

**VISUAL CUES IN OVIPOSITION SITE SELECTION BY
SOMATOCHLORA ARCTICA (ZETTERSTEDT)
(ANISOPTERA: CORDULIIDAE)**

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Behaviour of ♂ and ♀ individuals was studied at natural oviposition sites and over dummies of black plastic foil, black cotton and glass splinters on various backgrounds. Choice experiments revealed that both sexes are attracted chiefly by reflecting surfaces (on dark background). Male individuals responded by patrol flights including hovering, repeated surface-touching and site defence. Females exhibited inspection flights and (rarely) oviposition movements. The frequency of arrivals and the duration of stay over dummies in comparison with natural oviposition sites were quantitatively analysed.

INTRODUCTION

Dragonflies accomplish their larval development in species specific habitats. In most cases the latter serve simultaneously as rendezvous where the reproductive activities take place. Obviously adults of each species are able to recognize their appropriate oviposition sites. It is generally assumed that habitat recognition is primarily visual, as mature adults even respond to shining surfaces which are entirely unsuitable for oviposition (CORBET, 1962). The first experimental approach towards the problem of habitat selection was done in *Leucorrhinia dubia* by STEINER (1948). However, his conclusions were severely criticized by SCHIEMENZ (1954), as the response of both female and male individuals to breeding site dummies did not show any reproductive character. Here we present observations on reproductive behaviour and results of field experiments which may give some information on habitat recognition of a puddle dweller.

Somatochlora arctica is a widely distributed but rare corduliid in Central Europe (ASKEW, 1988). The larvae inhabit chiefly small and partly overgrown

pools of peatmoors and similar biotopes. The ecological requirements of this species were studied in Germany (ZIEBELL & KLINGER, 1980; STERNBERG, 1985, 1990) and in Switzerland (WILDERMUTH, 1986). Based on findings concerning the structural features at the oviposition sites it was suggested that the sparkling reflections of the uneven water surface, caused by vegetation, are an essential cue for the adults in recognizing the egg deposition place (WILDERMUTH, 1987). This hypothesis was examined in the course of the present study.

STUDY SITE, MATERIAL AND METHODS

The study was carried out between 30 August and 14 September 1990 at a small alpine bog, 2 km SSW of Nauders (Tyrol, Austria), 1.5 km E of the Swiss border. The area (200x50 m) is situated at 1600 m NN and consists of a slightly inclined clearing surrounded by pine and spruce forest. Superficial water is restricted just to a few places and comprises two turf wallows (used by red deer), a number of tiny puddles sparsely covered by vegetation (*Carex rostrata*, *Trichophorum caespitosum*) and a rivulet. The rest is densely overgrown with stalky vegetation. Observations were possible between 10.30 am and 5.30 pm Central European summer time, provided weather conditions were optimal (temperature $\geq 20^{\circ}\text{C}$, sunshine, calm).

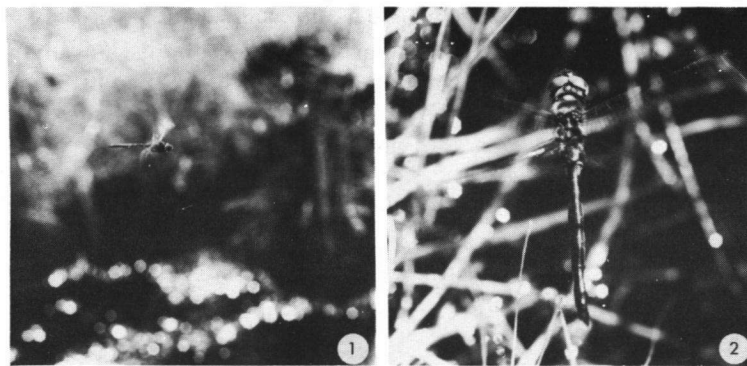
For the experiments we used black, shining plastic foil (2x4 m and 1x1 m), black, non-shining cotton cloth (1x1 m) and tulle (1x1 m). The material was mounted 20 cm above ground and stretched between sticks. Depending on the experiment, the various dummy elements simulating possible oviposition sites could be set up in different ways. In some cases the material was strewn with glass splinters from a car window in order to imitate the sparkling light reflection pattern of the natural breeding sites. For dummies feigning tiny puddles we placed a group of 8 little boards (size varying from 150 to 320 cm²) coated with black plastic foil in the vegetation on superficially dry ground. The same was done with 8 rectangular pieces of black cotton cloth, the total area of each group being 0.2 m².

