HABITAT SELECTION AND OVIPOSITION SITE RECOGNITION BY THE DRAGONFLY *AESHNA JUNCEA* (L.): AN EXPERIMENTAL APPROACH IN NATURAL HABITATS (ANISOPTERA: AESHNIDAE)

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The behaviour of ♂ and ♀ individuals was studied at natural and artificial breeding stites. In order to detect the stimuli by which the adult insects recognize their larval habitats dummies varying in size (0.02-8 m²) and material (black plastic foil, black and white cotton cloth, tulle) were set up in the vicinity of or apart from natural pools. In multiple choice experiments black plastic foil proved highly attractive to both sexes. They exhibited the complete repertoire of behavioural elements which belong to reproduction including site defence and oviposition. Two behavioural elements were analysed quantitatively, that is the number of arrivals and the duration of stay at dummy sites and at natural pools. The males frequented large foil areas more often than small ones and they stayed over them longer. Glass splinters feigning the sparkling light reflections present at natural breeding sites did not enhance the attractiveness of a dummy. In full sunshine a natural pool was preferred to a dummy of about the same size. However, the attractiveness of these sites was reversed when the sun became covered by a cloud. From the results of the choice experiments it may be concluded that the most effective stimuli by which the adult dragonflies recognize suitable oviposition sites comprise a coarse pattern of reflecting areas on dark background. They prefer large areas to small ones. Non-shining black areas have little effect and white ones have none or even repel insects. Sparkling light reflection patterns alone are obviously poor cues, as they evoke only weak responses or none at all.

INTRODUCTION

According to their developmental stage, maturity and disposition, many animals, including dragonflies, select different habitats to satisfy the specific requirements appropriate to the situation which individuals face (e.g. CORBET, 1962; PARTRIDGE, 1978, for reviews). Thus adult dragonflies seek out places·which

differ in structural features for hunting, drinking, sleeping, maturation and repro-
duction (STERNBERG, 1990).

Among the spatial resources the oviposition site is of particular importance.
By a female's choice of the oviposition site she influences the survival rate of
eggs and larvae. For males breeding habitats signify sites with a high probability
for encountering mates. Relatively high abundance and spatial clumping of recep-
tive females at the oviposition site selects for male strategies to focus their search
on such concentration points (PARKER, 1978; VAN BUSKIRK & SHERMAN,
1985).

As each dragonfly species only develops successfully in certain types of waters,
adults of both sexes must be able to find their specific breeding sites. This is
particularly important for ecological specialists which are confined to a few or
only one type of larval habitat. These species have to be capable of detecting
and recognizing specific parts of their environment suitable for the development
of eggs and larvae by using defined proximate factors.

Habitat selection may depend on physical traits of habitats as well as on
vegetation, predators and conspecific individuals present in available sites (UBU-
KATA, 1984; VAN BUSKIRK & SHERMAN, 1985; WAAGE, 1987; WOLF &
WALTZ, 1988; MARTENS, 1989; MARTENS & REHFELDT, 1989; REH-
FELDT, 1990). In this paper I consider habitat choice by males and females of
Aeshna juncea. I am concerned only with habitat choices based on structural
features including vegetation, which are independent of other biotic factors.

Different methods may be used for the study of habitat preferences by dragon-
flies: (1) Description of the places where they breed (e.g. DEMARMELS &
SCHIESS, 1977; WILDERMUTH, 1986; STERNBERG, 1985; BUCHWALD,
1989; BUCHWALD & SCHMIDT, 1990; MÜLLER, 1989; WILDERMUTH,
1992a); − (2) Experimental alterations of the oviposition sites and records of
the subsequent reactions of the adults (BUCHWALD, 1989; STERNBERG, 1990)
and − (3) Choice experiments with natural materials (WAAGE, 1987; WILDER-
MUTH, 1992a) or dummies (WILDERMUTH & SPINNER, 1991).

Based on various incidental observations (e.g. KENNEDY, 1917; 1938; MUL-
LER, 1937; WYNIGER, 1955; NEVILLE, 1960) it has been generally assumed
that habitat selection in dragonflies is primarily visual (CORBET, 1962) and that
the verdict of sight may be confirmed or amplified by chemical and physical
stimuli (STEINER, 1948; MOORE, 1960). However, more precise information
about the question how dragonflies recognize their oviposition site has only
recently been obtained. Choice experiments with *Somatochlora arctica* (WIL-
DERMUTH & SPINNER, 1991) and *Perithemis mooma* (WILDERMUTH,
1992b) revealed that specific visual and tactile cues are of great importance in
finding their oviposition sites.

