

**FEMALE PERCHING BEHAVIOUR IN
SYMPETRUM SANGUINEUM (MÜLLER) AT FEEDING PLACES
(ANISOPTERA: LIBELLULIDAE)**

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In field observations and experiments the sequence of occupation of perches by females, occupation duration and changes of perches by individuals at places of feeding were studied. Females defend their perches from conspecific and closely related individuals. Spontaneous locomotor activity is directed towards the apical part of a branch and to higher perch levels. Changes of perch after failure are usually directed to lower perch levels or more basally along the perch. The number of successful attempts is considerably lower after previous failure than during spontaneous attempts. Sitting time increases with high perches. Females occupy distal perches for a longer time than proximal ones. Dragonflies on high perches try to occupy even higher perches more often. Generally on a perch a dragonfly compensates for the slope of a branch by its body posture and indicates perch occupation by wing and/or abdominal displays both after landing on a perch and when other individuals approach. At feeding places a female defends its feeding territory from conspecific individuals of both sexes as well as from individuals of closely related species. In experiments with models has been shown distant sex differentiation by dragonfly females. The behavioural strategy of *S. sanguineum* females at places of feeding was compared with behaviour of territorial males at the places of pairing.

INTRODUCTION

In mid-summer *Sympetrum sanguineum* begins emergence from larval stage. After emergence they fly from ponds, lakes, river arms to glades of woods and parks, as other Libellulidae (WATANABE & HIGASHI, 1989). Here they concentrate at leeward places and feed actively. A great number of individuals fly out simultaneously, and their density increases rapidly at feeding places. Representatives of the genus *Sympetrum* as well as other Libellulidae are typical

perchers according to chase strategy (ZAIKA & VORONOVA, 1977). Usually these species hunt from selected perches. They rush after flying insects, then return to their perches. In the morning dragonflies occupy warm sunny perches. Leaves of trees, bushes and high blades of grass usually serve for this purpose; dry branches and twigs are especially attractive. During day-time regular transferences of individuals from perch to perch take place. What is the strategy of these transferences, how is sitting time connected with perch peculiarities, what are the peculiarities of changing and keeping of a perch? This research is devoted to solving of these problems. Female threat activity, postures on perches and some other peculiarities of communication of individuals in this behavioural situation were studied too.

BACKGROUND

Territorial behaviour of adult libellulid dragonflies has been reviewed by PARR (1983). The role of visual morphological stimuli in Odonata has been studied in *Platycnemis pennipes* (BUCHHOLTZ, 1956), *Cordulia aenea amurensis* (UBUKATA, 1983), *Nesiothemis nigeriensis* (PARR & PARR, 1974) and *Sympetrum* species (FRANTSEVICH & MOKRUSHOV, 1984). The role of different behavioural demonstrations has been studied very rarely (PAJUNEN, 1963; UTZERI, 1988; GORB, 1992). Territorial behaviour of imagoes has been studied mainly for sexual behaviour of males. Territoriality and aggressive behaviour at the places of feeding are known for larvae (ROWE, 1980; BAKER, 1981; RYAZANOVA & MAZOKHIN-PORSHNYAKOV, 1988; CONVEY, 1988; SANT & NEW, 1989). Information about female territorial behaviour is fragmentary. Territoriality by adult females was described by JACOBS (1955). Females of the libellulid dragonfly *Pachydiplax longipennis*, as well as males, defend territories and demonstrate aggressive interactions at foraging places. Such behaviour differs from sex-related behaviour at places of paring. Strategies of perch selection are different not only for different dragonfly species, but for a given species in different behavioural contexts, for example when resting, pairing, feeding (MILLER, 1989; EBERHARD, 1986).

METHODS

Field observations and experiments were carried out in July, 1991-92 in the park on the bank of Supoy Lake (Kiev Province, Central Ukraine). Some data were collected in July, 1989 in Kanew State Reserve (Cherkassy Province).

