at 11.00-12.00 MST, while long flights were rare and did not show any clear tendency. In females all flight types showed a similar pattern. Flight activity remained low before noon. Feeding even seemed to decrease and to reach its lowest point at 12.00 MST. In the afternoon, however, activity increased rapidly and reached a maximum around 14.00-14.30 MST. During low-activity hours females

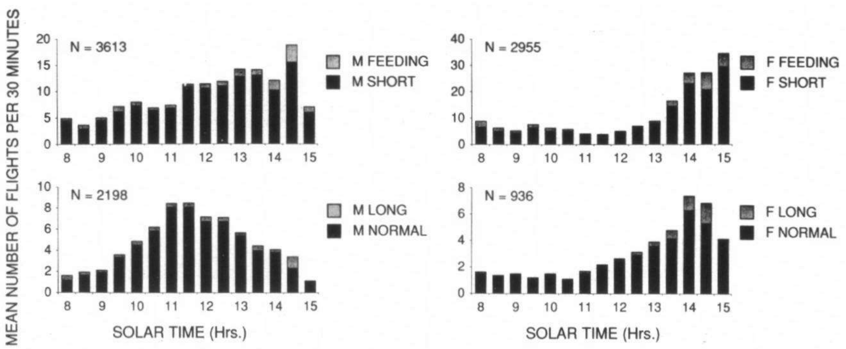

Fig. 3. Mean number of short, normal, long and feeding flights per 30 min as observed in male (M) and female (F) *S. danae*. – [Note different scaling of Y-axes].

remained perched or even adopted the roosting posture (see HASSAN, 1976), irrespective of the temperature.

Searching and patrolling males were seen only during part of the day (Fig. 4). The more common searching flights were almost exclusively seen before noon, peaking at 10.30 MST ($\bar{x}$=11h01′ ± 46′ MST). Patrolling was less frequent and occurred over a wider time range but significantly later than searching, reaching a peak at 11.30 MST ($\bar{x}$=11h50′ ± 56′ MST): M-W U-test: z= -12.02, P<<0.001.

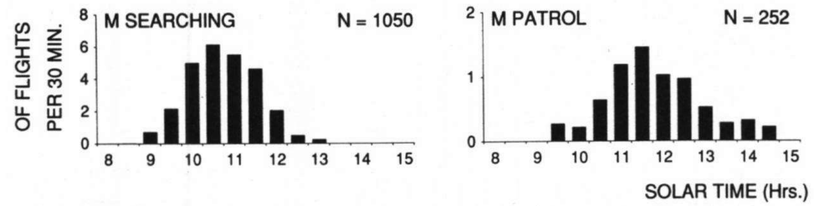

Fig. 4. Mean number of search and patrol flights as observed per 30 min in male *S. danae*. — [Note different scaling of Y-axes].

No significant differences were found in the timing of searching and pair formation in the surroundings on the one hand (M-W U-test: z= -1.28, P=0.20) and patrolling and pair formation at the pond on the other (M-W U-test: z= -1.33, P=0.18). Note however, that only a part of the pair formations occurred during search or patrol flights. A perched male attacking a flying female was a commonly observed alternative sequence as well, as e.g. in *Enallagma hageni* (FINCKE, 1985).

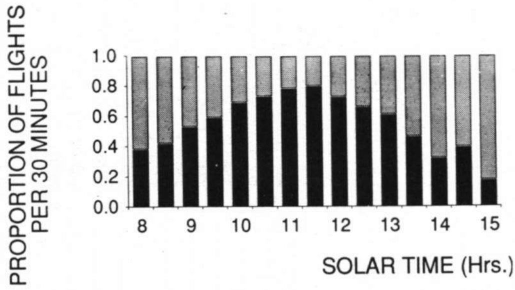

Fig. 5. Proportion of flights made by male (black) and female (grey) *S. danae* each 30 min interval, showing the relative activity of each sex throughout a day. Based upon 11,004 flight-recordings.

The results show that males and females had more or less opposite activity patterns, resulting in a diurnal switch of the activity-per-sex ratio (Fig. 5). During morning hours, females were more active than males, although the absolute number of flights was low (Fig. 3). At noon, however, at moments of maximal male and reproductive activity, females became inactive and, relative to males, "disappeared" from sight, unless reproducing. During the afternoon, the ratio changed again in favour of the females (Fig. 5), their number being now much greater (Fig. 3). Occasional observations after 15.00 MST indicated no important further changes in activity: most individuals remained perched and gradually moved to their final roosting perch for the night.

