Season and temperature dependent location of mating territories in *Somatochlora flavomaculata* in a heterogeneous environment (Odonata: Corduliidae)

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Key words: Odonata, dragonfly, *Somatochlora flavomaculata*, mating territories, seasonal change, phenotypic plasticity, thermoregulation.

Abstract

In a heterogeneous environment, males of *Somatochlora flavomaculata* regularly occupy site-fixed locations away from water, adjacent to vertical landscape elements, and to a lesser extent, also at water, i.e. at oviposition sites. Territories both over land and over water are typically patrolled by continuous site-fixed flights. These places serve as rendezvous sites where copulation is initiated. The results of a seven-year study in a heterogeneous mire habitat of Central Europe with scattered oviposition sites demonstrated that the rendezvous sites changed over the flight season in both location and quality. At the beginning of the reproduction period territories were established almost exclusively over land. Subsequently, there was a significant shift from sites over land to sites over water, and towards the end of the flight season virtually all territories were situated over water. Areas with overgrown puddles were also attractive for establishing territories, even at the beginning of the flight season. When the puddles desiccated during hot and dry spells in the first half of the reproduction period, these sites were no longer used as rendezvous sites. However, no shift towards territories over water was observed in this situation. Small-scale transfer of territories was also related to ambient temperatures. Below 28°C all males patrolled in full sunshine, but when temperatures rose they shifted their patrol sites gradually to the shade, presumably for thermoregulatory reasons. It appears that the mate search strategy of *S. flavomaculata* is characterised by extensive phenotypic plasticity with respect to time and space.

Introduction

Territoriality is widespread in Odonata (Corbet 1999: 430 ff.). In general it is associated with reproductive activity (Suhonen et al. 2008) and only exceptionally with feeding alone (Orr 2004). Occupancy of fixed sites has been reported from both perchers and fliers (sensu Corbet 1962: 126 ff.). Perchers, when territorial, generally occupy species-specific oviposition sites and typically spend most of their time on a

perch from which they monitor the place, make short flights, chase intruders, intercept arriving females and guard them during oviposition. Male perchers may hold a territory for a number of consecutive days at least during some hours of the day (e.g. Krüner 1977; Miller 1983) and return to it over a period of several weeks (e.g. Fincke 1992; Clausnitzer 1996). In contrast, territorial fliers remain on the wing, patrolling a defined stretch or area and staying at one site for only a few minutes, but sometimes return repeatedly to the same place, occasionally on a number of successive days (e.g. Kaiser 1974; Brooks et al. 1997; Inden-Lohmar 1997; Schneider & Wildermuth 2009).

Both perchers and fliers may exhibit different mating patterns (Suhonen et al. 2008). In corduliids, which are considered fliers, two or three tactics of mate search exist, i.e. active mate search by scanning large areas in slow flight, by intruding deeply into dense emergent vegetation and looking for ovipositing females, or by site-fixed patrolling (Ubukata 1975; Wildermuth & Knapp 1996; Wildermuth 2003, 2008b: 220 ff.). *Somatochlora flavomaculata* (Vander Linden) uses two tactics, both being dependent on the habitat structure (Wildermuth 1998a). At homogeneously structured oviposition sites larger than 0.05 ha, the males generally criss-cross slowly over open areas and search actively for arriving or ovipositing females. On the other hand, in habitats with a heterogeneous landscape structure and scattered oviposition sites, the males become territorial. They occupy fixed areas, preferably in the close vicinity of bushes, trees and other vertical landscape elements that protrude from the herbaceous vegetation (Wildermuth 1997, 1998a). According to Flöss (1998), who studied this spatial correlation by using sites selected at random, the males establish their territories preferentially at locations where bushes and small water bodies occur in combination.

It is assumed that reproductively active males establish their territories at places where they are likely to encounter receptive females. Hence, in most cases the primary rendezvous corresponds to the oviposition site while regular pair formation away from water is rather exceptional (Corbet 1999: 651; Wildermuth 2008b: 213 ff.). One of these exceptions is found in *S. flavomaculata*, a corduliid the males of which frequently occupy territories away from water, but not exclusively as stated by Ris (1886), as aquatic territories are also regularly recorded although less frequently (Wildermuth 1997, 1998a).

