

**INTERSPECIFIC COMPETITION IN SYMPATRIC *SYMPETRUM*
SANGUINEUM (MÜLLER) AND *S. FLAVEOLUM* (L.)
(ANISOPTERA: LIBELLULIDAE)**

G.E. REHFELDT and H. HADRYS

Zoologisches Institut der Technischen Universität, Pockelsstrasse 10a,
D-3300 Braunschweig, Federal Republic of Germany

Received April 30, 1987 / Revised and Accepted May 5, 1988

The influence of interspecific interactions between adults of sympatric *S. sanguineum* and *S. flaveolum* on the perching and flight behaviour of the males and the reproductive behaviour was studied at waters near Brunswick (FR Germany). Grid mappings show a horizontal habitat selection. *S. flaveolum* preferred perch and oviposition sites at earlier successional stages with lower height of the emergent vegetation. The overlapping indices and cumulations of the males' perches were density-related. In areas with common oviposition sites there was a vertical separation of both species. The perches of the males of *S. sanguineum* were higher vertical stalks whereas *S. flaveolum* males remained perched lower on broad sloping stalks. The height of the perch site was influenced by the presence of heterospecific males. — Site-tenacious *S. flaveolum* males showed a longer total time of flight and more flights over longer distances. They were involved in interactions with males of the other species more frequently than *S. sanguineum* was with conspecific males. Males with neighbouring heterospecifics were more site-fixed and their flight activity decreased. In *S. sanguineum* 48% (versus 40% in *S. flaveolum*) of the ovipositing tandems were interfered with by heterospecific males mostly when changing the oviposition site. Possible ultimate factors selecting for the spacing out of the species (different horizontal habitat selection and interspecific interactions) are discussed.

INTRODUCTION

The importance of interspecific competition for limited resources in the evolution of species differences and community organization in insects seems unclear (WIENS, 1977; SCHAEFER, 1981). In dragonflies most studies provide indirect evidence of competition by showing partitioning along some resource gradient (MOORE, 1952; LUTZ & PITTMAN, 1969; PAULSON & JENNER, 1971;

CONSIGLIO et al., 1972; MIZUTA, 1974; BENKE & BENKE, 1975; KAISER, 1975; TENNESSEN, 1975; VAN NOORDWIJK, 1978; MILLER, 1982). Because of their overlapping habitats adult dragonflies frequently interact interspecifically. Males patrolling or occupying a perch at the reproductive site fly not only against conspecifics but also against males of other species (WESENBERG-LUND, 1913; ST. QUENTIN, 1934; JOHNSON, 1963; PETERS, 1972; WAAGE, 1973; PARR, 1983).

We studied *Sympetrum sanguineum* and *S. flaveolum*, which co-exist in central Europe in marshes, secondary waters and bogs. Their flight season and niches overlap in a wide range. Males perching in emergent vegetation fly against heterospecific males and interfere with tandems at water. We discuss the influence of this behaviour on the spatial distribution of the males and the reproductive behaviour of both species.

MATERIAL AND METHODS

The study was conducted at a sand-pit northwest of Brunswick (FR Germany) in 1985. The area (70 × 50 m) is covered in small waters with *Phragmites australis* and *Typha latifolia* and in moist parts mainly with *Carex* spp. and *Juncus effusus*. In spring, it is flooded to a depth of 0.2-0.5 m and during summer becomes almost dry. Temporarily heavy rains can moisten the area again.

The spatial and temporal distribution of adults was recorded by marking and grid mapping from July to October, 1985. We divided the area into 48 study plots (8 × 8 m each). Each census, up to three in a day, lasted about 45 min. After each recording — in total 37 — the surrounding fields and meadows of the study area were thoroughly searched. Netted males and females were individually marked with waterproof spots on the front and rear wings.

We observed site-tenacious males from about 10.00 a.m. Civil time, when both species showed reproductive behaviour. To characterize the structure of the plots and the males' perches we determined the composition and height of the emergent vegetation. The density of the vegetation was measured counting the number of stalks on 0.25 m² at 0.5 and 1.0 m above the ground. *Typha* stalks were exposed in areas with common perch sites of both species to analyse differences in perch height. Each of the 12 test groups consisted of 5 stalks with heights of 0.15, 0.30, 0.45, 0.60 and 0.75 m and spaced at regular distances apart of 0.20 m. Here, between 21-31 August, site-tenacious males were recorded at noon at intervals of 30 min.

We recorded flight activity of site-tenacious males at intervals of 10 min in 1985 and 1986. The flight time and different flight styles were noted. We distinguish between spontaneous flights, flights against conspecific and heterospecific perching males, wandering males and changes of perch sites. To attain a measure of the flight distances around the perch sites, positions of the males and their flyways were noted on maps and we determined the distance from the first to the most distant perch site during the observation interval. We distinguished between situations with or without nearby other conspecific or heterospecific males at a radius of 3 m around the site-fixed male.