EXPERIMENTS WITH PERCHES were carried out at feeding places 500-800 m from the bank of the lake. A system of artificial perches was made from dry branches. This perches system was similar to a natural one and had seven levels (Fig. 1). It was used for quantitative recordings. Recordings of female transferences were carried out on warm sunny days from 11 a.m. to 4 p.m. After every 50-100 recordings, the system was moved to another place. When a male appeared at

the perches structure, the experiment was stopped, the male was captured and then recordings were renewed. The data were then classified: successful or unsuccessful attempt to occupy a perch; was perch free or occupied; from what point of the perches structure (level, distance from the branch top) and to what new point did the dragonfly move; direction of transference (up/down to new level, up/down along this level); reaction of other individuals to the attempt at transference. Then the information about direction of spontaneous transferences and transferences after previous unsuccessful attempts was extracted from consecutive series of recordings. Locomotor activity very much depends on changes of weather conditions. That is why, not absolute time, but an attempt to transfer in perch structure was used as the unit of time in recordings.

BEHAVIOURAL POSTURE RECORDINGS was carried out visually and with photographs. Angles of substrata slopes and angles of abdomens' slopes in relation to the substratum were measured from photographs. Duration of posture (in seconds after occupation of a new/old perch), perch position and character (top/base of a branch, leaf) were recorded during visual observations.

EXPERIMENTS WITH MODELS were carried out to find female reactions to models of males and females at feeding places. Reactions of mature males to these models at places of pairing on the bank of the lake were used as controls. Models were made of freshly-killed males and females and were constructed in a resting pose. They were presented for 3-4 s using a fishing rod, with a distance from model to dragonfly on perch of 20-30 cm. Reactions were scored using FRANTSEVICH & MOKRUSHOV's (1984) method but with the following differences: reaction "indifference" was scored as "pure indifference" (1) — individual reacted to model only with saccadic head movements, and "threat display" (TD). The second reaction is resembles the first one, but is more aggressive. In the field experiments nearly 1500 reactions were recorded.

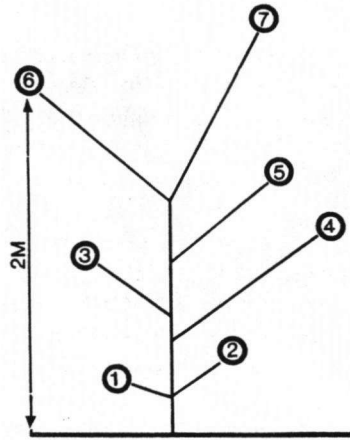


Fig. 1. The artificial experimental perches system.

RESULTS

PERCH SELECTION

In the morning when the sun warmed the park glades, *S. sanguineum* began to occupy perches in leeward places. On bushes, trees and in grass dragonflies orientated their bodies with the anterior to open space (Fig. 2). In meadows and glades, no regularity in body orientation was observed.

PERCHERS CHASE TYPE

Sympetrum species are typical "perchers". But sometimes, when there are many little high flying insects, they become "flyers". This type of feeding behaviour was observed on August 5, 1991 from 5 to 7 p.m. Great aggregations of *S. sanguineum* rose 2.5-5.0 m and made long feeding flights among chasing

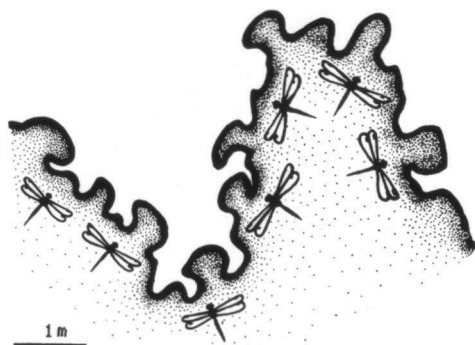


Fig. 2. *S. sanguineum* body orientation at feeding places in studied area. Dragonfly's field of vision is directed to open space.

Aeshna mixta. At the same time larger numbers of dragonflies chased from perches on trees.

During a feeding chase an individual occupies a specific feeding place. When prey appears, the dragonfly rushes after it, then returns to its own perch, rarely to another. The owner of the perch (female as well as male) guards its perch and pursues intruders in 6% of cases. After this the resident returns to its perch. If the intruder was very active we observed some cases of co-rotating

flights of two individuals. They moved around a centre, and a "ring" moved horizontally. Rarely a persistent intruder drives a resident away. But mostly it occupies another perch, when a resident is capturing its prey. At feeding places males are more active, more aggressive, but the behaviour of both sexes is similar.