In the course of a qualitative study on the habitat use of *S. flavomaculata* (Wildermuth 1997) a tendency for a shift in space and quality of the territories was noted as the season proceeded. In the beginning and around the peak of the reproduction period most territories were situated over land, often far away from any water bodies. Later in the season the relative frequency of these terrestrial territories appeared to diminish in favour of territories situated over ponds with open water surface. However, this shift remained to be verified. The aim of this study was to examine the hypothesis that the rendezvous-sites change as a rule in the course of the reproduction period, gradually moving from mainly terrestrial to mainly aquatic locations. Furthermore, based on an earlier study on thermoregulatory behaviour of *S. flavomaculata* (Wildermuth 2006), it is predicted that the precise location of the patrol stretch with respect to vertical landmarks depends on the ambient temperature.

Material and methods

Study area

The study was carried out from 2002 to 2008 in a 15 ha mire near Wetzikon Switzerland (47°18.21'N, 8°47.86'E; 540 m a.s.l.). The area named 'Ambitzgi/Böndlerriet' was part of the nature reserve 'Drumlinlandschaft Zürcher Oberland', the Odonata fauna of which has been studied for almost four decades (Wildermuth 2008a). This terrain comprised a largely exploited peat-bog with a mosaic of fen vegetation ('litter meadows') and regenerating bog fragments, interspersed with scattered small wood strips, single trees and bushes (Fig. 1). The immediate surroundings consisted of mostly forested drumlins – elongated whale-shaped hills formed by glacial action – and intensely used agricultural land. Three types of water bodies served as oviposition sites and therefore also as potential rendezvous-sites of *Somatochlora flavomaculata*: (1) partly overgrown peat diggings and (2) water-filled ditches, both regularly maintained for conservation reasons, and (3) shallow, vegetated puddles over peat ground of which the water evaporated partly or completely during hot and dry weather periods, but leaving moist mud below the surface that allowed the larvae to survive.

Records of reproductive behaviour and habitat use along transects

The reproductive activities of *S. flavomaculata* comprising territorial behaviour and copulation were recorded along a 750 m transect during the seven consecutive years 2002-2008, from the beginning of the emergence period to the end of the flight season. The transect was laid out along all relevant landscape elements of the area such as open fen and bog vegetation, peat ponds, ditch sections and vertical landmarks, i.e. wood edges, trees and bushes (Fig. 1). From 2005 to 2008 this transect was extended for 330 m in order to include an area with scattered puddles. In general, the censuses took place during favourable weather conditions (sunshine, calm, ambient temperature generally > 20°C, rarely 17-20°C) between 09:30 h and 14:30 h solar time and required 1.5-2.0 hours. Altogether more than 200 transect runs were conducted, ca 25% of them without records of reproductively active *S. flavomaculatata* individuals as the censuses either lay outside the reproduction season or the weather conditions were unfavourable. In some cases, following a spell of rainy and cool days during the reproduction season, no or only single *S. flavomaculata* individuals were seen along the transect even in ideal weather. The data of these transect runs were discounted. Thus, the records of 147 censuses were analysed for the short transect and 97 for the long transect.

During each transect run the territorial males were observed by eye or with the aid of close-focusing binoculars and mapped within a strip ca 30 m wide along the transect line. The scanned area of the 750 m transect encompassed ca 20,000 m^2 of which 530 m^2 (2.6%) consisted of open water. The searched area along the additional transect section leading through puddle areas but without peat ponds measured ca 10,000 m^2. A male was considered territorial when it regularly patrolled a more or less fixed stretch or criss-crossed within a fixed space (Wildermuth 1998a). Territorial disputes between conspecifics were also noted but individuals just passing

