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TERRESTRIAL AND AQUATIC MATING TERRITORIES IN *SOMATOCHLORA FLAVOMACULATA* (VANDER LINDEN) (ANISOPTERA: CORDULIIDAE)*

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In search of receptive females, the males of many corduliids patrol over open water. Additionally, some species exhibit localized patrol flights also over terrestrial sites. In open fen habitats, *Somatochlora flavomaculata* may be an extreme case in this respect as it conspicuously patrols often away from water. In consideration of its possible function the terrestrial patrol flights were investigated in a descriptive and experimental field study and compared with those at aquatic sites. Typically, the males patrolled close to vertical structures such as trees and bushes or over footpaths in glades of reedbeds. No relevant differences between the patrol fligths at aquatic and terrestrial localities were found. Both types of flight were territorial in function as conspecific males were vigorously driven away. It is speculated that the males establish territories away from ponds because the occurrence of females is unpredictable, the preferred ovipostion sites (shallow and largely overgrown puddles) being scattered over large areas. Hence, the best strategy for males for intercepting mates would be to patrol near vertical structures serving as landmarks and guidelines for arriving females.

INTRODUCTION

Territoriality, connected with reproduction, is suggested to be a widespread phenomenon in corduliid dragonflies. However, this behaviour and its variability is poorly understood, as it has been investigated intensely in only very few species. *Epitheca cynosura* (Say) was the first to be studied in detail in this respect (KORMONDY, 1959). Males occupy fixed areas at lake shores, aggressively expel conspecific intruders and mate with arriving females. The flight pattern is characterized by extended periods of hovering, considerable manoeuvering and no alighting. In contrast to the sexual patrol flight, the feeding flight occurs away from the

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* This paper is dedicated to the memory of the late Dr P. L. Miller.

water, and there is much horizontal and vertical displacement, almost no area localisation, little or no hovering and no aggressive interactions between individuals.

Cordulia shurtleffi Scudder was shown to patrol for short periods about 15m of shoreline at a bog pond, attempting to drive away any rivals (HILTON, 1983). By way of contrast, territorial individuals of *Hemicordulia australiae* (Rambur) are extremely site-fixed, spending most of their time hovering in a very small volume (ROWE, 1988). *Cordulia aenea amurensis* Selys becomes territorial at ponds only if male density exceeds a given value. Otherwise the males search for females along the shore over long distances, lacking aggression towards conspecifics (UBUKATA, 1975). In both species males initiate copulation exclusively at water by intercepting females which visit the site for oviposition.

In some corduliids localization of males ready to mate may depend on the type of habitat. At ponds male *Procordulia smithii* (White) intercept females over the water, whereas at lakes copulation is initiated away from the shore (ROWE, 1988). Hence, this species may use alternative mate finding strategies. *Somatochlora flavomaculata* (Vander Linden) may be an extreme case with respect to territorial behaviour. A number of authors have stressed that adults would avoid areas with open water, thus almost exclusively using terrestrial sites for patrol flights (e.g. RIS, 1885; SCHIEMENZ, 1957; ROBERT, 1959). Referring to *S. flavomaculata*, ST. QUENTIN (1932, 1964) distinguished between territories at water and territories away from water ("Wasserreviere" und "Landreviere"). He considered site--fixed patrolling individuals at terrestrial locations unambiguously to hold feeding territories ("Jagdreviere"). However, the function of the terrestrial patrol flights remained unclear as it was not demonstrated what resources were defended.

In this study the terrestrial patrol flights of *S. flavomaculata* are described and compared with those at aquatic sites with respect to the hypotheses that the former primarily serve mating, and not feeding. It will be speculated that the establishment of mating territories away from water may be connected with ecological constraints, i.e. the specific geometry of the oviposition sites.

STUDY SITE, METHODS AND DEFINITIONS

STUDY SITE. – This field study was conducted from 1995 to 1997 near Wetzikon (47°16'45"N/ 8°48'11"E, 540m alt.), 20km ESE of the city of Zürich (Switzerland). The area consists of a mosaic of elongated and gently sloped hills (drumlins), mostly covered with woods, and correspondingly shallow valleys laying between them, comprising moorland, meadows, hedges, small woods and scattered groups of trees and bushes (WILDERMUTH et al., 1982). Most investigations were carried out at the Böndlerried (Ambitzgi), a broad and shallow depression with bog and fen vegetation, peat ponds, ditches and densely overgrown puddles (Fig. 1; for further details cf. WILDERMUTH, 1992). Additional observations were made at the Oberhöflerried as well as at forest edges, wood clearings and treefall gaps, all in the vicinity of the main study locality. Supplemental data were collected near Ribnica (Slovenia) at an extended fen area along a dammed river.