PERCHING BEHAVIOUR

TOTAL LOCOMOTOR ACTIVITY. — There were more unsuccessful than successful attempts to displace an individual already on a perch. Attempts to transfer along the branch and up to another branch usually failed. Only 3.5% of attempts to take over an occupied perch succeeded. Only 8.6% of all transferences are directed to the base of the branch. More than 90% of these attempts succeeded. Dragonflies more often transfer from one level to another than along the branch of a perches system (Fig. 3).

SPONTANEOUS LOCOMOTOR ACTIVITY. — In classic ethology this refers to changes in the output of a system without a corresponding change in input (HINDE, 1975). In my experiment I consider movement of individuals following a successful previous attempt to be "spontaneous activity". Usually rest precedes cases of spontaneous activity. After this period individuals tend to move along a level and to higher level more often although in these cases the percentage of successful attempts was rather low (Fig. 3.3). Sitting time before transferring for differing directions differs. Locomotor activity after unsuccessful previous attempts was also recorded.

LOCOMOTOR ACTIVITY AFTER FAILURE. — I took into account only directions of subsequent transferences but not cases of returning to the perch after failure. After an unsuccessful attempt an individual frequently moves down along the perch or down to another level, rather than up. Repeated attempts to occupy

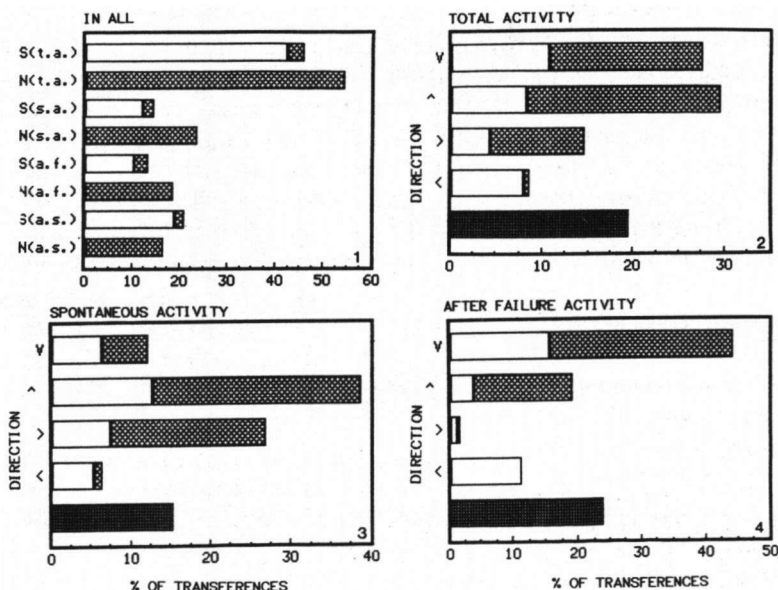


Fig. 3. Success of transferences in artificial perches system: (1) in all: to free perch (uncoloured bars), — to occupied perch (coloured bars), — S = successful attempts, — N = unsuccessful attempts, — t.a. = total activity, — s.a. = spontaneous activity, — a.f. = after failure activity, — a.s. = activity of intruders (n=370); — (2) total activity (n=427); — (3) spontaneous activity (n=190); — (4) activity after failure (n=179); — [V = down to new level, — ^ = up to new level, — < = basally along the level, — > = apically along the level, — white bars = successful attempts, — shaded bars = unsuccessful attempts, — dark coloured bars = fly away from perches system].

upper/lower perches fail twice as often compared with spontaneous locomotor activity. The percentage of individuals that leave the perches structure after these failures is twice as much compared with spontaneous locomotor activity.

SEQUENCE OF OCCUPYING OF PERCHES. — Upper perches (NN 6,7) are occupied first of all, the lower perches (NN 1-3) being occupied by later arrivals (Fig. 4). The sequence of occupying perches depends on the direction of an intruder's movement. If an individual arrives from low vegetation, e.g. grass, low perches can be occupied first. In this case the occupier of a low perch can rest for some time. Then it may try to occupy higher perches.