SPATIAL ACTIVITY PATTERN

Figure 6 shows that males shifted their flight activity from the surroundings to the pond during the day. At 13.00 MST more than 60% of male activity was seen around the pond, whereas this was less than 20% during the morning. From 14.00 MST onwards, males gradually seemed to return to the surroundings. Female activity was always higher in the surroundings than at the pond itself. The maximum at the pond, still below 40%, coincided with the minimum of absolute female activity (Fig. 3) and the maximum of male and reproductive activity (Figs 3, 4, 5): these were mainly pre- or post-oviposition females.

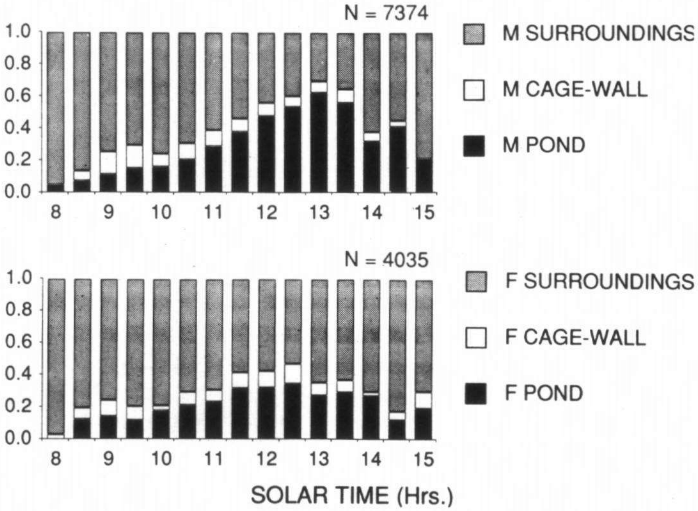

Fig. 6. Proportion of flights of male (M) and female (F) *S. danae* in each major part of the field cage at each 30 min interval.

Figure 7 shows the observed flights in each main sector of the surroundings. As more vegetation implies more unseen flights, the apparent highest numbers of both sexes in less vegetated sectors, is at least partly an artifact. Yet, a comparison between both sexes is allowed. Males flew relatively more in the western, less vegetated sectors NW, W, and SW, whereas females were relatively more active in the eastern, more overgrown parts, C, N, E, NE and SE ($G=445$, d.f. 7, $P << 0.001$), indicating sexual differences in microhabitat preferences.

Excluding perching on the cage wall, 1446 perch heights were recorded (males: 836; females: 610). Males and females showed a significant difference in perch height selection (Fig. 8) (G=246, d.f. 5, P << 0.001). Males preferably perched at low heights (< 50 cm) and were mostly seen sitting on the ground (median=0.06--0.50 m). Females, on the other hand, usually perched well above the ground, with a maximum in the 1.51-4.50 m class (median=0.50-1.50 m).

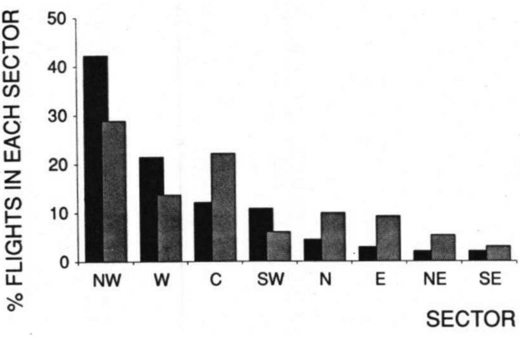

Fig. 7. Relative distribution of flight activity of *S. danae* in the 8 main sectors in the surroundings of the cage pond. — [Black: males (N=3484); — grey: females (N=2395); see Fig. 1 for situation size and vegetation of each sector].

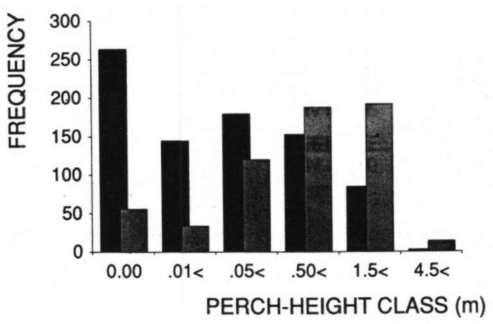

Fig. 8. Frequency distribution of perch height classes selected by *S. danae*. — [The X-axis labels indicate the lower limit of each class; — black: males (N=836); grey: females (N=610)].