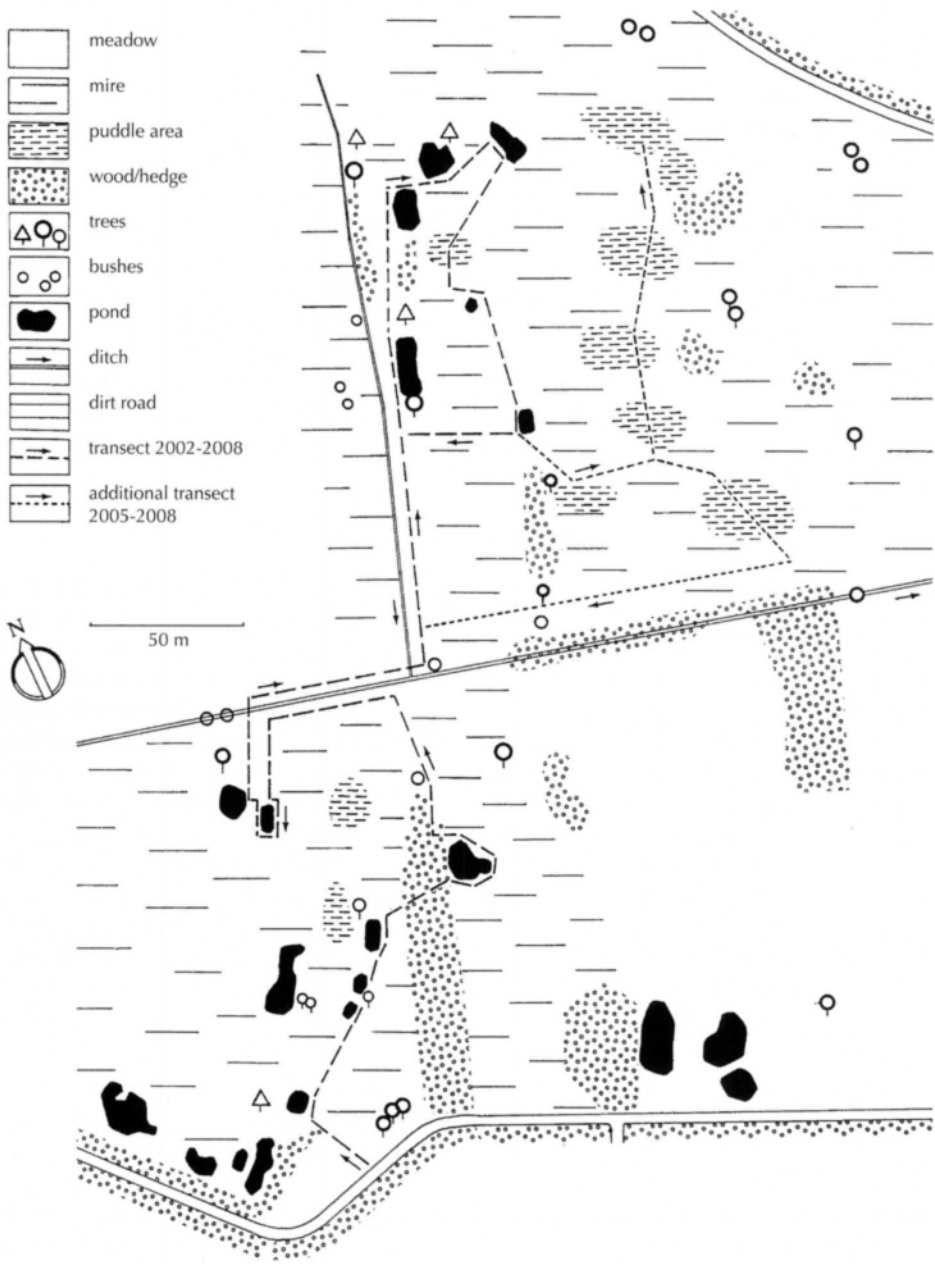

Figure 1: The study area 'Ambitzgi/Böndlerriet' with the transect along different landscape elements including 13 peat ponds in the heterogeneous environment of a nature reserve.

by were not considered. Territories over land were classified as terrestrial, and those over open water of ponds or ditches as aquatic. Territories along the transect extension over puddles with shallow water were counted separately. In order to record the annual phenology of *S. flavomaculata* I collected the exuviae and noted roaming copulation wheels as well as ovipositing females. Additional observations on reproductive behaviour were made in the nature reserve outside the transects.

Effects of ambient temperature

In warm weather the territorial males patrolled completely in the sun, and in hot weather completely in the shade of trees and bushes. In between they patrolled partly in the sun and partly in the shade. In order to locate the exact position of the patrol stretches with respect to adjacent landmarks at different ambient temperatures between ca 19 and 35°C, I estimated the sunlit and shaded portions of the patrol stretches by eye. Considering the inaccuracy of these estimations, the results of 304 assessments were allocated to four categories only: 0-10%, 11-50%, 51-90% and 91-100% in the sun (cf. Fig. 6).

Data analysis

To analyse the results of the records from the short transects I summarised the data for each quarter of each of the seven local annual flight seasons (cf. Fig. 2, bars) and figured out the relative portion of terrestrial and aquatic territories. This removed the annual variation in the flight season as well as the number and temporal distribution of the transect runs over the season. A MANOVA test (Wilks-Lambda method; Sokal & Rohlf 1995) was used to examine the differences between the quarters, which thus served as a fixed factor, with respect to the proportions of terrestrial and aquatic territories, both types of territories representing the interdependent variables. The seven recording seasons served as replicates in this analysis ($n = 7$). The data of the long transect runs were summarised for periods of 10 days, and differentiated by three types of territories: those over land (terrestrial), those over ponds (aquatic), and those over puddle areas. These periods were approximately fitted to seasonal periods with dry, partly dried and water filled puddles, thus allowing to estimate the effect of occasional desiccation of the puddles on the spatial distribution of the territories.