To what and from what perches are attempts of occupation made? Upper perches are more attractive for occupancy and they become springboards for new transferences. At the same time locomotor activity from/to the highest perch (N7) decreases compared with lower perches (Fig. 5).

PERCHING TIME — does not increase significantly with the height of the perch. There is a positive association between the length of time spent perching and

the position of a dragonfly relative to the top of the perch. Individuals on the highest perches keep their position for the longest time (Fig. 6). Consequently, individuals that are far from the top are more likely to transfer.

POSTURES ON PERCHES

As it is shown on Figure 7.1, the majority of individuals prefer perches with slope angle of $85-100^\circ$ relative to the horizontal. At the same time abdomen angles relative to the substratum can vary within rather wide limits ($25-125^\circ$). Freshly-emerged insects often hang on to the substratum like some aeshnid dragonflies (such cases were not taken into account). Thus the majority of individuals try to compensate for substratum slope with their body postures (Fig. 8). Some individuals keep their abdomens elevated. Dragonflies can adopt this posture by jerky movement of the abdomen when an intruder arrives. Subsequently the female adopts a resting

posture in most cases, rarely keeping the abdomen elevated for long. The resting female also raises her wings (Fig. 9.3-6), that in the resting state are held forward and depressed (Fig. 9.1,2). This behaviour is the threat display (TD) that for females is called "refusal display" when approached by a male (UTZERI, 1988).

		No. OF PERCHES							sum
		1	2	3	4	5	6	7	
No. OF PERCHINGS	1								10
	2								9
	3								10
	4								9
	5								9
	6								8
	7								7
	8								8
	9								8
	10								8
	11								8
	12								8
	13								8
	14								8

Fig. 4. Number of perchings in relation to the number of perches ($n=118$). — [sum = total number of occupations, — one darkened block (■) = single occupation].

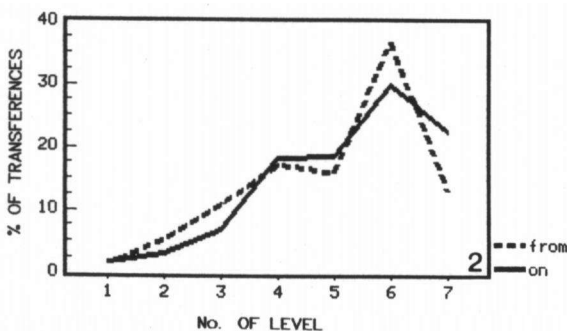


Fig. 5. Dependence between duration of sitting and height of perch ($n=662$). — [continuous line = transferences to the perch, — dotted line = transferences from the perch. An attempt to transfer in perch structure was used as the unit of time in recordings].

Such TD-behaviour of *S. sanguineum* is characterized by wing, abdominal and mixed demonstrations. Individuals keep the wings spread and abdomen raised for some time after landing; then the wings move gradually to the fore position and abdomen lowers slightly. A female which has settled demonstrates the TD for 10 sec in most cases, but sometimes for a longer time (Fig. 7.2) for example on a new substratum. Wing displays occur more often and last for a longer time than abdominal displays. TD-duration is not evidently connected with the substrata characteristics. When individuals sit on a branch close to one another multiple jerky abdominal lowering was often observed. This may be TD-demonstration too. The female landed on the branch from the acute angle walked off on the branch, and finally occupied the perch in an obtuse angle.

FEMALE REACTIONS TO MALE AND FEMALE MODELS

Undoubtedly, experiments with models give results that differ slightly

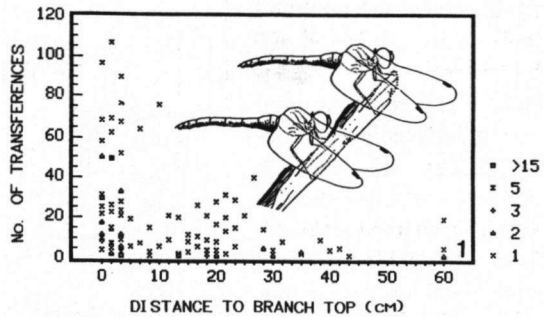


Fig. 6. Dependence between duration of sitting and distance to branch top (cm) $n=138$. An attempt to transfer in perch structure was used as the unit of time in recordings.