Preliminary studies showed that males and females of *A. juncea* react in similar
ways to dummies feigning oviposition sites as do both sexes of *S. arctica*. In

contrast to the latter, *A. juncea* is a common species at many localities, thereby offering favourable conditions for various experiments which can be quantitatively analysed. In order to determine the cues by which adult individuals detect their oviposition places I conducted multiple choice experiments, thus testing the hypothesis that reflections of the water surface in combination with other structural features, which are visually recognizable, are essential in guiding the animals to their breeding sites.

ECOLOGY OF *AESHNA JUNCEA*

A. juncea is a holarctic aeshnid dragonfly which occurs in Europe from the Iberian Peninsula to the North of Scandinavia (ASKEW, 1988). In the alpine countries of Central Europe it is found from 200 to 2200 m NN (MAIBACH & MEIER, 1987; LEHMANN, 1985; SCHORR, 1990). In that area it colonises a great variety of habitats such as moorland pools, peat diggings, ditches, slowly running rivulets in inclined bogs, alpine lakes and other still waters of any size which provide patches of emergent plants (PETERS, 1987; STERNBERG, 1982; LEHMANN, 1990). At low altitude up to ca 800 m NN however, it is almost exclusively confined to shallow and overgrown waters on peaty ground (MAIBACH & MEIER, 1987; WILDERMUTH, 1992a).

Details on the habitat requirements of *A. juncea* are known from Black Forest bogs in SW Germany (STERNBERG, 1985, 1990). There, in contrast to other moorland species, it prefers relatively large and deep pools (mean area 30 m², mean depth 23 cm) with acid water (mean pH 4.78) and a comparatively high concentration of electrolytes (mean electric conductivity 53 μS). On the average 72% of the water area is covered with emergent vegetation (*Caricetum rostratae* or *Caricetum lasiocarpae*). However, studies in various habitats at different locations and altitudes in Switzerland revealed that the values for the ecological parameters may vary considerably (WILDERMUTH, 1992a). The only necessary condition for the colonization of shallow stagnant waters by *A. juncea* is presumably the presence of emergent vegetation with vertical structures growing on peaty or peatlike ground.

STUDY SITES, MATERIALS AND METHODS

This study was carried out in August and September 1990 at the following localities:
(1)   H a r t k a i s e r a l m nr Ellmau, N Tyrol (Austria), alt. 1550 m. − Small bog (100 x 30 m) with large pool and a number of scattered small and shallow pools, surrounded by alpine pastures and spruce forest.
(2)   T i e f h o f nr Nauders, N Tyrol (Austria), alt. 1600 m. − Bog-like clearing (200 x 50 m) with a few small wallows, used by red deer, and scattered shallow pools, surrounded by spruce forest.
(3)   G r ü n s e e nr Nauders, N Tyrol (Austria), alt. 1840 m. − Bog similar in size and feature to location 2, adjacent to small lake with vast areas of emergent vegetation.
(4)   B o s c h   d e   l a   F u r c e l a nr Maloja GR (Switzerland), alt. 1860 m. − Circular bog with one large pool and a number of small and shallow pools, ca 100 m in diameter, surrounded by pine forest.
(5)   P a n ü ö l / T a n n e n b o d e n a l p nr Flums SG (Switzerland), alt. 1900 m. − Scattered pools of different sizes in alpine pasture with numerous depressions, situated above tree line.
The behaviour of male and female individuals was observed at traditional breeding sites where *A. juncea* develops regularly (proved by findings of exuviae) and at experimental simulations in
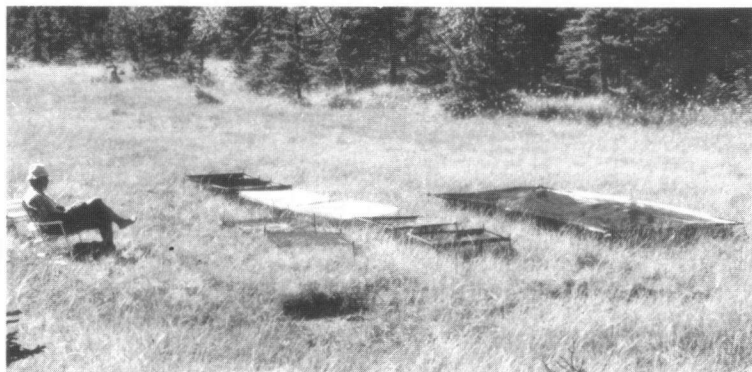
Fig. 1. Experimental device with 8 dummy elements in the vicinity of a small natural pool.