Results

Annual phenology of the local population

According to the records of tenerals and exuviae of *Somatochlora flavomaculata*, which were mostly found scattered and as single individuals at ponds, ditches and puddles, the emergence season started in the first half of May and peaked in the second half of the same month (Fig. 2). The first territorial males along the transect appeared in early June and the last were seen in September. However, the start as well as duration and end of the reproduction season varied annually. In a number of years a few territorial males were observed in the study area outside the transect strips slightly earlier and later than along the transects.

Reproductive behaviour

Tandem formation within the territories and subsequent mid-air copulation occurred very quickly and was witnessed only five times over land and twice over water. Most of the 194 copulating pairs were not detected until they passed by on the wing in the wheel position. Typically, the pairs circled or roamed rather low over the vegetation, or above ponds and puddles, for several minutes before perching in herbaceous vegetation or flying to a bush or tree (Plate III). Copulating pairs were predominantly observed from the beginning of June until mid-August, with a peak in the first half of July (Fig. 2). The exact copulation time was not determined because pairs often moved and I lost sight of them, but a few pairs that perched in low vegetation were observed for 15-20 min before they moved on. Termination of copulation was seen twice. After the partners had separated they remained perched on vegetation rather close to each other and then flew away one after the other. Oviposition occurred unguarded and mainly hidden in dense vegetation. Ten ovipositing females were seen during the study period.

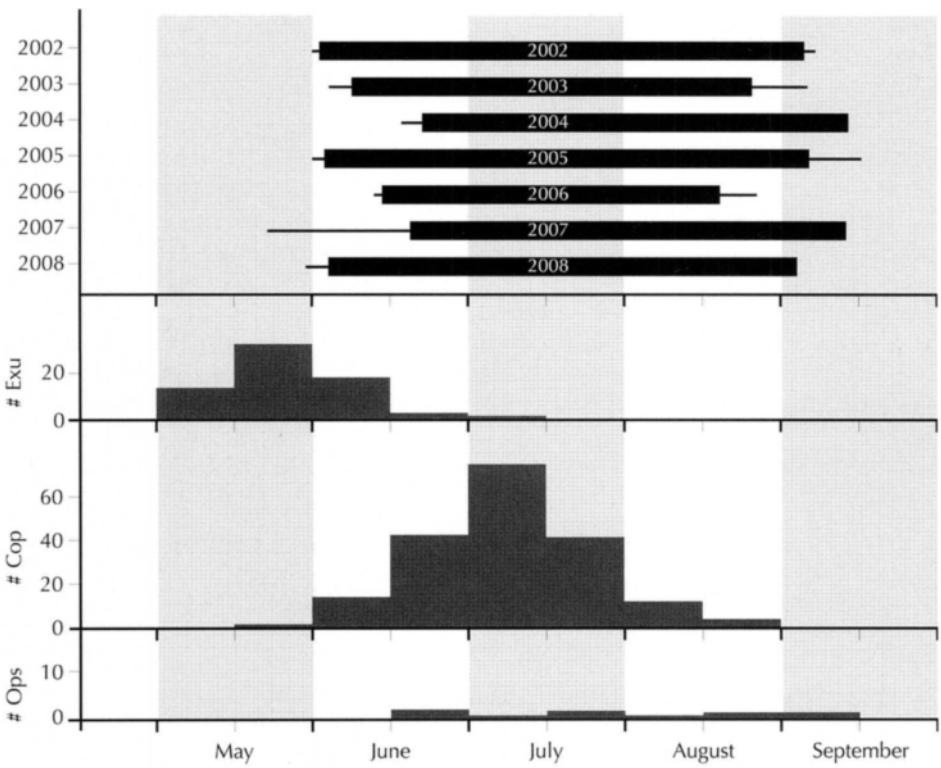

Figure 2: Phenology of *Somatochlora flavomaculata* from 2002 to 2008 in the study area. Bars represent individuals on the wing within the transects and lines those outside the transects, thus corresponding to the local annual flight season. — Exu: exuviae; Cop: copulations; Ops: ovipositions. The records for Exu, Cop, and Ops are summarized for 2002-2008.