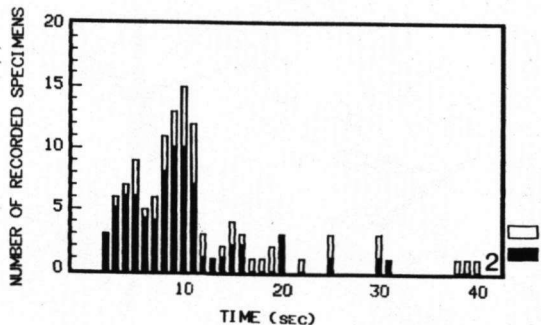
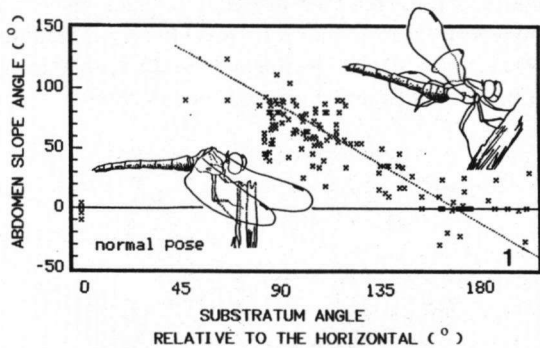


Fig. 7. Threat display (TD): (1) dependence between abdomen slope angle and substratum slope angle ($n=150$). [Dotted line delimitates usual postures and abdominal TD-displays], — (2) duration of wing or/and abdominal TD-display on new (white bars)/old (black bars) perch ($n=100$).

from natural behaviour of individuals, but it is possible to draw some conclusions about the communication between individuals at places of feeding. Perching female reactions to female models and male models resemble territorial male reactions to male models. The ethogramm (Fig. 10) characterizes territorial individuals with respect to aggressive orientation. It differs from the ethogramm of male territorial individuals demonstrating positive orientation. Such male behaviour is shown to female models at places of pairing. Thus females at feeding places demonstrate agonistic behaviour to all conspecific and closely related intruders, but aggressive reactions to male models are expressed more strongly.

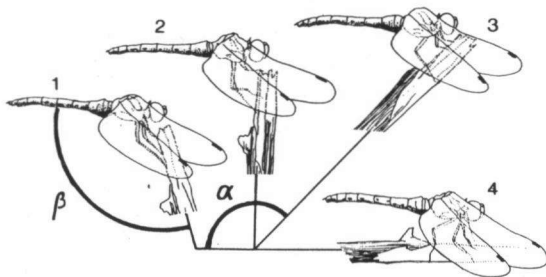


Fig. 8. Usual (resting) dragonfly postures on different slopes: (1) least acceptable substratum slope; (3) preferred substratum slope [α = slope substratum angle, β = abdominal angle].

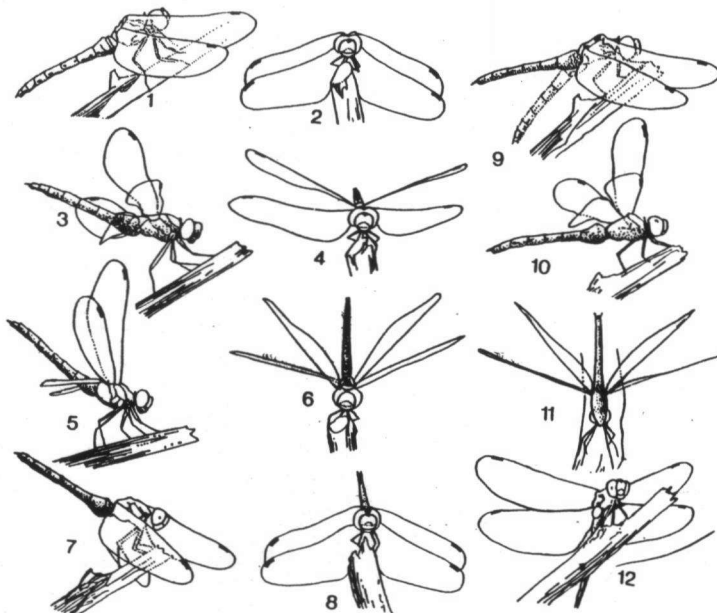


Fig. 9. Different female postures on perches: (1-2) — usual (resting) posture; — (3-4, 5-6, 11) different stages of TD-demonstration (wing-abdominal demonstration); — (7-8) TD-demonstration (abdomen raising); — (9) jerky down-movements of abdomen; — (10) TD-demonstration (wing raising); — (12) dragonfly's posture after emergence from larval stage. — [(1, 3, 5, 7, 9, 10) side view; — (2, 4, 6, 8, 12) anterior view; — (11) posterior view].