METHODS. – Flight velocity of patrolling individuals as well as flight and rest periods were determined with a stop watch. Selected examples of flight courses were simultaneously watched and outlined on paper. At the peak of the flight season all territorial males in the study area were mapped on two selected days with ideal weather conditions. A number of males were marked individually with nail varnish.

For the experiments I netted males and females. They were subsequently released individually in front of patrolling males at terrestrial territories. Fishing-line experiments were carried out with males of *S. flavomaculata* and *Libellula quadrimaculata* as well as small pieces of round stick (7 cm in length, 0.5 cm in diameter), tethered to a thin thread of ca 1m which was fastened to a rod. The animals were fixed at the thorax in a manner which allowed them to fly as freely as possible.

In order to mimic water (and thus oviposition sites), black plastic foil or dark brown perspex (1x1m), usually combined with aluminium foil or differently coloured plastic sheets, were placed side by side on dry vegetation in the vicinity of a ditch where *S. flavomaculata* males occasionally patrolled. The responses to the dummies of all dragonfly species present at the experimental site were recorded as in a previous study (WILDERMUTH & SPINNER, 1991).

For microscopic studies three patrolling males were captured at terrestrial sites and dissected in Ringer solution. I investigated sperm vesicles and testes separately with respect to mature sperm under the microscope using phase contrast.

DEFINITIONS. – The term patrol flight is used here for site-fixed imaginal adults cruising back and forth over a specific beat or flying slowly criss-cross for at least some minutes in a confined and narrow space at a certain level above ground. These areas are defended by the residents against conspecific intruders and therefore are considered as territories.

PATROL FLIGHTS

SEX. – Individuals performing patrol flights were males in all controlled cases (65 animals netted). Females could only be watched copulating and ovipositing.

SITE. – The places where the localized males stayed were distinguished by conspicuous topographic features such as trees or shrubs obviously serving as landmarks. Strongly site-fixed adults were never recorded in wide and open space lacking any vertical structure. They preferred the immediate vicinity of single bushes or trees as well as rows and groups of woody plants, hedges, woods, forest edges, forest clearings, treefall gaps in forests and glades or footpaths in reed beds.

Territorial males were encountered at or near the breeding sites, but often completely away from any water body. However, the patrol areas were situated at most some hundred metres away from the nearest possible larval habitat. Aquatic territories were situated at peat-diggings and ditches as well as partly overgrown areas of puddles with open water clearly visible for the human observer from the air. At the terresrial territories the ground consisted of moist or dry soil with dense wetland or heath or hay-meadow vegetation, even with grass freshly cut, or of gravel and clay without or with sparse short vegetation. In a few cases it was impossible to differentiate clearly between terrestrial and aquatic territories, since the males patrolled over water-logged vegetation with very little or no open water visible. At the peak of the reproductive period a census in the study area yielded 29 terrestrial and 15 aquatic territorial males (Fig. 1). Although the potential terrestrial territorial sites outnumbered the aquatic sites, not all of the oviposition places available were occupied.

Certain places seemed to be preferred to others, as they were nearly permanently occupied during the flying season. These were glades or footpaths between walls of reed or bush rows, meadow corners confined by woods, and bays at hedge or forest edges 2 to 6m in diameter adjacent to areas with low vegetation, overlooking open space. Generally the individuals patrolled in the sun and parallel to the vertical structures, but flight courses perpendicular to the woods edges, radially to the centres of single shrubs, and between bushes or trees were also recorded. At ambient temperatures of ≥28° C the animals flew partly in the shadow.

At coherent and homogeneously structured oviposition sites larger than 1/20 ha (open water with dense vegetation of *Carex elata* or *Equisetum fluviatile*), the males were not clearly site fixed. Instead, they slowly criss-crossed over the area, thus actively searching for females. This behaviour was observed outside the main study site.