Interspecific interactions of males with ovipositing tandems were recorded at a small *Sphagnum* bog (1800 m²) in 1987. We observed and filmed tandems of both species with a video-camera from the end of copulation to the end of oviposition and the following separation. Only complete sequences were analysed. The oviposition site, the number of flights of heterospecific males against tandems and the responses of the affected pairs were noted.

The overlappings of the niches were determined with the formula of SCHOENER (1970):

$$C_{ih} = 1 - \frac{1}{2} \sum_j |p_{ij} - p_{hj}|$$

Local cumulations of the individuals were calculated with the formula of IWA0 (1972):

$$P = \frac{m_{ci} - m_{ci-1}}{\bar{x}_i - \bar{x}_{i-1}} \text{ and } m_c = (1 + \frac{s^2 - x}{\bar{x}^2}) x$$

where $i = 1$ for the smallest plot.

The population sizes were estimated with the method of DU FEU et al. (1983):

$$(1 - \frac{N}{\hat{p}}) = (1 - \frac{1}{\hat{p}})^{(N+R)}$$

where \hat{p} = population size, N = number of marked individuals and R = number of recaptures.

RESULTS

At the sandpit, 215 males were marked (179 *S. sanguineum*, 36 *S. flaveolum*). 69 *S. sanguineum* males (= 38.5%) and 25 *S. flaveolum* males (= 69.4%) were found again at least once. The population estimates and densities from censuses show much higher numbers in *S. sanguineum* (Tab. I).

Table I
Numbers of males (\pm SD), derived from mark-recapture studies and grid mappings

Method	<i>S. sanguineum</i>	<i>S. flaveolum</i>	Ratio
Mark-recapture studies	224.9 \pm 32.0	34.0 \pm 17.4	7.8:1
Grid mapping	32.9 \pm 8.8	15.5 \pm 6.2	2.1:1
Mark-recapture/mapping	6.8:1	2.2:1	

The distribution of the adults and the perch behaviour of males were studied only in the second half of August 1985, when the densities of both species and the oviposition activity were highest (Fig. 1b, c). The spatial separation was largest when the density of *S. flaveolum* males was relatively low. In this period the overlapping index was small (Fig. 1d). Site-tenacious *S. sanguineum* males concentrated in permanent wet areas with higher emergent vegetation (1.84 \pm 0.57 m, $n=70$). *S. flaveolum* males and ovipositions of this species were restricted to the drier study plots of earlier successional stages with lower *Juncus* stands (1.60 \pm 0.49 m, $n=53$). The height of the vegetation around the perch and oviposition sites differed significantly for the two species (Mann-Whitney-test; $p < 0.01$).

We describe local cumulations of males with the formula of IWA0 (1972). At low densities *S. flaveolum* ($P = 3.6$) showed a stronger concentration in only a few plots (*S. sanguineum* $P = 2.6$). High densities of both species, however, led to cumulations especially in areas with common oviposition sites (*S. sanguineum* $P = 1.7$, *S. flaveolum* = 2.0; Fig. 2b). In *S. sanguineum*, however, only a part of the total number of males perched in the study area. Mostly pair formation took place in the morning outside the sandpit and from there the tandems flew to the

oviposition sites. We did not record comparable flight movements in *S. flaveolum*. The frequency relationships comparing the individual numbers from the mark-recapture study and the actual densities from censuses support these observations (Tab. I).

Preferred perches of both species were the broken and withered *Typha* stalks of the preceding year. 76.4% of the *S. sanguineum* males and 68.9% of the *S. flaveolum* males were recorded on this type of perch. The average perch height of both the species was different. *S. flaveolum* remained perched on lower stalks, often near the ground (0.37 ± 0.21 cm; $n=34$). Males of the other species were found on higher stalks (0.58 ± 0.22 cm; $n=50$; Mann-Whitney-test, $p < 0.001$). Evidently, the species preferred certain kinds of perches (Tab. II). *S. flaveolum* males perched on broad sloping and inclined stalks whereas *S. sanguineum* males preferred vertical *Typha* stalks ($\chi^2=9.88$, $p < 0.01$).