Location of the territories

Within the short transect strip males usually established their terrestrial territories near conspicuous topographic features such as bushes, trees, and wood edges, but also in aisles of reed stands or against outstanding walls of herbaceous vegetation (Figs 3a, b; Plate III). Territorial males regularly occupied a few sites – a particular single bush or a tree or a lane between two rows of woody plants – during the main reproduction season in all study years. Thus these places appeared to be especially attractive for the rendezvous. At aquatic territories the males patrolled or criss-crossed over ponds and ditches in the same way as they did over land (Fig. 3c).

Seasonal shift of the territories

From 2002 to 2008 males were recorded 1,315 times in their territories within the transect strips, mostly between mid-June and mid-August. Along the short transect, terrestrial territories were recorded 672 times and aquatic territories 241 times. In the first quarter of the reproduction period terrestrial territories amounted to nearly 100%, then their proportion diminished in the second and third quarter and averaged 10% in the fourth quarter (Fig. 4). The proportions of terrestrial and aquatic territories differed significantly within the reproduction season (MANOVA: $F = 38.954$, d.f. = 1, 24, $p < 0.001$) with the preferred mating territories moving from terrestrial to aquatic sites in the course of the season.

Along the extended transects territorial males were encountered 956 times from 2005 to 2008. Altogether 502 territories were recorded over land, 102 over ponds, and 352 over puddles (Fig. 5). The proportion of territories over puddles was rather

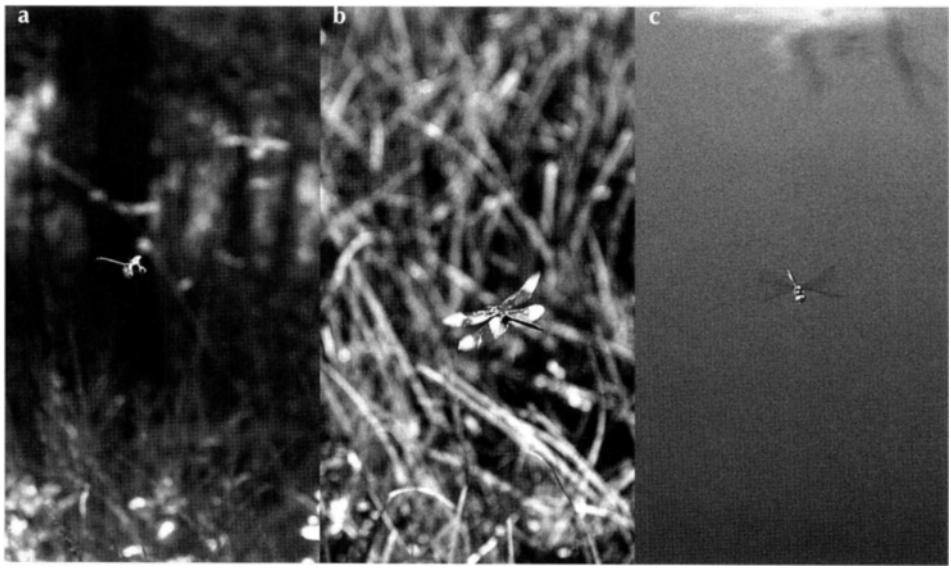

Figure 3: Territorial males of *Somatochlora flavomaculata* during hover stops on patrol flights — (a) typical terrestrial territory adjacent to sunlit edge of wood; (b) terrestrial territory over low vegetation bordered by tall reed, occupied by a wing-marked male; (c) aquatic territory over water surface almost bare of aquatic vegetation.

high, even in the early reproduction period; e.g. in 2005 and 2007 the percentage was 83-100% during the first 20 days of June, and the corresponding values for the end of the flight season (18 vii - 06 ix) varied from 17-100%. All in all the proportion of territories over puddles fluctuated considerably over the season, and no clear preference for this type of territory was apparent. However, males hardly ever established territories at these areas when the puddles dried out during hot spells devoid of precipitation in 2005 and 2006. Even in periods with partly desiccated puddles only a few territorial males were present over the puddle areas. They patrolled either above the remaining water or over land near outstanding vertical structures. No transfer of the territories to the ponds became apparent during these periods of drought even at the beginning or at the peak of the reproduction season.