DURATION OF STAY. – As no individuals were marked and the residents sometimes left their territories during aerial fights while chasing an intruder, it was impossible to determine which of the contestants returned. Therefore the duration of stay for a resident male could not be determined exactly, especially during the peak of the flying season when intraspecific competition was heavy. However, towards the end of the reproduction period the frequency of interferences with conspecifics

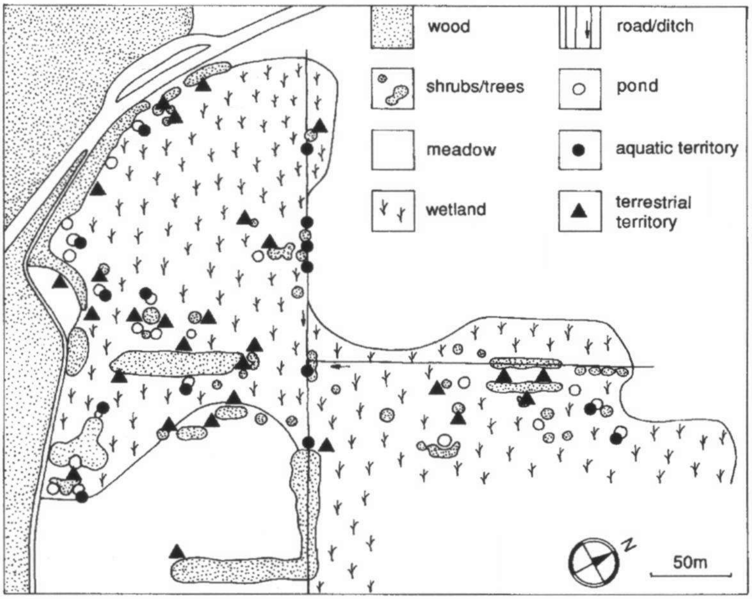

Fig. 1. Distribution of aquatic and terrestrial territories in the study area on July 23, 1996, 12:00 - 14:30 h CEST. Note the close vicinity of the territories to shrubs and trees. Each black circle or triangle indicates one site-fixed male.

decreased and territorial males could be observed uninterruptedly for half an hour or more at the same place. Maximum periods for five individuals were 40, 45, 55, 60, and 70min. Other individuals interrupted their patrol flights and perched on plant stems. In one recorded case flights lasted 15-130s (mean = 59s, n = 15) and rests 10-435s (mean = 81s, n = 18).

FLIGHT ALTITUDE. – At ditches and ponds without emergent vegetation the animals patrolled 0.3 - 0.5m above the water surface. In the presence of water plants (e.g. *Equisetum fluviatile*) the distance was 0.5 - 1.5m. On average males kept about the same height for longer periods. They lowered their flight altitude at intervals or raised it for short instances, sometimes dashing at an insect above them. On terrestrial territories the constant flight height was occasionally only 0.2m over gravel or freshly cut grass. However, flight between 0.8 - 1.5m was also observed at these sites. The flight height was usually 0.7-1.2m above ground in places where the grass or herbaceous vegetation had not been cut yet. Over puddles with sparse vegetation a flight height of 0.5-1.0m was found.

RANGE AND FLIGHT COURSE. – At terrestrial sites the individuals cruised back and forth over a specific beat using the the same horizontal line dozens of times subsequently (Fig.2). The distance between two turns was individual, but more or less constant for the same male at one site. It varied from 3 to 10m. Instead of straight lines also irregular zigzag or curved courses were seen, e.g. at areas of 2x3m (adjacent to bush), 1.5x1.5m and 2x15m (footpath between reed beds), 4x5m (puddle area with dense vegetation). At ditches and peat-diggings the animals kept rather close to the water.

FLIGHT VELOCITY. – The flight speed was only measured in individuals keeping periodically a straight flight course at terrestrial territories. Patrol flights were rather slow, ranging from 0 (hovering) to 4m/s. Average speed was 2.0-2.5m/s. One individual which patrolled evenly covered 1600m in 12 min (Ø v = 2.2m/s). The flight velocity of individuals patrolling a straight line was occasionally different back and forth, e.g. 1.9m/s from S to N (n =21) and 4.1m/s from N to S (n = 21). In some cases this was due to the wind, but the reasons for the differences were not always obvious.

FLIGHT STYLE. – Patrolling males advanced with alternating wing beats and turned back abruptly at the ends of their flight stretches. Other individuals showed zigzag courses with sharp turns or wide curves. Gliding was regularly observed, however mostly for short distances of 0.1 - 0.3m only, rarely up to 2m. Returning from pursuits or inspection flights up to 10m upward, the males flew wide loops and glided over distances of 4-5m. Hovering on the spot was a frequent component of patrol flights and usually lasted 0.5 - 3s (Ø 1.6s, range 0.5 - 20s, n = 112). Many individuals patrolled for 15min or longer without interruption and without a single hover stop.

FEEDING DURING PATROL FLIGHTS. – Cruising males now and then dashed at some objects above them which sometimes could be identified as small flying insects.

However, only on few occasions I clearly saw that the prey item was captured and that detached parts of them dropped after a short instant.