These different perch heights were verified by exposing groups of vertical

Typha stalks at common oviposition sites (Fig. 3). *S. flaveolum* males were perched lower (0.24 ± 0.15 m; $n=26$) than *S. sanguineum* (0.37 m \pm 0.19 m; $n=36$; Student's t-test, $p < 0.01$) The height of the perch site was influenced by the

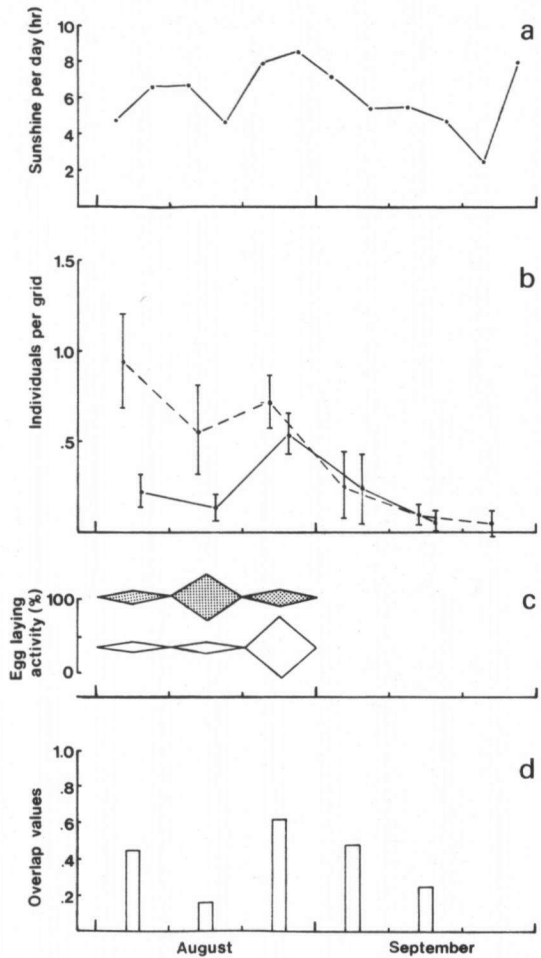


Fig. 1. Distribution of the *Symptetrus* species at the sand pit in August-September: (a) Period of sunshine per day; — (b) Male density per grid and per decade after noon recordings (broken-line: — *S. sanguineum*, — unbroken line: *S. flaveolum*, — vertical line: SD; — (c) Oviposition activity (%): *S. sanguineum* (dotted, $n=46$), — *S. flaveolum* (open $n=18$); — (d) Overlapping indices (C) of the males' records.

presence of males of the other species (Fig. 4). With neighbouring heterospecific males, both *Sympetrum* species perched lower than in the presence of conspecific males (Mann-Whitney-test, $p < 0.01$).

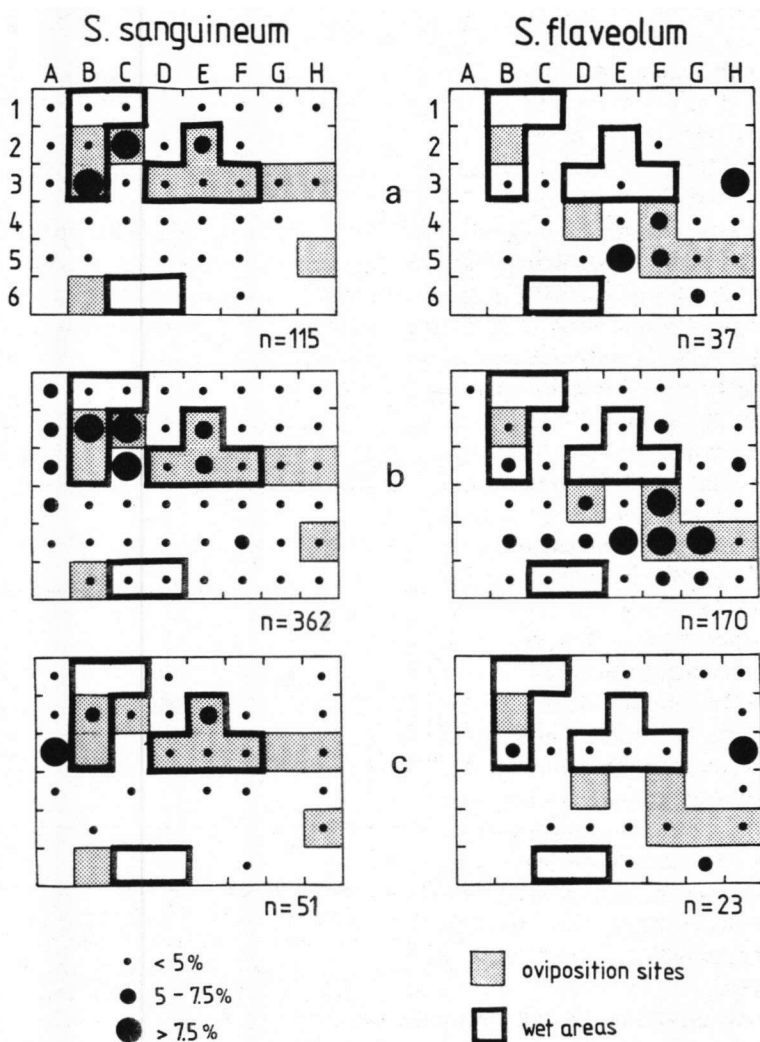


Fig. 2. Distribution of: (a) males in the morning; — (b) males at noon at the end of August 1985; — (c) females during the whole investigation period. — [Small points indicate < 5%, middle-sized points 5-7.5% and large points > 7.5% of the total number of individuals. — Plots with thick lines: permanent wet areas, — shaded plots: oviposition sites]