Temperature dependent small-scale transfer of territories

Territorial males were generally on the wing at ambient temperatures from 20 to 34°C. But three individuals were recorded at temperatures below 20°C, one of them at 18.6°C. Two males were encountered at 34.8°C and 35.1°C, the highest temperatures measured during any transect runs. At temperatures up to 28°C all males patrolled in full sunshine. Then, with rising ambient temperatures they transferred their patrol stretches gradually to the shade of bushes and trees, spending progressively more time in the shade and making longer flights between turns in the shade. Above 30°C, 46% of the recorded individuals flew completely in the shade, and above 32.2°C all males patrolled only in the shade (Fig. 6). At temperatures above 28°C the territorial males interrupted their patrols irregularly and perched in the shade for a few seconds up to several minutes.

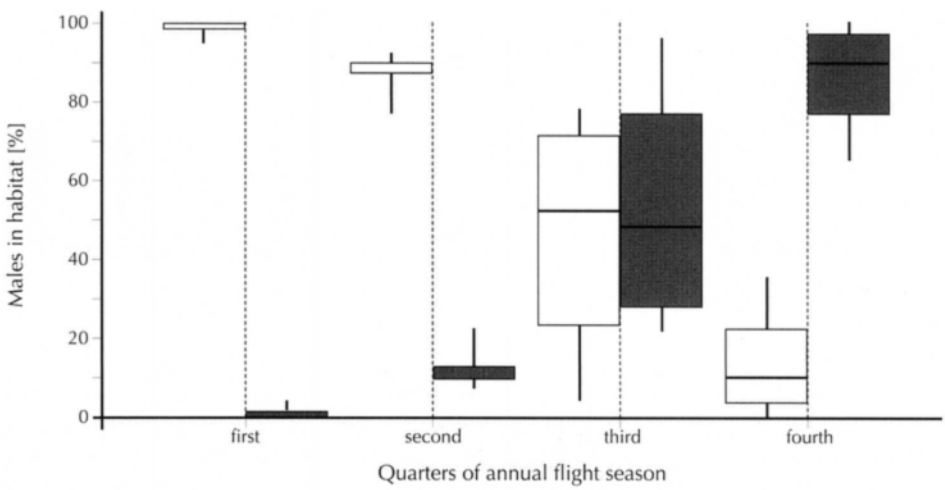

Figure 4: Seasonal proportion of terrestrial [white boxes] and aquatic [grey boxes] territories of *Somatochlora flavomaculata* along the unextended transect in 2002-2008. Boxplot with median, 25th and 75th percentiles (boxes) and 10th and 90th percentiles (bars). The annual flight seasons were divided in quarters. The percentages differ significantly between the quarters (see text).