REACTIONS TOWARDS FLYING NON-PREY OBJECTS. – Territorial males dashed at any fast flying objects of a certain size, even though it was not suitable as prey. Targets such as butterflies, dragonflies and falling tree leaves were approached for

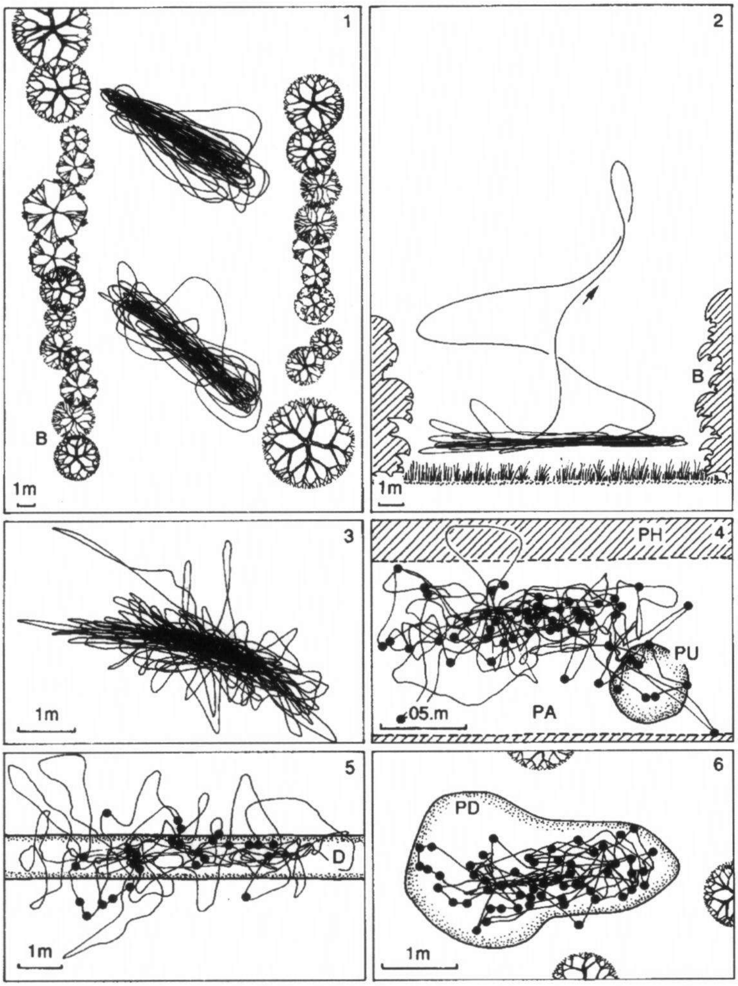

Fig. 2. Flight courses of site-fixed males. (1) Two adjacent terrestrial territories in lane between rows of trees and bushes (B), view from above; – (2) terrestrial territory between bushes (B), view from the side; – (3) terrestrial territory over fen vegetation; – (4) terrestrial territory over dirt path (PA) with rainwater puddle (PU) in glade of reed bed (*Phragmites australis* PH), black dots indicate hover stops; – (5) aquatic territory over ditch (D); – (6) aquatic territory over peat pond (PD); (3) to (6) view from above.

closer examination with accelerated speed. This was observed at both aquatic and terrestrial sites. However, the residents hardly showed any reactions towards dragonflies and butterflies passing at low speed. Fast flying dragonflies were detected at distances up to 12m, approached closely but only occasionally chased.

REACTIONS TOWARDS CONSPECIFICS. – Encounters between conspecific males proceeded in the same manner at both aquatic and terrestrial territories. In all cases which were watched (n = 24) the resident darted immediately at the intruder as soon as he was detected and attacked him from below or from the side. Generally the newcomer retreated. Sometimes the latter was chased far beyond the territory. Typically aerial fights started about 1m above ground or water, the contestants facing each other with body axes held obliquely and spiralling upward up to 6-12m (Fig. 3). Occasionally they extended all legs for short grapples with body contact. Chases could also be performed at a horizontal plane, the animals swiftly curving or circling several times. The pursuer followed the escaping opponent very closely (Fig. 3). Some chases ended up far away from the territory and one individual occasionally returned to the site after 15-30s. As pursuits occurred at high speed it was difficult recognise details. Therefore it is possible that one or the other of the chased individuals was a female. However, definite encounters between territorial males and females could be recorded neither at aquatic nor at terrestrial locations.