Table II
Distribution of site-tenacious *Sympetrum sanguineum* and *S. flaveolum* males among different types of perches

Type of perch site (height)	<i>S. sanguineum</i> (n=50)	<i>S. flaveolum</i> (n=34)
Inclined stalks (0.47 ± 0.16 cm; n=52)	10	18
Vertical stalks (0.60 ± 0.26 cm; n=154)	40	16

At these perching and oviposition sites we examined the flight behaviour of the site-fixed males. If the total flight times are compared, *S. flaveolum* stayed in the air almost twice as long (45.6 ± 28.2 s/10 min) as *S. sanguineum* (24.8 ± 16.3 s/10 min; Mann-Whitney-test, $p < 0.001$), resulting from spontaneous long-lasting flights connected with a change of perches (Figs 5a, e).

In low male densities spontaneous flights ($p < 0.001$) and changes of perches ($p < 0.01$) were longer in *S. flaveolum* and predominated (83.1% of flights) (Figs 5d, e). With neighbouring males the time of flights against conspecifics increased in *S. sanguineum* to almost 80%, and in *S. flaveolum* against heterospecifics to 54% (Fig. 5b). However, in this species the total number of flights in situations with neighbouring *S. sanguineum* decreased compared with situations without other males ($p < 0.05$). The number of records of flights by *S. flaveolum* against conspecific males was too small to be evaluated. Flights against wandering males by both species were only short (Fig. 5c). Feeding or flights against females were not noticed.

We observed interspecific competition in reproductive behaviour at a *Sphagnum* bog with high densities of both species. Here, the oviposition sites could be in different parts of the habitat: open *Sphagnum* areas without higher

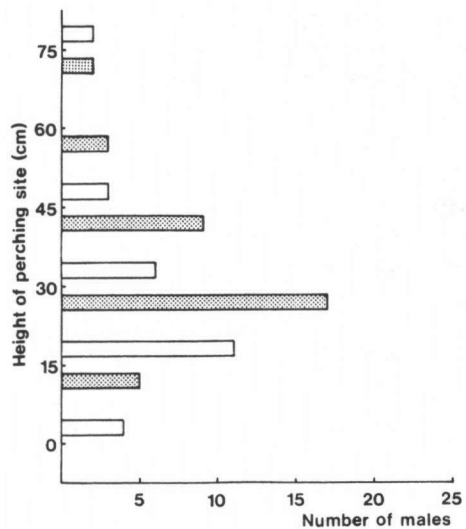


Fig. 3. Distribution of males on exposed perches of different height: *S. sanguineum* (dotted, n=36); — *S. flaveolum* (open, n=26).

vegetation, transitional areas with *Sphagnum* and little grass and areas with dense, 45-55 cm high stands of grass or *Carex* spp. Both species differed in their oviposition sites ($\chi^2 = 12.5$, $p < 0.001$; Tab. III). *S. sanguineum* was restricted to areas with higher vegetation around the periphery of the bog whereas ovipositing *S. flaveolum* in tandem preferred the moist or wet inner parts of the bog, mainly those covered with *Sphagnum*. The actual number of perching males was 25-30 in *S. flaveolum* and 15-25 in *S. sanguineum*. Ovipositing tandems were interfered with by encounters with

conspecific as well as heterospecific males. In *S. sanguineum* 48% of ovipositing tandems were interfered with by heterospecific males versus 48% by conspecifics. However, in this species reproductive encounters with heterospecific males occurred more often in the transitional area than in the dense grassland ($\chi^2 = 3.88$, $p < 0.05$). Among 10 tandems disturbed eight interrupted oviposition and

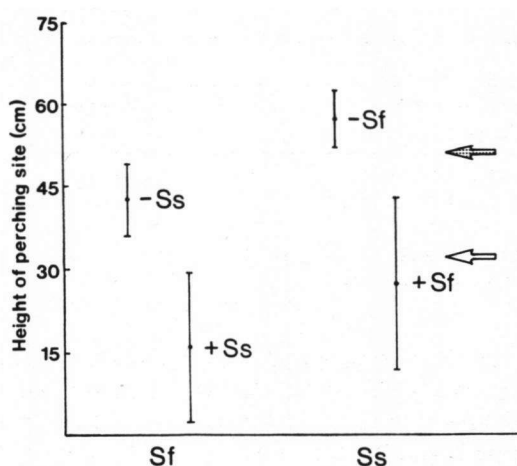


Fig. 4. Height of perches when a heterospecific male was present (+) or absent (—) within a radius of 3 m. — [Arrows: total average of *S. sanguineum* (Ss, dotted, $n=50$) and *S. flaveolum* (Sf, open, $n=34$). — Vertical lines: 95% confidence limit].