natural habitats. In order to test the reactions of the different possible stimuli coming from natural oviposition places, artificial sites (dummies) varying in material and size were offered to adults ready for reproduction. For site choice experiments I used black shining plastic foil (2 x 4 m and 1 x 1 m), black non-shining cotton cloth (1 x 1 m), white cotton (1 x 1 m) and tulle (1 x 1 m). Foils and tissues were mounted in the vegetation, 20 cm above superficially dry ground, stretched between sticks and fixed with clothes pegs.

According to the experiment, single dummy elements or groups of them were placed next to a natural oviposition site (small pool) or fully isolated from open water (e.g. Fig. 1). A complete experimental set consisted of 9 elements, i.e. 1 black plastic foil of 8 m^2 in size and 8 areas of 1 m^2, the latter consisting of pairs of different material. Among each pair one area was strewn with glass splinters from a car window in order to mimic the sparkling light reflection pattern of natural breeding sites. For dummies feigning tiny puddles I placed a group of rectangular boards (size varying from 0.015 to 0.032 m^2) coated with black plastic foil in the vegetation. A similar set was arranged with pieces of black cotton cloth, the total area of each group being 0.2 m^2.

Observations were made by eye or with the aid of binoculars (Nikon Travelite II, 7 x 20) whose shortest working distance was 2.8 m. At artificial oviposition sites I recorded the responses towards the various dummies qualitatively. In choice experiments which were to be quantitatively analysed I noted the frequency of arrivals, of aggressive interactions and of dipping movements. Additionally I measured the duration of stay with a stop watch. For comparison purposes the same measurements were carried out at natural breeding sites.

Observations and experiments were possible from 09.30 to 16.30 h Solar time, provided there were suitable weather conditions (temperature > 18°C, full sunshine or slightly cloudy, calm or slightly windy).

BEHAVIOUR AT NATURAL BREEDING SITES

MALES. — At isolated ponds with distinct margins and a free water surface of more than 100 m^2 the individuals patrolled slowly along the edge, 0.8-1 m above the water table, hovering at irregular intervals (Fig. 2a). They frequently lowered their flying height in search of ovipositing females, presumably for closer inspection of the vegetation. By repeated short dipping movements, they
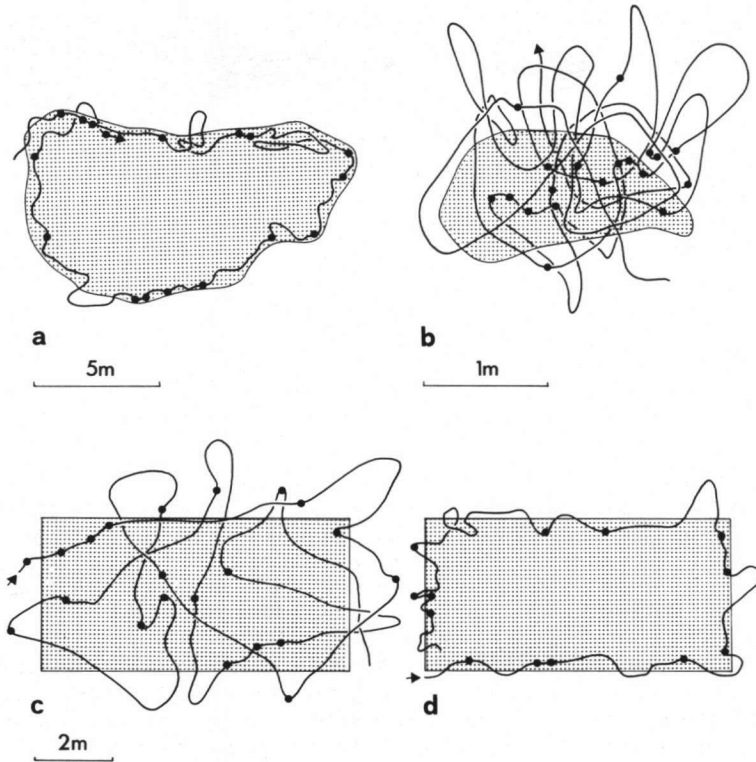
Fig. 2. Examples of flight manoeuvres (males) at natural and artificial oviposition sites: (a) flight path along the margin of a large pool; − (b) flight path over a small pool; − (c, d) flight paths over plastic foil (8 m²). − The rectangular dummy is either flown over randomly (c) or investigated along the margin. Dots indicate sites of hovering.

often touched the vegetation with their wings; individuals apparently intended to startle females in the process of oviposition. Obviously the males are not able to detect females hidden in the vegetation, unless the latter move.