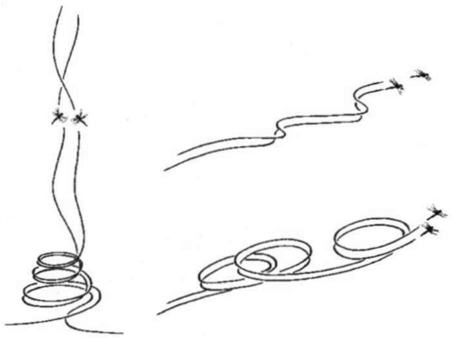

Fig. 3. Examples of flight courses during aerial fights of male *S. flavomaculata* at terrestrial territories.

FEEDING FLIGHTS OF NON-TERRITORIAL INDIVIDUALS. – Besides strictly localized patrolling males, adults also were observed which performed flights using wider spaces and showing a different flight style, interpreted as feeding flights. In one typical case recorded, the individual patrolled on a small sunlit forest clearing. It hunted uninterruptedly at altitudes between 1 and 10m above ground, over an area of 30 x 40m. The flight was characteristically erratic and undulating, alternating with calm flight and gliding stretches along straight lines and periodically interrupted by darts upwards or sidewards, presumably directed toward small insects. Occasionally prey items or parts of them were seen dropping against the sunlight. The individual was obviously feeding. Neither hover stops nor interactions with other dragonflies could be recorded.

EXPERIMENTS

FISHING-LINE EXPERIMENTS. – Six tethered males of *S. flavomaculata* were released in the territories of patrolling males approaching the experimentalist on a straight flight course. They elicited immediate attacks by the resident towards the fleeing individual, followed by short but vigorous clashes. The contestants circled 3 to 5s, occasionally grappling with perceivable clattering of wings. Soon afterwards the territory owner mostly left the site. Males flying in an untypical manner or staying motionless were only approached for short inspections or not noticed at all. On the other hand, the reactions were the stronger the faster the tethered individual tried to escape. Flying males of *Libellula quadrimaculata* tethered to the fishing-line were approached up to ca 0.2m, and then no longer noticed. Repeated releases did not evoke further reactions.

Patrolling males also pursued a small piece of wood tethered to the fishing-line, swiftly circling around the experimentalist (n = 8). The strongest reactions were obtained when the object passed horizontally at high speed in front and slightly above the approaching male. The dummy was followed 2 to 3m, in some cases up to a complete turn. Then the males resumed the patrol flight. However, this experiment was successful only a few times subsequently with the same individual. After two or three bouts of swinging, the residents did no longer show positive reactions. Males at aquatic territories reacted exactly the same as those at terrestrial sites.

EXPERIMENTS WITH UNTETHERED MALES AND FEMALES. – Six males were released individually at six different terrestrial territories. They fled swiftly upwards and were immediately chased by the resident up to ca 10 m. Subsequently the latter returned to his territory. Corresponding experiments were carried out with five females. The males reacted promptly and tried to intercept them. In four cases tandem formation could be watched. However, only three pairs completed copulation. One female dived into a bush nearby and remained motionless. The male hovered 20 cm in front of her during ca. 20s but did not recognize her. The same experiment was conducted by L. Börzsöny (pers. comm.) at a fen near Munich. He obtained similar results.

REACTIONS TOWARDS OVIPOSITION SITE DUMMIES. – In contrast to *Libellula quadrimaculata* and *L. depressa*, *S. flavomaculata* showed only weak reactions to the plastic material. In the course of 45 experimental sessions (distributed over 3 years, in June and early July, each session lasting 2-4h) the libellulids exhibited ca 1800 positive reactions, whereas in *S. flavomaculata* only 7 clear reactions could be recorded. The males examined the sheets very shortly from a close distance and subsequently moved on. Some returned once or twice. No individual stayed longer than a few seconds at the site.

SPERM VESICLE CONTENTS OF MALES AT EXTRA AQUATIC TERRITORIES

In order to learn whether the males patrolling away from the water had their sperm vesicle filled with sperm and therefore were ready to copulate, patrolling individuals were captured and then microscopically studied in the laboratory. The sperm storage organs of every male contained mature sperm cells. Presumably *S. flavomaculata* fills the sperm vesicle before the patrol flight as described for *Cordulia aenea* (UBUKATA, 1984).

DISCUSSION

According to BROWN's (1964) concept of economic defendability, the establishment of a territory is only rewarding if the benefits of priority of access to the site-fixed resource exceed the costs such as time and energy expenditure. Hypothetically, the resources which *S. flavomaculata* males claim for exclusive access might comprise food, locations for thermoregulation, oviposition sites, or females. Combined functions may not be excluded.