Table III

Numbers of ovipositing tandems at different sites of the *Sphagnum* bog, and interspecific interference with males

Oviposition site	<i>S. sanguineum</i> ($n=21$)	<i>S. flaveolum</i> ($n=15$)
Grass		
total	13	4
interfered with	4	1
Grass <i>Sphagnum</i>		
total	8	4
interfered with	6	2
<i>Sphagnum</i>		
total	0	7
interfered with	0	3

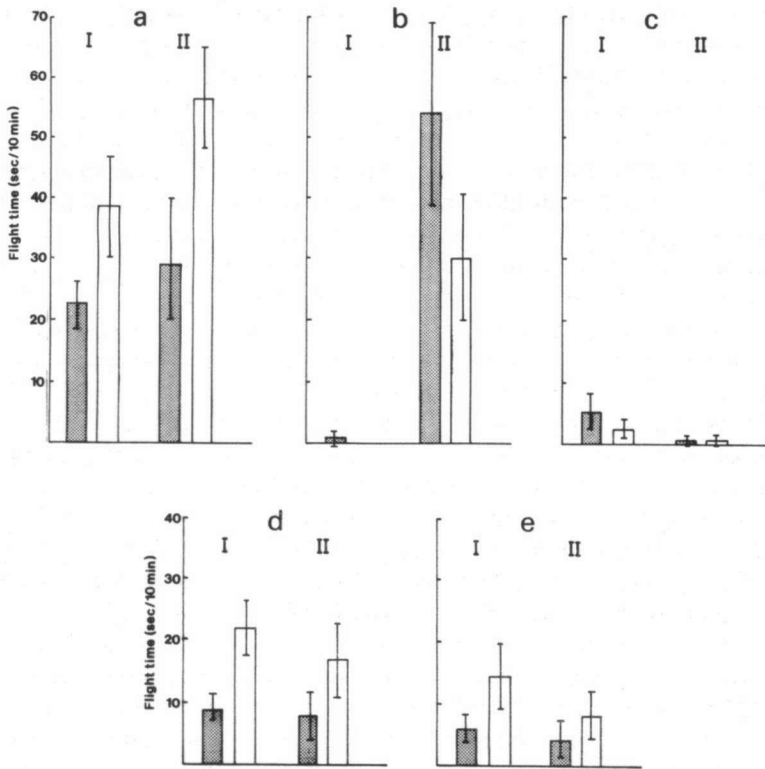


Fig. 5. Flight time: (a) total; — (b) against *S. sanguineum* males; — (c) against wandering males; — (d) spontaneous flights; — (e) changes of perch sites in males of *S. sanguineum* ($n=54$, dotted) and *S. flaveolum* ($n=48$, open) without (I) and with (II) neighbouring males. [Vertical lines: SD].

changed site. In *S. flaveolum* egg-laying tandems at the open *Sphagnum* areas were especially interfered with by conspecific males. 73% of the encounters were with conspecifics whereas 40% were with heterospecifics. We recorded up to six approaches of heterospecific males per oviposition and changes of site occurring over distances up to 8 m.

DISCUSSION

MAPPING METHOD

In most dragonfly studies concerning survival rates, estimates of population size or dispersal mark-recapture methods are applied (e.g. MANLY & PARR, 1968; CONNOR, 1971; SOUTHWOOD, 1978; HIGASHI, 1969; PARR &

PARR, 1974; HILTON, 1983; WATANABE, 1986). GARRISON (1978) used mark-recaptures and a grid net to determine individual movements. In this study the formula of DU FEU et al., (1983) allowed iterative population estimates with only a few recaptures. Especially in Anisoptera, however, the preconditions for population estimates with mark-recaptures, e.g. a closed population, are seldom fulfilled; so there are considerable estimation errors. *Sympetrum sanguineum* males were more easily detectable than *S. flaveolum* males because of the vigorous flight movements of tandems between different parts of the habitat. Therefore, recaptures of *S. sanguineum* were more probable explaining the high male frequencies derived from population estimates (Tab. I).