DISCUSSION

The strategy of waiting on a perch for flying prey to approach is most energy-economical and is probably the most advanced in evolutionary sense (ZAIKA & VORONOVA, 1977). The advantages of perch and chase are especially strong when there is a shortage of prey. Male "perchers" guard the territory at places of pairing by perching and flying at intruders (PARR, 1983) and male "flyers" defend the territory by patrolling. Thus perch selection by perchers is an important aspect of their territorial behaviour. Patrolling species select a perch only for egg laying or rest; perching species can use a perch for different functions [(feeding — (EBERHARD, 1986); roosting — (REHFELDT, 1986); pairing — (MOKRUSHOV, 1982; EBERHARD, 1986)].

Agonistic territorial behaviour on perches at the places of pairing resembles the behaviour on feeding perches. Perch keeping strategy is to return as quickly as possible after pursuing prey, because the perch could be occupied by another dragonfly. The presence of a conspecific dragonfly on the perch and its behavioural displays (PAJUNEN, 1963; UTZERI, 1988; GORB, 1992) may signal about perch occupation. Wing and abdominal displays are usual for dragonflies and are typical for some other insects: Coleoptera (OBATA, 1988), Lepidoptera (OBARA, 1984). For example, the close presence of a conspecific individual results in abdominal movements of *S. sanguineum*. Such behaviour is known in *Xanthocnemis zealandica* larvae as a threat posture (ROWE, 1980). In *S. sanguineum* females such displays may be connected with threat behaviour too.

Active aggression with territory guarding is known for females of some other libellulid dragonflies (JACOBS, 1955; BAIRD & MAY, 1988). Co-rotating flights were described for some butterflies by SIBATANI (1989). Such behaviour is

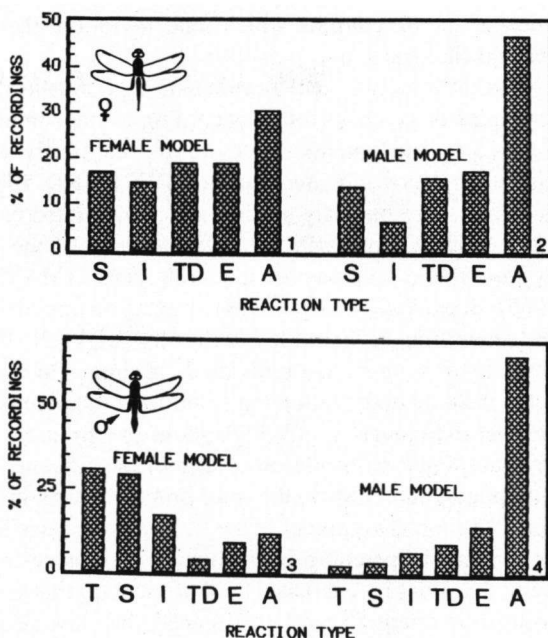


Fig. 10. Experiments with models: (1-2) female reactions at feeding places (n=320); — (3-4) male reactions at places of pairing (n=214). — [(1, 3) female models; — (2, 4) male models; — reaction types: t = tandem, — s = survey, — i = indifference, — td = threat display, — e = escape, — a = attack].

unusual for dragonflies which tend to follow their escaping intruder along a straight line trajectory.

PERCH SELECTION AND TRANSFERENCES ON PERCHES. — Insects have different strategies of perch selection according to their motivations.