In the case of aquatic territories food as a resource with exclusive access may be left out of consideration, since the residents only occasionally feed. The sites may be regularly visited for egg deposition. Indeed, oviposition could be witnessed only rarely, but exuviae were found at most waters where the males occasionally patrolled (WILDERMUTH, 1997). Hence, the defended aquatic sites will at least partly serve as rendezvous, as described for other corduliids such as *Cordulia aenea* (UBUKATA 1975) and *Procordulia smithii* (ROWE, 1988). However, as demonstrated by the experiments with plastic sheets mimicking possible oviposition sites, areas with open water do not prove specially attractive for male *S. flavomaculata*. This is in contrast to *S. arctica* (WILDERMUTH & SPINNER, 1991). Terrestrial territories, on the other hand, may be completely excluded as resources rewarding defence with respect to egg deposition, since females have only been observed to oviposit into open water (e.g. SCHMIDT, 1990; BUCHWALD, 1983; ULLRICH, 1995). At the study site these are shallow and densely overgrown puddles on organic mud ground, ditches, and small peat ponds (WILDERMUTH, 1997).

ST. QUENTIN (1932, 1964) interpreted the terrestrial territories of *S. flavomaculata* as defended feeding sites. However, if the individuals claimed food resources, it should be expected that the prey items were clumped and stationary, at least for a certain time. In the field no such concentrations of prey insects were present at the territory sites. Furthermore, the females having considerable food requirements for egg production should also be territorial. However, no territorial females have been reported. As mentioned above, hunting individuals differ in their flight style from patrollers. Regular or occasional feeding of territorial males may be explained by the fact that *S. flavomaculata* is a "flier" sensu CORBET (1962), staying on the wing for long periods and therefore consuming corresponding amounts of energy. On the other hand, occasional prey capture was also recorded in territorial males of *Libellula quadrimaculata*, considered a typical "percher", and therefore supposed to have lesser energy requirements (MOORE, 1960; personal observations).

Many locations where males patrolled were characterized by favourable microclimatical conditions due to high insolation and/or wind shelter suggesting a thermoregulatory function of the terrestrial territories. Hence, the males would gain maximum agility for encounters with females. This might be true for "perchers" which regulate their body temperature to a great extent by behavioural means. However, "fliers" will hardly seek the sites in order to warm up their body since they rely on endothermic heat generation (HEINRICH, 1993). On the contrary, at high ambient temperatures they may be faced with overheating problems. Strikingly, males of *S. flavomaculata* patrolled partly in the shadow when the air temperature exceeded 28° C, hardly showing any hover stops. At lower temperatures the territorial flights were performed exclusively in the sun, and hovering was frequently interspersed, as recorded in *Epitheca cynosura* (MAY, 1987).

The most likely function of the terrestrial territories is sexual. This assumption is supported by a number of facts: (1) The territorial behaviour is exclusively performed by males. (2) The males are ready to mate, as their sperm vesicle is filled with sperm. (3) Intruding conspecific males are vigorously driven off, to a lesser extent also other dragonflies species. (4) Released or tethered conspecific males are vigorously attacked by the territory owner. (5) Any passing insects of a certain size and dummies swiftly sweeping through the air are dashed at and approached for close inspection. (6) Feeding during patrol flights is rather infrequent and the flight style is different from typical foraging flights. (7) Conspecific females released within terrestrial territories are immediately seized, followed by tandem and wheel formation. (8) There is no relevant difference in territorial behaviour at aquatic and terrestrial sites.

Direct evidence for the reproductive function of the terrestrial territories with receptive females rewarding defence would be the record of mating. Although pairs adopting tandem or wheel position were seen at some occasions at or near the territories (L. Börzsöny, pers. comm.; this study), the complete sequence of mating has not been recorded at terrestrial sites. However, it may not be excluded that seizure and tandem formation have not been witnessed because the procedures occur suddenly, rapidly, after a short pursuit and therefore away from territory. This might have happened when a terrestrial territory stayed empty for a while after a wild chase with the prosecuted individual possibly being a female. Nevertheless, WEBEL (1932) observed on forest paths that males grasped females and flew rapidly to the ponds nearby.

Most corduliids so far studied patrol at selected sections of pond or lake shores where female arrivals are most likely (e.g. KORMONDY, 1959; ROWE, 1987; WILDERMUTH & KNAPP, 1995). However, as reported in *'Procordulia' grayi* and *P. smithii*, one species may concentrate the reproductive behaviour either to aquatic or to terrestrial sites, depending on the type of habitat. At ponds tandem and wheel formation proceeds exclusively over the water, whereas at lake shores the males intercept the females mostly away from water, and the animals reach the oviposition sites in wheel position (ROWE 1988).