There are hardly any studies concerning census and mapping methods for adult dragonflies. In libellulids direct counts were used at small waters to determine population densities (PAJUNEN, 1963, 1966; CAMPANELLA & WOLF, 1974; GREEN, 1974; WOLF & WALTZ, 1984; TSUBAKI & ONO, 1986). Linearly distributed species at the shore of larger waters were recorded with transect counts (KOENIG & ALBANO, 1985). Repeated studies of adult distribution, e.g. individual territories, require quantitative mapping methods (e.g. WOLF & WALTZ, 1984; HILDER & COLGAN, 1985). With a net of grids it is possible to get actual individual numbers and local changes of the dispersion over short periods. Best recordings give fixed count units as territorial males or individuals on resting sites. Flying odonates often can be censused better with line transects or point censuses. The size of the plots depends on the density of the individuals, their specific flight behaviour and the nature of the investigated area. Recordings should be made under favourable weather conditions with short investigation periods to avoid errors from flight movements. Successional censuses should follow a random walk. With a high number of plots it is possible to determine grid frequencies (REHFELDT, 1982).

INTERSPECIFIC INTERACTIONS

For insects there are only a few works concerning competition on the basis of interspecific territorial behaviour (BAKER, 1983; FITZPATRICK & WELLINGTON, 1983). MOORE (1964) has shown that aggressive interactions between males of different dragonfly species can lead to an exclusion from certain areas of the water. Our study supports notion of a stronger spatial partitioning of different species caused by interspecific competition. The interactions between site-tenacious, heterospecific males and flights against ovipositing tandems which are chased away, promote different distributions.

Both *Sympetrum* species prefer different oviposition sites, but they overlap in a wide range of their habitat (Fig. 2, Tab. III). In the r/K-continuum (PIANKA, 1970), *S. flaveolum* is more a pioneer species and an r-strategist. This can be seen from the shorter time of larval development (MÜNCHBERG, 1930) as well as

from the types of waters in which it breeds. *S. flaveolum* is restricted to earlier successional stages of marshes, secondary waters and *Sphagnum* bogs with low vegetation. These types of waters have an oligo-/mesotrophic character. At the sandpit new open oviposition sites, resulting from drying up, were quickly occupied by males. In contrast, *S. sanguineum* also develops at larger ponds and pits with fluctuating water levels and higher reeds or wet grassland (e.g. ROBERT, 1958; GEIJSKES & VAN TOL, 1983; FRANTSEVICH & MOKRUSHOV, 1984). The water quality is mesotrophic to eutrophic.

S. flaveolum recognizes conspecifics by the colour of the wings whereas *S. sanguineum* does not (FRANTSEVICH & MOKRUSHOV, 1984). This could explain the higher frequency of interactions in *S. sanguineum* males with wandering males approaching the surroundings of the perch site. *S. flaveolum* males were more often intruders than were site-tenacious males of the congeneric species because of their frequent long-distance flights and changes of perch site. They were always chased away (see WOLF & WALTZ 1984). The study of perching behaviour also shows a vertical partitioning of males that can be expected in a poorly structured environment featuring emergent vegetation. However, with neighbouring heterospecifics the males of both species change their perch height. In these situations *S. flaveolum* is fixed closer to the perch site and the males are placed lower in the vegetation. This could be also correlated with the different abilities of the species to recognize each other. *S. flaveolum* males seem to avoid interference with heterospecifics to a higher degree.

The influence of interspecific interaction on ovipositing tandems could be shown in both species. In the transitional area between the open *Sphagnum* bog and the dense grassland the highest rate of aggressive interactions against tandems of *S. sanguineum* was observed. Tandems ovipositing in more open areas were frequently intercepted and chased away. Here, in contrast to the main oviposition sites of both species, interspecific interactions seem to be more frequent than intraspecific ones. They influence the distribution of tandems in areas with common oviposition sites and promote habitat partitioning.

In both species horizontal habitat selection as well as interspecific interactions lead to a strong spatial separation. Possible factors mediating this are competition for food, competition for females or oviposition sites and a reduction of predation pressure. In productive environments competition for food is unlikely to be important. In co-existing species that are similarly coloured, such as those of *Lestes*, *Enallagma*, *Gomphus* and *Sympetrum*, hybrids and mixed species tandems have been found (BICK & BICK, 1981; ASAHINA, 1974). However, heterospecific sexual competition may occur only exceptionally. We observed only one heterospecific copulation and an egg-laying tandem of a male *S. flaveolum* and a female *S. sanguineum* at the *Sphagnum* bog.

Competition for oviposition sites seems to be more important in species with endophytic oviposition (BICK & BICK, 1972; WAAGE, 1975). In exophytic

species the main advantage of partitioning seems to be related to predation of adults or eggs. In *Sympetrum*, especially, ovipositing tandems are vulnerable to potential predators such as frogs (RÜPPELL, 1984). Guarding males in *S. sanguineum* were caught in dense grass by spiders. We suppose that interspecific interactions regulate the distribution of the co-existing species and decrease the risks of predation.