In corresponding preliminary experiments with *Aeshna juncea* and other alpine Anisoptera white cotton cloth proved to be completely unattractive. Only males of *A. caerulea* did sometimes settle on it. Based on those observations, we abandoned offering white dummies to *S. arctica*.

All observations were made by eye or with the aid of binoculars. Besides the uninfluenced behaviour at the oviposition sites we recorded the responses towards the dummies and noted the frequency of arrivals at both natural breeding-waters and their imitations. The duration of stay of the individuals at certain sites was measured with a stop-watch.

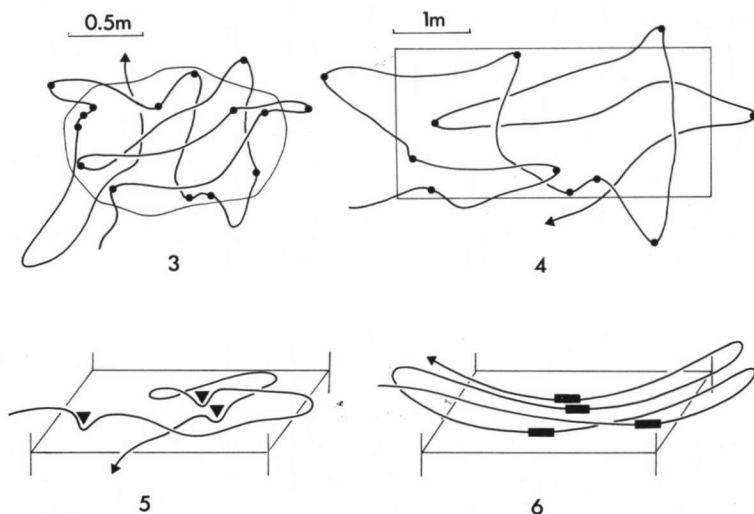
BEHAVIOUR AT BREEDING SITES

0-3 flying males were simultaneously present at the area under observation. Immediately after arriving at the mating place they showed typical patrol flights, mostly over puddle areas but also over vegetationless wallows and, rarely but repeatedly, over vegetation lacking any visible water. The individuals stayed between 1 and 44 seconds at the same locality. However, site-tenacity could be less easily observed at places with scattered, indistinctly confined puddles partly hidden in vegetation than at open turf pools. Here the males hovered 0.5-1.0 m above the water surface (Fig. 1), often near the edge, their heads directed towards



Figs 1-2. *Somatochlora arctica* at natural oviposition sites: (1) Male hovering over wallow; — (2) Female oviposition at puddle hidden among vegetation. Note light reflections on dark background.

the centre of the pool. They frequently changed position abruptly, but also gradually. A typical example of a flight path is shown in Figure 3. Sometimes they lowered their flying height, possibly for closer inspection of the ground. "Water-touching", as observed in many other Anisoptera (CORBET, 1962), was only recorded once. The individual touched the surface four times running. Patrol



Figs 3-6. Examples of flight manoeuvres (males) at natural oviposition site and plastic foils: (3) Flight path over pool (dots indicate hovering); — (4) Flight path over foil; — (5) Flight path over foil including dipping movements without touching the surface (arrows); — (6) "Water-touching" movements (reinforced lines indicate touch with surface).

flights were often interrupted by aggressive interactions with conspecifics and males of *Aeshna juncea*. Arrivals of the latter mostly diminished the duration of stay of *S. arctica* at the same place. Females visited both puddles and wallows for oviposition, however, they preferred the pot-holes hidden in vegetation. Oviposition took place on the water surface close to plant stems, on soaked moss pads and emergent turf mud (Fig. 2). All these sites had a similar appearance, exhibiting a sparkling pattern of light reflections on dark background (Figs 1, 2, 10, 12). "Water-touching" in females was observed once at a mud-pool. Concerning the additional elements of reproductive behaviour the findings of PRENN (1935) and SONEHARA (1985) could be confirmed.