EFFECTS OF TEMPERATURE

Of all observed flights, 95% occurred above 21.3° C body surface temperature (T_{bs}), which equals 81.6% of total observation time. 5% were observed above 37.78° C T_{bs} during 5% of the observation time. Heat-avoidance, by pointing the abdomen to the sun (obelisk-posture, MAY, 1976) was seen at a mean T_{bs} of 39.8° C (± 1.73, N=10). The only observations of voluntary shade seeking were made at this T_{bs} as well. This suggests that the maximal voluntarily tolerated temperature (MVT, see MAY, 1978) must be around 40° C T_{bs}, a temperature that was achieved only during 1.0% of the observation time.

A direct relationship between number of flights and temperature would be biased by the number of times each temperature interval was "sampled". We therefore corrected by dividing the daily number of observed flights at each interval of 1° C by the number of times this interval was measured (1-minute/1° C intervals) and by the number of individuals present. This yields a daily number of flights per individual, per minute and per 1° C (Nf_c). Figure 9 shows that, within the "sampled" temperature interval, a positive exponential relationship between Nf_c and T_{bs} existed for the 4 general flight types in males and females. In males the slope was steeper than in females (95% Conf. Int.: 0.082-0.110 and 0.043-

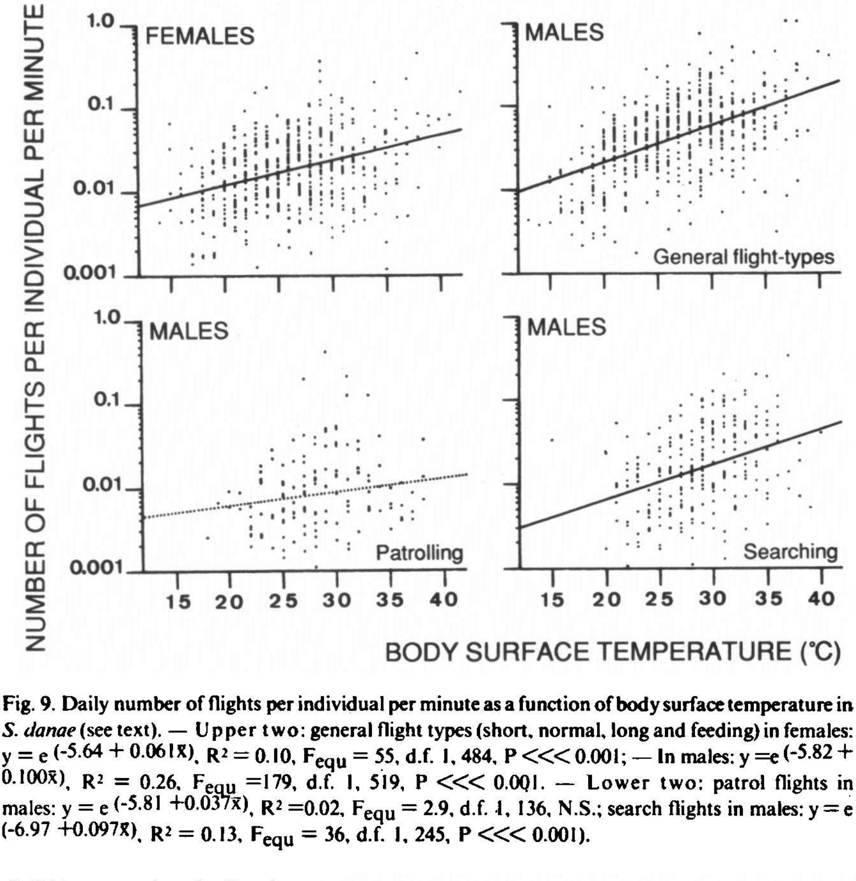

Fig. 9. Daily number of flights per individual per minute as a function of body surface temperature in *S. danae* (see text). — Upper two: general flight types (short, normal, long and feeding) in females: $y = e^{(-5.64 + 0.061\bar{x})}$, $R^2 = 0.10$, $F_{equ} = 55$, d.f. 1, 484, $P <<< 0.001$; — In males: $y = e^{(-5.82 + 0.100\bar{x})}$, $R^2 = 0.26$, $F_{equ} = 179$, d.f. 1, 519, $P <<< 0.001$. — Lower two: patrol flights in males: $y = e^{(-5.81 + 0.037\bar{x})}$, $R^2 = 0.02$, $F_{equ} = 2.9$, d.f. 1, 136, N.S.; search flights in males: $y = e^{(-6.97 + 0.097\bar{x})}$, $R^2 = 0.13$, $F_{equ} = 36$, d.f. 1, 245, $P <<< 0.001$).