ACKNOWLEDGEMENTS

We are grateful to Professor P.S. CORBET for valuable comments and to Mr D. HAUPT for correcting the English version of the manuscript. The study was supported by the DEUTSCHE FORSCHUNGSGEMEINSCHAFT.

REFERENCES

- ASAHINA, S., 1974. Interspecific hybrids among the Odonata. *Jap. J. Zool.* 17: 67-75.
- BAKER, R.R., 1983. Insect territoriality. *A. Rev. Ent.* 28: 65-89.
- BICK, G.H. & J.C. BICK, 1972. Substrate utilization during reproduction by *Argia plana* Calvert and *Argia moesta* (Hagen) (Odonata: Coenagrionidae). *Odonatologica* 1: 3-9.
- BICK, G.H. & J.C. BICK, 1981. Heterospecific pairing among Odonata. *Odonatologica* 10: 259-270.
- BENKE, A.C. & S.S. BENKE, 1975. Comparative dynamics and life histories of coexisting dragonfly populations. *Ecology* 56: 302-317.
- CAMPANELLA, P.J. & L.L. WOLF, 1974. Temporal leks as a mating system in a temperate zone dragonfly (Odonata: Anisoptera). I. *Plathemis lydia* (Drury). *Behaviour* 51: 49-87.
- CONNOR, W.F., 1971. Marking and recapture techniques for adult Odonata. *Can.Fld Nat.* 85: 68-70.
- CONSIGLIO, L., R. ARGANO & L. BOITANI, 1972. Ecological niches in two communities of adult Odonata. *Abstr. XIVth Int. Congr. Ent.*, Canberra, p. 193.
- DU FEU, C., M. HOUNSOME & I. SPENCE, 1983. A single-session mark/recapture method of population estimation. *Ring. & Migration* 4: 211-226.
- GARRISON, R.W., 1978. A mark-recapture study of imaginal *Enallagma cyathigerum* (Charpentier) and *Argia vivida* Hagen (Zygoptera: Coenagrionidae). *Odonatologica* 7: 223-236.
- FITZPATRICK, S.M. & W.G. WELLINGTON, 1983. Insect territoriality. *Can. J. Zool.* 61: 471-486.
- FRANTSEVICH, L.T. & P.A. MOKRUSHOV, 1984. Visual stimuli releasing attack of a territorial male in *Sympetrum* (Anisoptera: Libellulidae). *Odonatologica* 13: 335-350.
- GEIJSKES, D.C. & J. VAN TOL, 1983. *De libellen van Nederland*. Kon. Ned. natuurh. Veren., Hoogwoud.
- GREEN, J., 1974. Territorial behaviour in some Nigerian dragonflies. *Zool. J. Linn. Soc.* 55: 225-233.
- HIGASHI, H., 1969. Territoriality and dispersal in the population of dragonfly, *Crocothemis servilia* Drury (Odonata: Anisoptera). *Mem. Fac. Sci. Kyushu Univ.* (E) 5: 95-113.
- HILDER, B.E. & P.W. COLGAN, 1985. Territorial behaviour of male *Nannothemis bella* (Uhler) (Anisoptera: Libellulidae). *Can. J. Zool.* 63: 1010-1016.
- HILTON, D.F.J., 1983. Territoriality in *Libellula julia* Uhler (Anisoptera: Libellulidae). *Odonatologica* 12(2): 115-124.
- IWAIO, S., 1972. Application of the m-m method to the analysis of spatial patterns by changing