BEHAVIOUR TOWARDS DUMMIES

The following responses were noted:

- Individuals flew past and took no notice (both sexes);
- Dummies were flown over slowly; sometimes individuals returned once or twice (both sexes);
- Hovering (Figs 9, 13); duration at least 1 s, often combined with change of position (males). A typical example of a flight path is shown in Figure 4;
- Hovering combined with short dipping movements (Fig. 5; males);
- Repeated audible surface-touching (Fig. 6); maximum record 52 times within 49 s. Sometimes individuals slid over the foil very close to the surface, touching the latter presumably with the abdominal tip over a distance of several dm (both sexes);

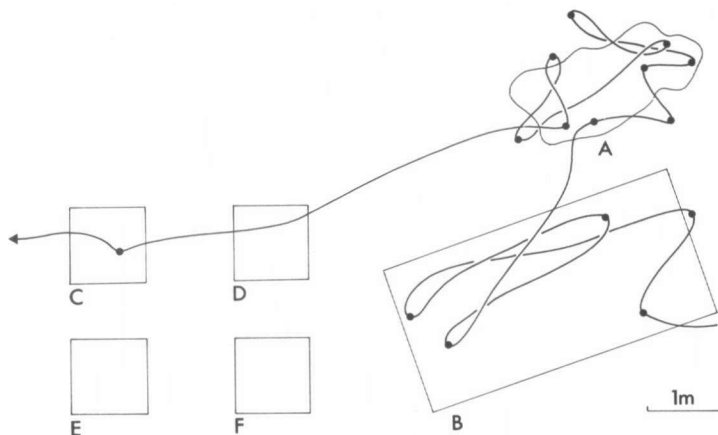


Fig. 7. Arrangement of dummies near a natural oviposition site (wallow), A) in experiment (2); — B, C black plastic foil; — D foil with glass splinters; E tulle; — F tulle with glass splinters. — The line indicates a typical example of flight path (male) including hovering (dots).

- Close inspection of possible oviposition site, potentially combined with oviposition movements (females);
- Defence of the site against intruders (males).

Females rarely visited dummies and natural oviposition sites under observation. Therefore only data from males could be used for quantitative analysis of the choice experiments.

EXPERIMENTS

(1) Two black plastic foils of square shape (each 1 m²), one of them with glass splinters on the surface, were placed near a pool (ca. 2 m²), the distance between their edges was 1 m. The results are shown in Table I. During the observation period of nearly 3 hours the sites were shortly overflown 47 times and the males remained hovering over them 180 times. Fights were only recorded at the pool. The frequency of arrivals at the natural site was significantly higher than at the foils. On the average, the individuals remained 4 times as long over the pool as over the dummies. Between the responses to plastic foils no difference was found. Indications to statistical tests are included in Table I.

(2) This experiment was carried out at the same place and with the same material as in experiment (1). In addition, a rectangular black foil (8 m²) and two squares of tulle each (1 m², one of them with glass splinters) were offered. The arrangement of the dummies is shown in Figure 7. As exemplified in the latter,

Table I

Results of choice experiment (1): responses of males to natural oviposition site (vegetationless wallow with coherent water surface) in competition with black plastic foils, 30 August 1990 (duration of observation 2.75 h) — [s: significant differences ($p < 0.01$); — ns. non significant differences ($P > 0.05$). — For the number of arrivals the χ^2 -test and for the duration of stay the Mann-Whitney U-test, two tailed, were used].

Behavioural features	Pool (2 m ²)	Foil (1 m ²)	Foil (1 m ² , with glass)
Number of slow over-flights	8 (17%)	20 (43%)	19 (40%)
Number of arrivals incl. hovering	89 (49%)	52 (29%)	39 (22%)
	(s)		(ns)
Number of fights	10	—	—
Duration of stay:	(s)		
— $\bar{x} \pm \text{SD}$ (sec)	8.6 \pm 8.2	2.3 \pm 1.2	2.1 \pm 1.0
— range (sec)	1-44	1-5	1-5

Table II

Results of choice experiment (2): responses of males to natural oviposition site (wallow) in competition with 5 dummies, 6 September 1990 (duration of observation 4.75 h) — [s and ns as in Table I, except for * ($P < 0.05$)].