At small pools not more than 1-3 m in diameter, the males did not follow the margins during their patrolling flights but flew over the water in any directions, describing loop-like flight patterns, and often hovering over the water surface or above the vegetation nearby (Fig. 2b). The mean duration of stay at small water bodies varied between the different localities as well as between subsequent days at the same place. If undisturbed, a male might stay up to 5 min at the same small pool and move on to another locality nearby. Patrolling flights were often interrupted or shortened by newly arriving individuals. Aerial fights occurred between conspecifics as well as with males of other aeshnids or corduliids.

Table I
Duration of stay of male individuals at natural oviposition sites (pools)

Locality & date	Duration of stay $\overline{X}$ + SD (s)	Range	Number of values
Ellmau, 16-VIII	81.8 ± 62.5	8 - 225	23
Maloja, 25-VIII	78.8 ± 87.8	6 - 300	8
Grünsee, 24-VIII	28.6 ± 18.1	2 - 53	10
Maloja, 28-VIII	16.5 ± 10.6	1 - 50	28
Maloja, 29-VIII	12.2 ± 11.0	2 - 27	149

In areas with scattered tiny pools which were hidden among vegetation and the wide edges of lakes homogeneously overgrown with sedge vegetation, *A. juncea* males changed their position continuously. In search of ovipositing females they often dipped deeply into dense vegetation. In areas with one large pool and
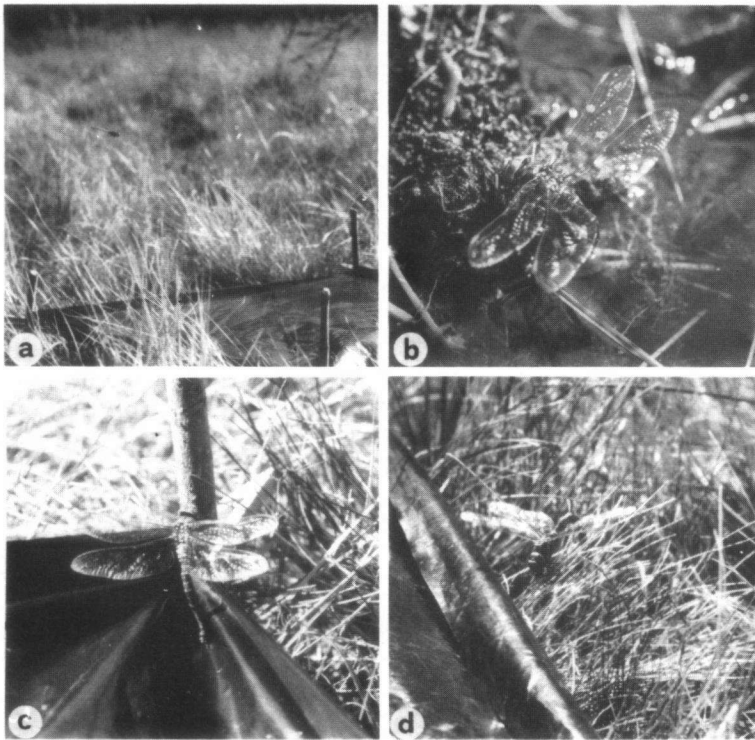

Fig. 3. *A. juncea* at natural and artificial oviposition sites: (a) male hovering over black plastic foil; — (b) female ovipositing at small and shallow pool [note light reflections on dark background]; — (c, d) female ovipositing on and beside black plastic foil.

a number of scattered small pools in the vicinity, the males preferred the bigger water body, since in the morning the latter was the first to be taken over, and during the course of the day it stayed almost permanently occupied.

FEMALES. − They deposited their eggs in areas with stalks of emergent vegetation, but also at sites with pads of moss or raw peat within shallow areas of bog pools and wallows (Fig. 3b). Oviposition sites were characterized by reflecting water surfaces broken by vegetation or soil structures which produced a pattern of sparkling light reflections.