Many authors stress that *S. flavomaculata* avoids water and prefers terrestrial sites (e.g. RIS 1885, ROBERT, 1959; SCHIEMENZ, 1957). Obviously, the males are encountered more frequently at terrestrial localities. On the other hand, territorial or reproductive behaviour at terrestrial sites is only exceptionally mentioned in faunistic or ecological publications, and no details are available (e.g. ST. QUENTIN, 1934; SCHEFFLER, 1969; BUCHWALD, 1983; SCHMIDT, 1990). Nevertheless, terrestrial territoriality seems to be a common phenomenon in the behaviour of this species, thus requiring a functional explanation.

At lake shores which hold several corduliids including *S. flavomaculata*, all flying simultaneously, the differerent species are spatially segregated (e.g. BAUER, 1977; GOFFART, 1990). *S. flavomaculata* is the only one which occupies terrestrial sites. It might be hypothesized that the species faces ecological constraints to establish terrestrial territories, since it prefers small and shallow waters offshore as larval habitats. For males of *S. flavomaculata* the occurrence of receptive females with respect to space and time is rather unpredictable, as the optimal oviposition sites are diffusely scattered over large areas. Hence, the best strategy for the males is to intercept females arriving at habitats of this kind by patrolling the routes taken by females in search of oviposition sites, flying along vertical structures which serve as landmarks and guidelines and thus controlling the entrances to the egg laying places. On the other hand, at localities with large and homogeneously structured oviposition sites the males use a different mate finding tactic by searching actively ovipositing females on the whole area.

The establishment of terrestrial territories might be a general mate finding strategy in species which use unconspicuous oviposition sites scattered over large areas. This view is supported by observations of other corduliids showing site-fixed patrolling or mating at localities away from the water, such as *Hemicordulia ogasawarensis* (SAKAGAMI et al., 1974), *Somatochlora viridiaenea* (MIYAKAWA et al., 1972; UBUKATA, 1979) and *Williamsonia fletcheri* (CHARLTON & CANNINGS, 1993).

For the great majority of Odonata it is assumed that the sexes meet and copulate at or near the oviposition site (CORBET, 1980). However, in some species, especially corduliids, localities away from water such as feeding sites, good locations for thermoregulation, or conspicuous landmarks may also serve as rendezvous. Many insects such as Diptera, Hymenoptera, Coleoptera, or Lepidoptera congregate at distinctive topographical or physical features of the environment

(THORNHILL & ALCOCK, 1983). For Odonata with oviposition sites diffusely scattered over large areas, landmarks may be optimal rendezvous sites. In order to obtain more insight into the variety of mate finding systems of corduliid species, detailed and experimental studies with marked individuals will be needed. *S. flavomaculata* would seem to be a suitable subject.

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REFERENCES

BAUER, S. ,1977. Untersuchungen zur Tierwelt des Moorkomplexes Fetzach-Taufachmoos - Urseen in Oberschwaben (Kreis Ravensburg). *Veröff. NatSchutz LandschPfl. Bad.-Württ.* 44/45: 166--295.

BROWN, J.L., 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76: 160-169.

BUCHWALD, R., 1983. Ökologische Untersuchungen an Libellen im westlichen Bodenraum. *NaturLandschGeb. Bad.-Württ.* 11: 539-637.

CHARLTON, R. E. & R. A. CANNINGS, 1993. The larva of Williamsonia fletcheri Williamson (Anisoptera: Corduliidae). *Odonatologica* 22: 335-343.

CORBET, P.S., 1962. *A biology of dragonflies.* Witherby, London.

CORBET, P.S., 1980. Biology of Odonata. *Annu. Rev. Ent.* 25: 189-217.

GOFFART, G., 1990. Compte-rendu de l'excursion à Virelles du 16 juin 1990. *Gomphus* 6(2): 12-15.

HEINRICH, B., 1993. *The hot-blooded insects.* Springer, Berlin Heidelberg.

HILTON, D.F.J., 1983. Reproductive behavior of Cordulia shurtleffi Scudder (Anisoptera: Corduliidae). *Odonatologica* 12: 15-23.

KORMONDY, E.J., 1959. The systematics of Tetragoneuria, based on ecological, life history, and morphological evidence (Odonata: Corduliidae). *Misc. Publ. Mus. Zool. Univ. Mich.* 107: 1--79.

MAY, M., 1987. Body temperature regulation and responses to temperature by male Tetragoneuria cynosura (Anisoptera: Corduliidae). *Adv. Odonatol.* 3: 103-120.

MIYAKAWA, K., K. NARUMI, A. SHIMIZU & H. ANDO, 1972. Odonata of Sugadaira and vicinity. *Bull. Sugadaira Biol. Lab. Tokyo Kyoiku Univ.* 5: 1-18.