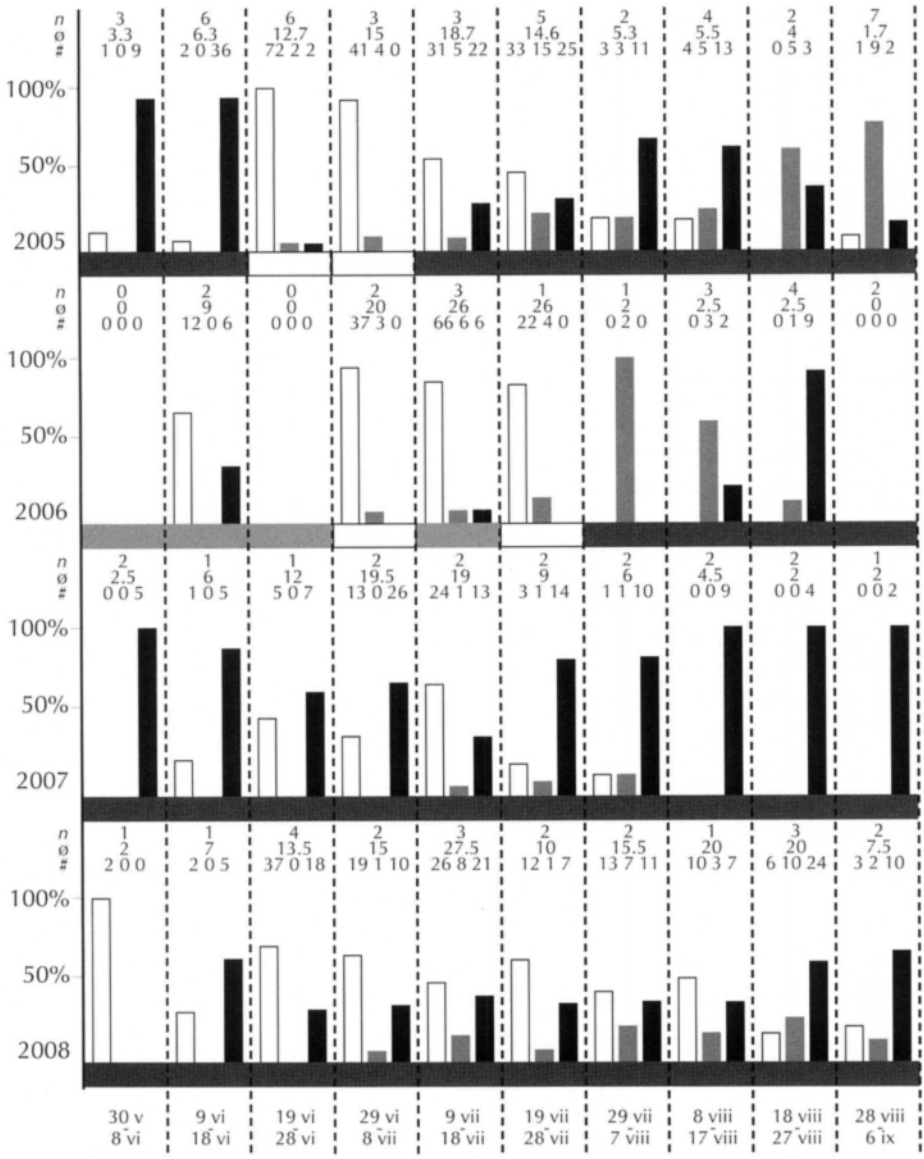

Figure 5: Territories of *Somatochlora flavomaculata* — proportions of terrestrial [white bars] and aquatic [grey bars] territories, and of territories at puddle areas [black bars] along the extended transect during the flight seasons 2005-2008. The horizontal bars represent periods with water-filled [dark grey], partly desiccated [light grey] and completely dry [white] puddles for each year. The flight season is divided into 10 periods of 10 days each and approximately fitted to periods with partly and completely dry puddle areas. — *n*: number of transect runs per 10 day-period; ø: average number of males encountered per transect run; #: total number of males recorded per 10 day-period at three different types of territories. Virtually no territories were established over puddle areas when these were dry.

Discussion

It is known that site-fixed, patrolling males of *Somatochlora flavomaculata* occupy territories both over land (terrestrial) and over water (aquatic) and there is strong indication that these places serve as rendezvous sites (Wildermuth 1998a). As prey capture is observed only very occasionally within territories (Wildermuth 1998a), food can be most likely excluded as the resource to be defended by occupying fixed sites. However, no unequivocal evidence for territories having a rendezvous role has previously been provided, as the initiation of copulation has not been directly observed. But in the course of the present study, pair formation was repeatedly witnessed at both types of territories, showing that males regularly await females at and also away from oviposition sites. Exceptionally, copulating pairs of *S. flavomaculata* are even seen in forest gaps, far from any water body (Webel 1932; HW unpubl.). Pair formation distant from breeding sites is also reported in other corduliids s.l. such as '*Procordulia*' *gray* (Selys) under special ecological conditions (Rowe 1988), and occasionally in *Oxygastra curtisii* (Dale) (Hoess 2005). In *S. flavomaculata*, terrestrial mating territories are established as a rule, in contrast to the co-inhabiting *Libellula quadrimaculata* Linnaeus in which site occupancy and copulation is observed exclusively at water bodies such as ponds, ditches and puddles (e.g. Walker & Corbet 1975: 165; Wildermuth 1998b and unpubl.; Sternberg 2000: 458). The establishment of terrestrial territories near conspicuous landmarks in *S. flavomaculata* may be explained by the low predictabilty of encountering females in areas with numerous scattered oviposition sites. Females, when visiting these sites, may use the same landmarks for orientation.

In *S. flavomaculata* no site fidelity was found during an earlier mark-release-resighting investigation at the study site (Flöss 1998). The resighting rate of marked males was 30.5% and only 50% of the resighted individuals were observed more than once and always at different localities within or outside the study area up to distances of 1.8 km from the marking site. Most of the time, males occupied localities distinguished by outstanding vertical landscape structures. Site fidelity in other territorial corduliids is also rather low, e.g. in *Cordulia aenea* (Linnaeus) (Brooks et al. 1997) and *Somatochlora alpestris* (Selys) (Knaus & Wildermuth 2002). Male individuals may occasionally return to the same place repeatedly within the same day or on a number of consecutive days, but they remain there for a few minutes at most. Thus, frequent change of the territory location appears to be a constant element of the male behavioural pattern in *S. flavomaculata*.