With respect to other details of the reproduction behaviour the findings of ROBERT (1959) and KAISER (1976) could be confirmed.

BEHAVIOUR AT ARTIFICIAL BREEDING SITES

Throughout the observation period with suitable weather conditions (78h) about 800 single positive reactions were recorded in total. Most responses to dummy elements were seen at the large black plastic foil. The individuals showed gradual differences with respect to the intensity of the reactions. The males having taken notice of the site, either did not react or they reduced their travelling velocity and flew over the foil slowly, sometimes returning once or twice before they moved on. The reactions were clearer to the observer when the individuals stopped, hovered and repeatedly changed their position as they did at natural breeding sites. The large foil was either investigated along the margin or flown over randomly, the insects describing loops similar to the flying manoeuvres observed at small pools (Figs 2c, d). The duration of stay ranged from 1-140 s and varied between different localities as well as between subsequent days at the same place (Tab. II). Usually the males hovered 0.5-1 m above the foil (Fig. 3a) but often they lowered their flying height up to 5-10 cm above the ground for closer inspection of the surface. Additionally they made short dippings. When the surface was touched a sound could be heard. Occasionally an individual tried to seize an object such as a clothes peg, a glittering wrinkle in the foil, a stone or a small pad of moss placed on the dummy. It appeared as if the male intended

Table II

Duration of stay of male individuals at dummies (black plastic foil, 8 m²)

Locality & date	Duration of stay $\bar{X}$ + SD (s)	Range	Number of values
Flums, 20-VIII	57.7 ± 48.3	5 - 140	16
Grünsee, 24-VIII	26.6 ± 25.2	3 - 89	10
Maloja, 25-VIII	12.2 ± 9.9	2 - 35	12
Maloja, 29-VIII	10.8 ± 9.5	1 - 37	103
Maloja, 23-VIII	10.7 ± 9.0	3 - 38	26
Maloja, 28-VIII	7.1 ± 7.0	1 - 28	21

to rouse an ovipositing female. The reactions towards arriving conspecific males and females were exactly the same as at natural breeding sites.

Females visited the dummy sites less frequently than males. When the latter were present they immediately rushed at the females, trying to grasp them for copulation. When males were absent, the females often followed the margin of the dummy material searching for oviposition sites at a low flying height. Short dippings and ground touching were also observed. Sometimes they landed at the edge of the dummy or immediately beside it and made oviposition movements, trying to insert their ovipositor into the foil, the tissue or the dry vegetation nearby (Figs 3c, d). However, they did not stay as long as they did at natural oviposition sites.

During the course of the observation period I noticed in total 36 attempts of oviposition at artificial sites, that is 25 at the large black plastic foil (8 m^2), 6 at the small plastic foil (1 m^2). 2 at the small plastic foil with glass splinters, 1 on tulle, 1 on tulle with glass splinters and 1 on a small piece of black plastic foil (0.015 m^2) hidden in dry vegetation. However, the number of females which intended to oviposit on plastic was actually higher, but the individuals did not land when the foil was heated up too much in full sunshine.
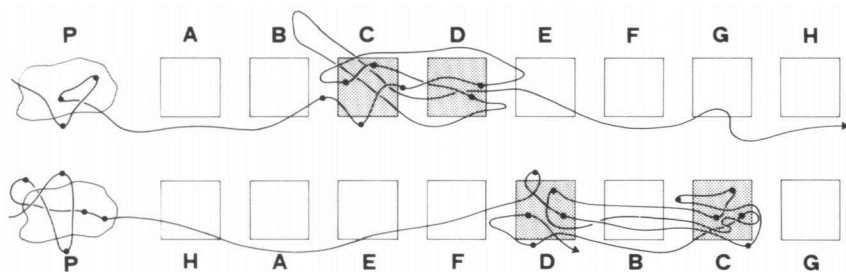

Fig. 4. Single row arrangement of 8 different dummies, each 1 m^2 in size, in vicinity of small natural pool (P). A: tulle; − B: tulle with glass splinters; − C: black plastic foil; − D: black plastic foil with glass splinters; − E: black cotton cloth; − F: black cotton cloth with glass splinters; − G: white cotton cloth; − H: white cotton cloth with glass splinters. − In both rows the single dummy elements are differently arranged. Each line indicates an example of a flight path of a male including sites of hovering (dots).