MOORE, N.W., 1960. The behaviour of the adult dragonfly. *In*: P.S. Corbet, C. Longfield & N.W. Moore, Dragonflies, pp. 106-126, Collins, London.

RIS, F., 1885. Fauna insectorum Helvetiae. Neuroptera. Die schweizerischen Libellen. *Mitt. schweiz. ent. Ges.* 7 (Appendix): 1-50.

ROBERT, P.-A., 1959. *Libellen (Odonaten).* Kümmerly & Frey, Bern.

ROWE, R.J., 1987. *The dragonflies of New Zealand.* Auckland Univ. Press, Auckland.

ROWE, R.J., 1988. Alternative oviposition behaviours in three New Zealand corduliid dragonflies: their adaptive significance and implications for male mating tactics. *Zool. J. Linn. Soc.* 92: 43-66.

SAKAGAMI, S.F., H. UBUKATA, M. IGA & M.J. TODA, 1974. Observations on the behaviour of some Odonata in the Bonin Islands, with considerations on the evolution of reproductive behaviour in Libellulidae. *J. Fac. Sci. Hokkaido Univ.* (VI) 19: 723-756.

SCHEFFLER, W., 1969. Die Odonatenfauna des Naturschutzgebietes Thymen. *Brandenburg. Naturschutzgeb.* 11: 1-14.

SCHIEMENZ, H., 1957. *Die Libellen unserer Heimat.* Franckh, Stuttgart.

SCHMIDT, B., 1990. Faunistisch-ökologische Untersuchungen zur Libellenfauna (Odonata) der Streuwiesen im NSG Wollmatinger Ried bei Konstanz. Auswirkungen und Bedeutung der Streuwiesenmahd und Überschwemmungen auf die Libellenbesiedlung. *Naturschutzforum* 3/4: 39-80.

ST. QUENTIN, D., 1932. Beobachtungen und Versuche an Libellen in ihren Jagdrevieren. *Konowia* 13: 275-282.

ST. QUENTIN, D., 1964. Territorialität bei Libellen (Odonata). *Mitt. münch. ent. Ges.* 54: 163-180.

THORNHILL, R. & J. ALCOCK, 1983. *The evolution of insect mating systems.* Harvard Univ. Press, Cambridge/MA.

UBUKATA, H., 1975. Life history of and behavior of a corduliid dragonfly, Cordulia aenea amurensis Selys. II. Reproductive period with special reference to territoriality. *J. Fac. Sci. Hokkaido Univ.* (VI) 19: 812-833.

UBUKATA, H., 1979. Behavior of Somatochlora viridiaenea viridiaenea Uhler in Kushiro district (Odonata, Corduliidae). *New Ent.* 28: 1-7.

UBUKATA, H., 1984. Intra-male sperm translocation and copulatory behaviour in the dragonfly, Cordulia aenea amurensis Selys (Odonata, Corduliidae). *J. Hokkaido Univ. Educ.* (IIB) 35: 43-52.

ULLRICH, K., 1995. *Stillwasservegetation in der südlichen Oberrheinebene: Pflanzengesellschaften-Synökologie und Besiedlung durch Somatochlora flavomaculata und Sympetrum sanguineum (Odonata).* DiplArb. Univ. Freiburg i.Br.

WEBEL, G., 1932. Die Libellen der Umgebung von Görlitz. *Abh. naturf. Ges. Görlitz* 31: 81-103.

WILDERMUTH, H., 1992, Habitate und Habitatwahl der Grossen Moosjungfer (Leucorrhinia pectoralis) Charp. 1825 (Odonata, Libellulidae). *Z. Ökologie NatSchutz* 1: 3-21.

WILDERMUTH, H., 1997. Phänologie und Larvenhabitate von Somatochlora flavomaculata (Vander Linden) in einem voralpinen Moorkomplex (Anisoptera: Corduliidae). *Libellula* 16: 17-32.

WILDERMUTH, H., R. HANTKE & J. BURNAND, 1982. Die Drumlinlandschaft des Zürcher Oberlandes. *Vjschr. naturf. Ges. Zürich* 57: 297-306.

WILDERMUTH, H. & E. KNAPP, 1995. Räumliche Trennung dreier Anisopterenarten an einem subalpinen Moorweiher. *Libellula* 15: 57-73.

WILDERMUTH, H. & W. SPINNER, 1991. Visual cues in oviposition site selection by Somatochlora arctica (Zetterstedt) (Anisoptera: Corduliidae). *Odonatologica* 20: 357-367.