It is a striking fact that in *S. flavomaculata* the mating territories change from terrestrial to aquatic sites in the course of the reproduction period. This happens not randomly, but regularly, at least in this structurally heterogeneous study site with many small and scattered breeding sites. Within the short transect strip, open water represented only 2.6% of the scanned area. If the spatial distribution of the territories were random and not changing during the reproduction period, an overall very low percentage of aquatic territories would have been expected. However, the proportion gradually altered from nearly zero in the first quarter to about 90% in the last quarter of the season. The shift was independent of the drying up of puddles: Although the males virtually no longer established their territories over desiccated puddle areas during early and medium flight season 2005 und 2006, no increase of aquatic territories was observed (cf. Fig. 5). On the other hand, when water filled puddle areas were available during the whole season like in 2007 and 2008, these were always attractive for territorial males.

The reasons for the seasonal shift from mainly terrestrial to mainly aquatic are poorly understood. Possibly the females identify suitable oviposition sites during their visits to the wetlands and approach these sites more and more directly as the season progresses. Furthermore, additional copulations may no longer be essential for the females later in the season. Hence, they try to avoid male harassment and fly furtively to the oviposition sites. Hence, terrestrial territories would gradually loose their value as rendezvous sites towards the end of the flight season and the males would react to the change by shifting their territories to the water.

The reason for the shift of mating territories from the sun into the shade of bushes or trees during hot weather is presumably related to the danger of overheating from high ambient temperature and irradiation (Wildermuth 2006). This thermoregulatory behaviour determines the precise location of the territory and may enable the males to stay in flight and intercept females even at relatively high ambient temperatures.

Based on the results of this study, the mate search strategy of *S. flavomaculata* appears to be characterised by considerable phenotypic plasticity with respect to space and time. Depending on environmental features such as availability, type and spatial distribution of the oviposition sites as well as the seasonal point of time and the ambient temperatures, the males establish territories at different locations. Hence, it appears that this conditional mate search strategy has evolved in response to variation in the physical environment. In Odonata, a comparable plasticity in the mating system with respect to environmental heterogeneity has only been described in *Protoneura amatoria* Calvert, a zygopteran for which the local light conditions are the essential environmental factor (Larison 2007).

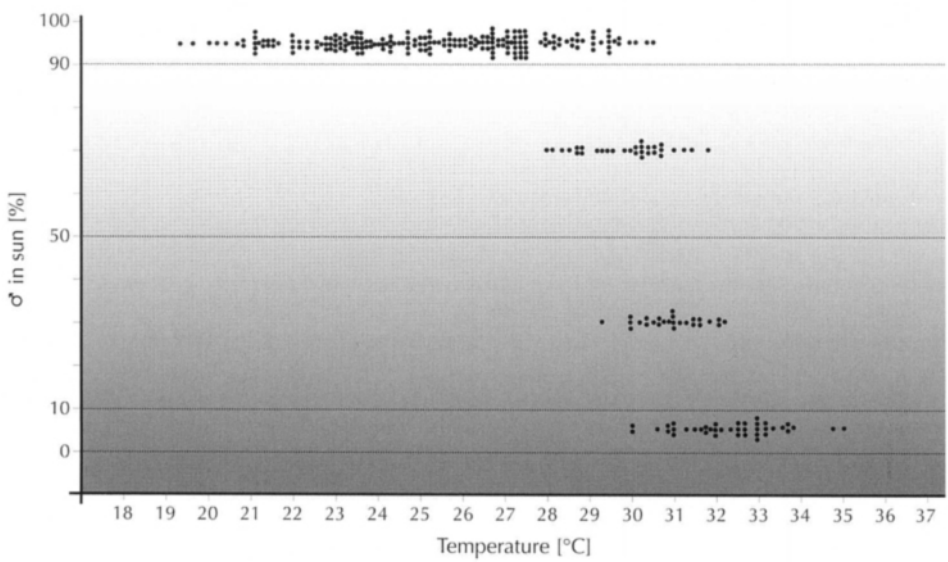

Figure 6: Proportion of *Somatochlora flavomaculata* males patrolling in the sun – as opposed to the shade – at different ambient temperatures. Each dot represents one individual (n = 304). The records are allocated to four unequal proportion categories. Vertical rows of dots within a catergory indicate the values obtained for different individuals at the same temperature.

Acknowledgements

I would like to thank Frank Suhling for his support in the statistical analysis of the results, Kamilla Koch for valuable comments on the manuscript, and Gordon Pritchard for polishing the language.

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Received 09 February 2009, revised and accepted 30 April 2009

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