EXPERIMENTS

CHOICE EXPERIMENT
WITH EIGHT DUMMIES OF THE SAME SIZE IN DIRECT VICINITY OF A POOL

Eight different dummy elements, each 1 m^2 in size, were placed in a single row next to a small pool. A few males just flew over the row slowly at a low height without stopping and then moved on. However, many individuals which

arrived at the site, halted at the pool as well as at one or more dummy elements. They approached the row from either end, but also from the side, and they could leave the row before they arrived at the end of it. The black plastic foils beside the pool were clearly preferred, independent from the place where they were mounted. Two examples of typical flight paths are shown in Figure 4.

CHOICE EXPERIMENT
WITH ONE LARGE AND EIGHT DIFFERENT SMALL DUMMY ELEMENTS

This experiment was carried out at 4 days at 2 different localities. On 3 days all the dummy elements were placed in a single row (Fig. 5a) and in one experiment the small dummies were mounted in 2 rows adjacent to the short side of the rectangular large foil. Male individuals reacted by overflying the whole arrangement or parts of it, exhibiting patrol flights at selected sites. Examples of flight paths are shown in Figure 5. The results of the quantitative analysis of this experiment are summarized in Table III. Altogether 490 positive reactions (arrivals incl. hovering) were recorded. The animals definitely preferred the large plastic foil, as 58% of all arrivals were noted here.
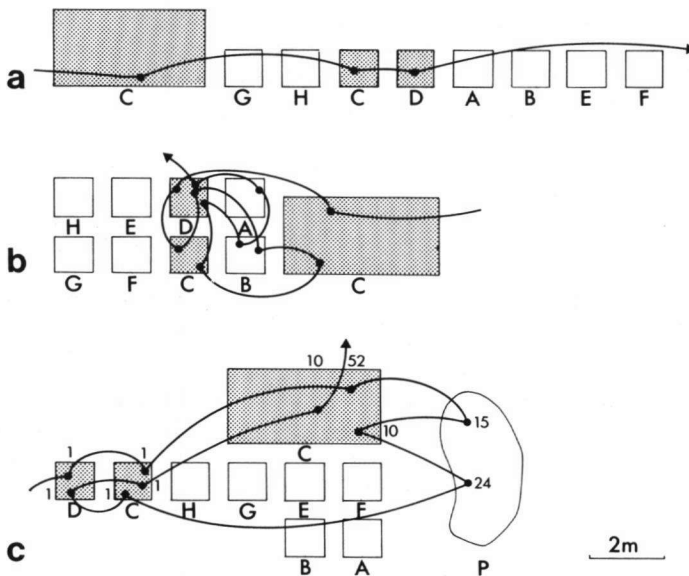

Fig. 5. Choice experiments with one large and eight small dummy elements. The lines show examples of simplified flight paths including sites of hovering (dots): (a, b) different arrangement of dummy elements isolated from natural oviposition sites; — (c) arrangement of dummy elements in vicinity of natural pool. — Figures indicate duration of stay at points of hovering (dots, in s). — [P, A - H as in Fig. 4].

The 2 small black plastic foils had also some attractiveness (31% of the arrivals). However, the differences between these similar sites were not significant on 3 of the 4 days. Only in one experiment did the foil without glass splinters prove significantly more attractive (χ^2-test, P<0.05). With white tissue just one, and with the black non-shining cotton cloth only 19 stops were observed in total. The reactions towards tulle were irregular; while in one experiment 13% of the arrivals were recorded at tulle, in another one it was only 1%.

Table III

Number of arrivals (incl. hovering) of male individuals at different dummies; choice experiment at various experimental sites. − [● = significant (P < 0.05); − ✳ = non-significant difference (P > 0.05). − χ^2 tests were used. − All dummies were 1 m² in size, unless stated]

Locality & date	Black foil 8 m²	Black foil	Black foil and glass	Black cotton	Black cotton and glass	White cotton	White cotton and glass	Tulle	Tulle and glass	Total number of arrivals
Flums, 20-VIII	28 (46%) ●	12 (20%) ✳	16 (26%) ●	2 (3%)	2 (3%)	0	0	0	1 (2%)	61 (100%)
Maloja, 22-VIII	63 (74%) ●	8 (10%) ✳	9 (11%) ●	2 (2%)	2 (2%)	0	0	0	1 (1%)	85 (100%)
Maloja, 23-VIII	106 (67%) ●	22 (14%) ✳	14 (9%) ●	2 (1%)	3 (2%)	0	1 (1%)	4 (3%)	4 (3%)	156 (100%)
Maloja, 25-VIII	85 (45%) ●	47 (25%) ●	25 (13%) ●	3 (2%)	3 (2%)	0	0	6 (3%)	19(10%)	188 (100%)