Behavioural features	Pool (2 m ²)	Foil (8 m ²)	Foil (1 m ²)	Foil (1 m ² with glass)	Tulle (1 m ²)	Tulle 1 m ² with glass)
Number of slow over-flights	2 (9%)	11 (50%)	1 (5%)	6 (27%)	—	2 (9%)
Number of arrivals incl. hovering	37 (46%)	31 (40%)	5 (7%)	5 (7%)	—	—
	(ns)		(s)			
Number of fights	6	8	—	—	—	—
Duration of stay:	(s)*					
- $\bar{x} \pm \text{SD}$ (sec)	8.5 \pm 7.4	11.1 \pm 10.5	1.4 \pm 0.5	2.4 \pm 1.0	—	—
	(ns)		(s)			
- range (sec)	1-31	1-37	1-4	1-2	—	—

Table III

Results of choice experiment (3): responses of males to natural oviposition site (puddles) in competition with dummies, 10 September 1990 (duration of observation 1.5 h) — [ns as in Table I].

Behavioural features	Puddle area (2 m ²)	Area with scattered foil pieces (2 m ²)	Area with scattered cotton pieces (2 m ²)
Number of slow over-flights	—	—	—
Number of arrivals incl. hovering	21 (44%)	26 (54%)	1 (2%)
	(ns)		
Number of fights	2	1	—
Duration of stay:	(ns)		
— $\bar{x} \pm \text{SD}$ (sec)	11.7 \pm 11.4	7.1 \pm 5.7	(1)
- range (sec)	1-35	2-26	1

individuals sometimes visited pool and plastic foils successively. Frequency of arrivals and remaining time at the wallow as well as at the big foil were essentially the same, as indicated in Table II. The bigger plastic area proved significantly more attractive than the smaller ones. Tulle, even when covered with glass splinters, apparently showed no visible effect (Fig. 14).

(3) In a preliminary test we placed a group of 8 little boards coated with black plastic foil in the vegetation near small puddles (Fig. 11). Males reacted promptly, hovering for long periods over the dummies, repeatedly returning to the site. One individual remained about 20 minutes (Fig. 13). According to the flight manoeuvres, the male seemed to have selected the dummy site as the center of his territorial activities. Females visited the little foil pieces only rarely approaching them up to 5 cm for some seconds, hovering and turning their body axis horizontally, the last two abdominal segments being erected as if ready for oviposition. However, typical up and down movements were only seen once and, unlike at natural sites, just for a short time.

For a quantitative study of the reactions, an area of 2 x 1 m, with hidden puddles, was marked out. The foil boards were then scattered over a place of equal size at a distance of 2 m. The same was done with 8 adequate pieces of black cotton. The results (Table III) indicate essentially the same attractivity of puddles and foil fragments, while the non shining cotton pieces were hardly ever noticed.

(4) In a further experiment the same locality and arrangement as in experiment

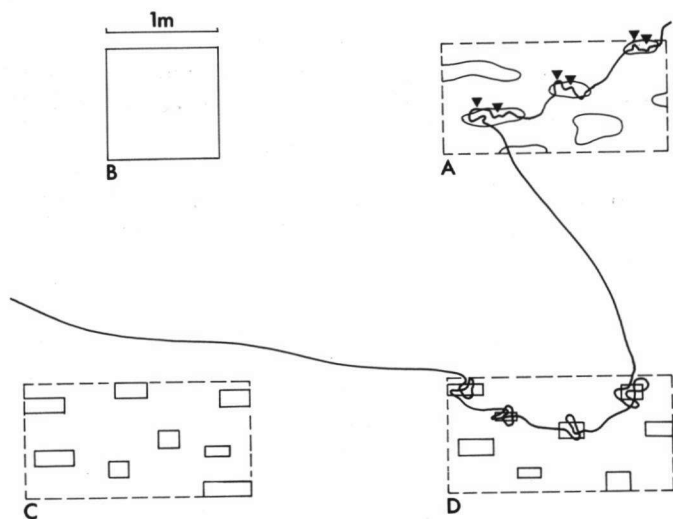


Fig. 8. Arrangement of dummies near a natural oviposition site (puddles, A) in experiment (4); — B coherent black foil; — cotton fragments; — D foil fragments. — The line indicates the flight path of a female including sites of oviposition (arrows).