Females and juvenile males of the damselfly *Hetaerina macropus* occupy higher perches than mature males (EBERHARD, 1986). During sexual behaviour males of some butterfly species are concentrated on the tops of hills (DENNIS, 1987; KELSON & MINNO, 1983). Males of the pompilid wasp, *Hemipepsis ustulata* prefer high perches at pairing places (MATTHES-SEARS & ALCOCK, 1985). Bees (*Xylocopa*, *Bombus*) foraging on trees demonstrate directional activity and move from higher to lower flowers (KEVAN, 1990). Selection of a foraging perch by *S. sanguineum* individuals is similar to that of *Hetaerina*. An "ideal" perch must meet the following conditions: (1) plentiful food, — (2) the minimum of other individuals, — (3) high above the ground, — (4) distal part of the perch structure. The first condition is the most significant. The second one is connected with population density, the third and the fourth give the possibility of the best field of vision. This model of the "ideal" perch can explain spontaneous locomotor activity in perching behaviour. Transferences to a higher level or distally along this level give a better field of view. In that way a high percentage of such occupation attempts can be explained. The low percentage of successes can be explained by occupation of the best perches by other dragonflies. Spontaneous activity succeeds in occupying a perch more often than attempts after previous failures. Probably, in the first case the dragonfly wittingly selects a better free perch for occupation. In the second case the insect has no time for perch selection and occupies any free perch or leaves this perches system. Percentage of successes in transferences down along this level depends on vacancy of the proximal part of the branch. After occupying the perch on the proximal part of the branch the dragonfly tries to move to the branch top. When females reach higher perches, they leave them willingly to examine new ones. Such behaviour was described for the wasp *Hemipepsis ustulata* (MATTHES-SEARS & ALCOCK, 1985). At the same time higher perches are more attractive for individuals from lower perches. The decrease of to/from-activity in an apical perch area seems surprising on the face of it. In nature dragonflies do not experience an infinite choice of perches but some definite and limited number of potential perches (a branch, a tree, a plant group). When an apical perch is occupied, the conditions of an "ideal" perch are fulfilled and consequently, from-activity decreases. Decrease of to-activity is caused by occupation of the apical perch for a long time. Sitting time decreases with increasing distance from top of any level. Thus dragonflies sitting proximally demonstrate from-activity more often.

POSTURE IN RELATION TO THE ANGLE OF THE PERCH. — Perches with slope angles of 90-120° appear to be more preferable, because they are more energetically advantageous. When the perch angle is less than 90°, the body centre of

gravity and fulcrum point are far separated. A dragonfly must spend additional energy to keep balance. When perch angles are more than 90° these points coincide.

DRAGONFLY THREAT DISPLAY WHEN PERCHING. — Occupying a perch or returning to it after flight, a female indicates a territory occupation by wing and/or abdominal displays for some time. The length of time varies very much and depends on many factors: perch type, distance between individuals, previous behavioural factors, and physiological state of the dragonfly. Usually nearly one third of individuals sitting on perches demonstrate TD. It is generally supposed that libellulid abdominal postures are functionally connected with thermoregulation (DELL'ANNA et al., 1990). This conclusion is based on the fact that the number of individuals with raised abdomens and abdominal angle increases as air temperature rises. These two factors are also correlated with an increase in the abdominal angle.

REACTIONS OF PERCHING FEMALES TO MODELS OF CONSPECIFIC MALES AND FEMALES. — Territorial males of *S. sanguineum* at places of pairing strictly differentiate conspecific males and females by morphological signs (FRANTSEVICH & MOKRUSHOV, 1984; MOKRUSHOV, 1987). Females are usually thought to be passive. But RÜPPELL (1989) shows that anisopteran females can repel males and prevent tandem formation using their fore legs. Nothing is known about distant sex differentiation by dragonfly females. It was found that at feeding places male models more often than female models are attacked by perching females. Other recorded behavioural reactions such as escape, indifference and survey were the same. Probably, in these behavioural situations the level of motivation connected with reproduction as comparing with level of motivation connected with feeding was rather low. In this case the female defends its feeding territory from conspecific individuals of both sexes as well as from individuals of closely related species. The ratio of negative (a, e, i) and positive (s) reactions in females absolutely corresponds to that of territorial behaviour of males at places of pairing. Probably, at feeding places sexual activity of *S. sanguineum* males must decline, as in the libellulid dragonfly, *Pachydiplax longipennis* (BAIRD & MAY, 1988).

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