-0.074, resp.), indicating that males responded more strongly to a temperature increase than females. In males the frequency of patrol flights was not temperature related, whereas search flights were, showing that most searching was seen at higher temperatures. The mean (uncorrected) T_{bs} at which searching or patrolling was observed, resp. 30.4 ± 3.9° C and 29.6 ±

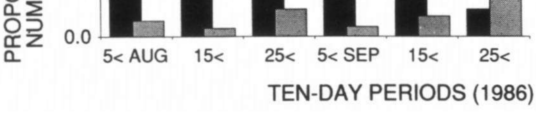

Fig. 10. Frequency of search (black) and patrol (grey) flights relative to total number of flights observed per 10 day period, as observed in male *S. danae* in 1986. —[The labels at the X axis indicate the lower limit of each class].

4.4° C, differed significantly (M-W U-test: $z=-4.19$; $N1=1022$, $N2=249$; $P \ll 0.001$). In agreement with this result, the relative number of search flights decreased towards the end of the season whereas this was not the case in patrol flights (Fig. 10) ($G=150$; d.f. = 5; $P \ll 0.001$).

The overall effect of T_{bs} on Nf_c for all flights types in males could be described by $y=e^{(-6.067 + .116x)}$ ($R^2=0.31$; d.f. 1, 525; $F_{equ}=239$; $P \ll 0.001$), amplifying the sexual difference.

On sunny days T_{bs} at the soil surface could raise at noon up to 10° C above the value measured at 1.5 m height, showing the existence of a vertical thermal gradient. This gradient was actively used by *S. danae:* a positive relationship existed between T_{bs} and perch-height both in males (Spearman $r=0.30$; $N=817$; $P<0.001$) and in females (Spearman $r=0.32$; $N=590$; $P<0.001$), showing that *S. danae* perches become higher when temperature increases.

DISCUSSION

We demonstrated that *S. danae* male and female activity patterns differ substantially: male activity peaks around solar noon, while female activity increases not before early afternoon and peaks in the late afternoon. Also activity patterns were found to differ in space: males show important (sexual) activity in the surroundings before noon, during which most pair formation occurs, and move to the pond at noon, whereas females fly predominantly in the surroundings, their (low) activity at the pond peaking around noon. The fact that spatial shifts could be observed on a 10x20 m surface proved that the distinction between "pond" and "surroundings" was meaningful, even on this small scale.

Our results indicate that, although observations at the waterside show the expected activity pattern (MICHIELS & DHONDT, 1987), they are misleading in relation to the total (sexual) activity. Relative mating frequencies or operational sex ratios, estimated at the waterside only, as done by e.g. BICK & BICK (1963), PARR & PALMER (1971), FINCKE (1986) and HINNEKINT (1987) therefore should be used with caution if sexual activity away from the pond exists, as individuals that are sexually active, but unmated, away from the water, are not included. CORBET (1980) argues that the male activity pattern at the water is a reflection of the arrival rate of receptive females, which was shown by KAISER (1985) and ALCOCK (1988). However, although the pattern is identical, this relation seems to be reversed in *S. danae:* female arrival at the pond is a function of male activity, as most females are brought in tandem by a male from the surroundings.

That important (sexual) activity away from the pond exists in *S. danae* also under natural conditions, is illustrated by observations during the summer of 1985. We noted that at a small, natural pond in De Tikkebroeken pair formation and copulation in *S. danae* were seen only in 13 (7.8 %) out of 167 tandem pairs of which the beginning of oviposition was witnessed. Most tandem pairs came to the pond from over the surrounding woodland and started oviposition without delay. Pair formation and copulation in roosting areas up to 200 m away, was observed occassionally (unpublished data). If in the cage the behaviour of *S. danae* would have been disturbed, we would also expect a high degree of escape behaviour. However, escape flights (discarded in the results section), amounted only to 281 (2.5%) out of 11409 flights. Furthermore, under natural conditions we would expect a relatively larger proportion of individuals to be found in the surroundings, since the proportion water to total space is certainly much smaller in nature than the 11% in the cage. All this suggests that our estimate of activity away from the water is probably conservative.