Table IV

Results of choice experiment (4): responses of males to natural oviposition site (puddles) in competition with dummies including a coherent foil area, 14 September 1990 (duration of observation 3.5 h)
— [s as in Table I, except for * (= $P < 0.02$) and ** (= $P < 0.05$)].

Behavioural features	Puddle area (2 m ²)	Area with scattered foil pieces (2 m ²)	Area with scattered cotton pieces (2 m ²)	Coherent foil (1 m ²)
Number of slow over-flights	5 (17%)	11 (36%)	4 (13%)	10 (34%)
Number of arrivals incl. hovering	43 (30%)	69 (47%)	16 (11%)	17 (12%)
Number of fights	2	9	—	—
Duration of stay:				
- $\bar{x} \pm \text{SD}$ (sec)	7.9 \pm 7.9	8.9 \pm 8.7	4.2 \pm 3.2	3.9 \pm 2.8
- range (sec)	1-43	1-43	1-10	1-10

3 was used. Additionally we mounted a black plastic foil in one piece, 1 m² in size (Fig. 8). Again natural puddles and foil fragments had about the same effect. On the other hand the 1 m² foil and the cotton pieces evoked only few and weak reactions.

The results of the four experiments cannot be compared unconditionally as probably not always the same individuals were involved. Furthermore, slight differences in weather conditions and daily observation time have to be considered.

CONCLUSIONS

In the experiments described here, *S. arctica* doubtless responded to oviposition site dummies with behavioural elements belonging to the scope of reproduction. Males showed site-tenacity combined with hovering, "water-touching", site-defence and search for females, while the latter exhibited oviposition site search and egg laying movements. Therefore it may be concluded that these reactions are closely related to the recognition of suitable larval habitats. These responses differ from those reported by STEINER (1948) in *Leucorrhinia dubia*. He found that



Figs 9-14. Responses by males to visual cues of natural oviposition sites and dummies: (9) Male hovering over large plastic foil; — (10) Natural puddles in stalky vegetation; — (11) Boards coated with foil among vegetation, feigning tiny water-holes; — (12) Male hovering over tiny puddle; — (13) Male hovering over scattered dummies; — (14) Tulle with glass spinters over vegetation.

males and females were attracted to, and settled upon, white paper. Steiner misinterpreted these reactions as behaviour in connection with habitat finding. However, as already stressed by SCHIEMENZ (1954), various Anisoptera tend to settle on any bright background, presumably to take up heat. In view of our observations this is especially true for *L. dubia* and *Aeshna caerulea* among the alpine species. Furthermore, according to STEINER (1948), black paper had almost no effect on *L. dubia*. We noticed similar weak reactions towards black cotton by *S. arctica*, and also by *S. alpestris* and *Aeshna juncea* (Wildermuth, unpublished). On the other hand, females of *L. dubia* and *Sympetrum danae* showed repeated "water-touching" and egg laying movements on the shining black foil (males were no longer present at the time of observation). Obviously both libellulid species were likewise deceived by reflections on black background.

From the different reactions to the various dummies it can be concluded that medium-range recognition of the oviposition site occurs visually in both sexes of *S. arctica*. The responses are released by simple stimuli, these being reflections (on a dark background). Sparkling light patterns alone (glass splinters on tulle over vegetation) had no effect, and when glass splinters providing a great number of reflecting light spots were added to a black foil no enhancement of the responses was recorded. This is somehow surprising as a glittering surface is characteristic of the natural breeding waters, a fact which led to the hypothesis that reflecting spots would suffice as cue for the recognition of the oviposition place (WILDERMUTH, 1987). However, it must be considered that the foils do not make up a homogeneous plane like the water surface of a pool. The slightly undulatory surface produces a coarse mosaic of reflections. Moreover, dragonflies might not be able to resolve a pattern of sharply defined light spots from a distance longer than 1 m. Therefore, relatively coarse and simple stimuli have to be sufficient for recognizing habitat structures and other crucial elements of their environment, as shown by FRANTSEVICH & MOKRUSHOV (1984) for the detection of conspecifics. In connection with reflecting surfaces, polarized light might play an important role (SCHWIND, 1985).