- the quadrat size. *Res. Pop. Ecol.* 14: 97-128.
- JOHNSON, C., 1963. Interspecific territoriality in *Hetaerina americana* (Fabricius) and *H. titia* (Drury) (Odonata: Calopterygidae) with preliminary analysis of the wing color pattern variation. *Can. Ent.* 95: 575-582.
- KAISER, H., 1975. Populationsdynamik und Eigenschaften einzelner Individuen. *Verh. Ges. Ökol., Erlangen* 1974: 25-38.
- KOENIG, W.D. & S.S. ALBANO, 1985. Patterns of territoriality and mating success in the White-tailed Skimmer *Plathemis lydia* (Odonata: Anisoptera). *Am. Midl. Nat.* 114: 1-12.
- LUTZ, P.E. & PITTMAN, 1970. Some ecological factors influencing a community of adult Odonata. *Ecology* 51: 279-284.
- MANLY, B.F.J. & M.J. PARR, 1968. A new method of estimating population size, survivorship, and birth rate from capture-recapture data. *Trans. Soc. Br. Ent.* 18(5): 81-89.
- MILLER, P.L., 1982. Temporal partitioning and other aspects of reproductive behaviour in two African libellulid dragonflies. *Ent. mon. Mag.* 118: 177-188.
- MIZUTA, K., 1974. Ecological and behavioral isolation among *Mortonagrion selenion* Ris, *Ceriagrion melanurum* Selys and *Copera annulata* (Selys) Zygoptera: Coenagrionidae, Platynemididae). *Odonatologica* 3(4): 231-239.
- MOORE, N.W., 1952. On the so-called "territories" of dragonflies (Odonata). *Behaviour* 4: 85-100.
- MOORE, N.W., 1964. Intra- and interspecific competition among dragonflies (Odonata). *J. Anim. Ecol.* 33: 49-71.
- MÜNCHBERG, P., 1930. Beiträge zur Kenntnis der Biologie der Odonaten Nordostdeutschlands. *Sber. Ges. naturf. Freunde Berlin* 130: 205-234.
- PAJUNEN, V.I., 1963. Reproductive behaviour in *Leucorrhinia dubia* v.d. Lind. and *L. rubicunda* L. (Odon. Libellulidae). *Annls ent. fenn.* 28: 108-118.
- PAJUNEN, V.I., 1966. The influence of population density on the territorial behaviour of *Leucorrhinia rubicunda* L. (Odon. Libellulidae). *Annls zool. fenn.* 3: 40-52.
- PARR, M.J., 1983. An analysis of territoriality in libellulid dragonflies (Anisoptera: Libellulidae). *Odonatologica* 12(1): 39-57.
- PARR, M.J. & M. PARR, 1974. Studies on behaviour and ecology of *Nesciothemis nigeriensis* Gambles (Anisoptera: Libellulidae). *Odonatologica* 3(1): 21-47.
- PAULSON, D.R. & C.E. JENNER, 1971. Population structure in overwintering larval Odonata in North Carolina in relation to adult flight season. *Ecology* 52: 96-107.
- PETERS, G., 1972. Gibt es Konkurrenz zwischen Libellenarten (Odonata)? *Ent. Ber. Berlin.*, 1972: 104-107.
- PIANKA, E.R., 1970. On "r" and "K" selection. *Am. Nat.* 104: 592-604.
- REHFELDT, G., 1982. Rasterkartierung von Libellen zur ökologischen Bewertung von Flußauen. *Beitr. Naturk. Niedersachs.* 35(4): 209-225.
- ROBERT, P.-A., 1958. *Les Libellules* (Odonata). Delachaux & Niestlé, Neuchâtel.
- RÜPPELL, G., 1984. *Rana esculenta* (Ranidae) — Beuteerwerb. *Publ. Wiss. Film.* (Biol. XVI) 31/2819.
- SCHAEFER, M., 1981. Interspezifische Konkurrenz — ihre Bedeutung für die Einnischung der Arthropoden. *Mitt. dt. Ges. allg. angew. Ent.* 2: 11-19.
- SCHOENER, T.W., 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. *Ecology* 51: 408-418.
- SOUTHWOOD, T.R.E., 1978. *Ecological methods, with particular reference to the study of insect populations*. Chapman & Hall, London-New York.
- ST. QUENTIN, D., 1934. Beobachtungen und Versuche an Libellen in ihren Jagdrevieren. *Konowia* 13: 275-282.
- TENNESSEN, K.J., 1975. Reproductive behavior and isolation of two sympatric coenagrionid damselflies in Florida. *Odonatologica* 6: 123-124.

- TSUBAKI, Y. & T. ONO, 1986. Competition for territorial sites and alternative mating tactics in the dragonfly, *Nannophya pygmaea* Rambur (Odonata: Libellulidae). *Behaviour* 97(3/4): 234-252.
- VAN NOORDWIJK, M., 1978. A mark-recapture study of coexisting zygopteran populations. *Odonatologica* 7(4): 353-374.
- WAAGE, J.K., 1975. Reproductive isolation and the potential for character displacement in the damselflies, *Calopteryx maculata* and *C. aequabilis* (Odonata: Calopterygidae). *Syst. Zool.* 24: 24-36.
- WATANABE, M., 1986. A preliminary study of the population dynamics of *Orthetrum j. japonicum* (Uhler) in paddy fields (Anisoptera: Libellulidae). *Odonatologica* 15(2): 219-222.
- WIENS, J.A., 1977. On competition and variable environments. *Am.Sci.* 65: 590-597.
- WESENBERG-LUND, C., 1913. Odonatenstudien. *Int. Revue ges. Hydrobiol. Hydrograph.* 6: 155-228, 373-422.
- WOLF, L.L. & E.C. WALTZ, 1984. Dominions and site-fixed aggressive behaviour in breeding male *Leucorrhinia intacta*. *Behav. Ecol. Sociobiol.* 14: 107-115.