Flight activity was almost absent below 20° C T_{bs}, but increased exponentially between this lower limit and the maximum voluntarily tolerated temperature (MVT), at about 40° C T_{bs}. The effect was stronger in males than in females. In addition, males perched on average lower than females, as found by EBERHARD (1986) for *Hetaerina macropus*. These findings, combined with the phenomenon of maximal male activity at maximal solar radiation, suggest that males prefer a higher body temperature (T_b) than females. Perhaps this explains why mature males are almost completely black, and thus absorbing more radiation, while females are brownish (see e.g. d'AGUILAR et al., 1985). The difference in temperature preference probably would have been even clearer if the Tbs of a dead female instead of a male would have been used to analyze female activity.

The positive relation between perch height and T_{bs} suggests that *S. danae* thermoregulates behaviourally, by choosing specific places on the vertical temperature gradient in its habitat, in addition to postural adjustments. Endothermic warming-up by means of wing-whirring was observed at low temperatures. The exact regulation of T_b in *S. danae* remains, however, unstudied.

SIGNIFICANCE OF FEMALE INACTIVITY

The sexual differences in spatial and temporal activity, and the preference of females for more overgrown parts, resulted in avoidance of male sexual activity by females. This could be caused indirectly, by differences in the response to the environment, or directly, by a negative effect of intersexual encounters. Observations during two days with only males or females present (resp. 20-21 August) showed, however, patterns of flight activity very similar to the global pattern illustrated in Figure 3, suggesting that female morning inactivity was not directly caused by the presence of the opposite sex.

A possible correlate for the avoidance of male sexual activity could be unreceptivity due to the periodic maturation of eggs. As the mean inter-clutch interval is 3-4 days (unpublished data) it can be expected that on average 66% to 75% of the females on a certain day are not receptive. As males can be aggressive and persistent, escaping from them when detected can consume time and energy. Hiding from males might therefore be necessary, as males react without hesitation to any female-like movement. A receptive female on the other hand, has no need to hurry: as the number of willing males always exceeds that of receptive females, it may still be advantageous to hide, as the male which is successful in finding her, could father good searchers among her progeny, since almost all the eggs of the next batch are fertilized by the last male (MICHIELS & DHONDT, 1988). If not found by a male in the surroundings during the morning, females can fly to the pond, and "present" themselves to the aggregated males active there. Even then, females can be observed to exert some degree of mate choice by rocketing into the open air as soon as a male detects them: this attracts other males, resulting in a whirling pack of competitors, of which only the quickest is successful in grabbing the female.

MALE MATE FINDING BEHAVIOUR

It is essential for a *S. danae* male to locate a mate as early as possible: any missing receptive female that copulates with another male, is a lost occasion, as females seldom mate more than twice a day, and probably lay most of their eggs while escorted by their first mate. Several arguments can be used to explain why *S. danae* males focus on the roosting areas early during the day and are so successful in obtaining mates. First, the probability of encountering a female at the shore is still very low. Secondly, assuming that the temperature rises more rapidly in the sheltered parts around the pond than along the exposed shores, earlier activity is possible away from the water. Thirdly, both sexes spend the night in these areas and therefore are present during the morning in relatively high numbers, at least higher than at the pond, and presumably in a less male biased sex ratio. Fourthly, in the energetically "patchy environment" of a temperature--dependent animal such as *S. danae,* the encounter of a female by a male can be assumed to be more likely than would be expected purely by chance, as the thermal preferences of both sexes are perhaps not identical on average, but certainly overlap largely. Under these conditions, searching the surroundings as early as possible seems to be a good strategy for a male *S. danae,* at least if the temperature rises sufficiently, because searching is costly and done only at higher temperatures. The same reasoning might hold for activity away from the water in other small libellulids and in damselflies as well.

Around noon, it becomes more and more unlikely to find a receptive female away from the pond: those who are paired, are brought to the pond, and those who are not, will come on their own. This would explain why males stop searching and shift their activity to the pond at noon in order to obtain (additional) matings. At the shore, however, they will encounter in part previously mated females, and also they will be involved in increased intra-male competition. From the early afternoon onwards, sexual activity diminishes and flying over larger distances (normal, searching & patrolling) changes to more localized flights (short & feeding). A similar shift to more feeding was observed in *Orthetrum coerulescens* by PARR (1983).

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