The effect of mat black areas is not quite clear, as in experiment (3) hardly any responses were noted while in experiment (4) the males showed evident, though weak, reactions. This evidence may explain the fact that males sometimes hover over superficially dry ground, with shady, dark-appearing depressions, possibly feigning small water holes.

In experiment (2), males showed a clear preference for the bigger of two foils. On the other hand, in experiment (4), small scattered foil pieces proved more attractive than one bigger foil. For the interpretation of these findings which appear inconsistent at first sight, it has to be taken into consideration that the experiments were conducted at different localities: experiment (2) next to a pool, and experiment (4) in an area with scattered puddles. This suggests that in male individuals there might exist two different dispositions or imprintings influencing

the preference of corresponding dummies.

Of special interest are the "water-touching" movements which both sexes exhibited on plastic foil, performing them occasionally many times in succession. This behaviour may be interpreted as a tactile examination of the oviposition substrate. From the flexible, but dry surface, the insect might be unable to obtain a clear information as to the nature of the substrate, which is possibly the reason for the frequent repetition of the touches. Females presumably received negative replies from dipping, as real oviposition movements could only be observed once and merely for a short moment. Immediately afterwards the female changed from the dummy to a puddle where she continued egg laying for minutes (Fig. 8).

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REFERENCES

- ASKEW, R.R., 1988. *The dragonflies of Europe*. Harley, Martins (Essex).
- CORBET, P.S., 1962. *A biology of dragonflies*. Witherby, London.
- FRANTSEVICH, L.I. & P.A. MOKRUSHOV, 1984. Visual stimuli releasing attack of a territorial male in *Sympetrum* (Anisoptera: Libellulidae). *Odonatologica* 13(3): 335-350.
- PRENN, F., 1935. Zur Biologie von *Somatochlora arctica* Zett. und *Som. alpestris* Selys. *Sber. Akad. Wiss. Wien* (I) 144: 119-139.
- SCHIEMENZ, H., 1954. Ueber die angebliche Bindung der Libelle *Leucorrhinia dubia* v. D.L. an das Hochmoor. *Zool. Jb. Syst.* 82: 473-480.
- SCHWIND, R., 1985. Sehen unter und über Wasser, Sehen von Wasser. *Naturwissenschaften* 72: 343-352.
- SONEHARA, I., 1985. Observations on the life-history of *Somatochlora arctica* in Nagano Prefecture. *Tombo* 28(1/4): 23-30.
- STEINER, H., 1948. Die Bindung der Hochmoorlibelle *Leucorrhinia dubia* Vand. an ihren Biotop. *Zool. Jb. Syst.* 78: 65-96.
- STERNBERG, K., 1985. *Zur Biologie und Oekologie von sechs Hochmoorlibellenarten in Hochmooren des südlichen Hochschwarzwaldes*. Diplomarbeit Univ. Freiburg, Freiburg i. Br.
- STERNBERG, K., 1990. *Autökologie von sechs Libellenarten der Moore und Hochmoore des Schwarzwaldes und Ursachen ihrer Moorbinding*. Diss. Univ. Freiburg i. Br.
- WILDERMUTH, H., 1986. Zur Habitatwahl und zur Verbreitung von *Somatochlora arctica* (Zetterstedt) in der Schweiz (Anisoptera: Corduliidae). *Odonatologica* 15(2): 185-202.
- WILDERMUTH, H., 1987. Fundorte und Entwicklungsstandorte von *Somatochlora arctica* (Zetterstedt) in der Schweiz (Odonata: Corduliidae). *Opusc. zool. flumin.* 11: 1-10.
- ZIEBELL, S. & P.U. KLINGER, 1980. Zur Oekologie von *Somatochlora arctica* (Zetterstedt 1980) (Odonata). *Drosera* 80(1): 17-24.