CHOICE EXPERIMENT:
NATURAL POOL VERSUS BLACK PLASTIC FOILS IN DIFFERENT SIZE

One large and 2 small black plastic foils, one of them covered with glass splinters, were mounted next to a natural pool of about 10 m² in size. This experiment was performed on 4 different days at 2 localities 80 km apart. The results of the quantitative analysis are summarized in Table IV and V. In 2 experiments the number of arrivals at the pool and at the large foil was essentially the same, however, there were significantly more arrivals at the pool in a third experiment (Tab. IV). Similar heterogeneous results were obtained for the duration of stay. On the other hand statistically significant differences between the responses to the large foil and the small foils were found since the animals visited the large foil more frequently and stayed longer than at the small areas (χ^2-test for the number of arrivals, P < 0.01; Mann-Whitney-test for duration of stay, p < 0.05). Glass splinters, however, had no effect on the attractiveness of the small foil areas.

REACTIONS TOWARDS NATURAL OVIPOSITION SITES AND DUMMIES
UNDER DIFFERENT WEATHER CONDITIONS

In a choice experiment with a natural pool, one large and one small foil the number of arrivals and the duration of stay of males were recorded under different

Table IV

Number of arrivals (incl. hovering) of male individuals at natural sites (pools) in competition with foil dummies of various size; choice experiment at different experimental sites. — [● and ✱ as in Tab. I. — n = number of values]

Locality & date	Pool ca 10 m²	Foil 8 m²	Foil 1 m²	Foil with glass 1 m²	Duration of observation (h)	n
Grünsee, 24-VIII	17 (44%) ✱	17 (44%) ●	3 (7%) ✱	2 (5%)	4.75	39
Maloja, 28-VIII	70 (46%) ✱	57 (37%) ●	12 (8%) ✱	14 (9%)	3.5	153
Maloja, 29-VIII	217 (47%) ●	164 (35%) ●	48 (10%) ✱	39 (8%)	6.5	468

Table V

Duration of stay of male individuals at natural oviposition sites and various foil dummies in two choice experiments. — [● = significant differences (P < 0.05); — ✱ = non-significant difference (P > 0.05); — Mann-Whitney test]

Locality & date	Pool ca 10 m²		Foil 8 m²		Foil 1 m²		Foil with glass 1 m²
Grünsee, 24-VIII							
X̄ ± SD (s)	28.6 ± 18.1	✱	26.6 ± 25.2	●	1.3	✱	1.0
Range	2 - 63		3 - 89		1 - 2		1
Number of values	10		10		3		2
Maloja, 25-VIII							
X̄ ± SD (s)	78.8 ± 87.8	●	12.2 ± 9.9	●	3.5 ± 1.5	✱	2.9 ± 1.5
Range	6 - 300		2 - 35		1 - 6		1 - 5
Number of values	8		12		25		29

weather conditions, that is in full sunshine and when the sun was covered by clouds, provided that the air temperature was high enough. This experiment was conducted on two subsequent days with similar weather conditions (sunny periods alternating with cloud shade). The results are shown in Table VI.

(a) Pool vs foils, full sunshine

The frequency of arrivals at the pool was higher than at the large foil and very much higher than at the small one. The same sequence of results was found for the duration of stay; the males stayed longer at the pool than at the large foil and much longer than at the small foil. All differences are statistically significant (x^2-test for the number of arrivals, P < 0.001; Mann--Whitney-test for duration of stay, P < 0.01).

(b) Pool vs foils, sun covered by cloud

The frequency of arrivals at the pool and at the large foil were almost the same, but significantly higher than at the small foil (x^2-test, P < 0.001). On the other hand the duration of stay was longest at the large foil and significantly higher than at the pool (Mann-Whitney-test, P < 0.05) and shortest

Table VI

Choice experiment with natural oviposition site and two foil dummies under different weather conditions. The data were obtained on two subsequent days with similar weather conditions. Experimental site: Maloja. — [● = significant; — ✱ = non-significant difference (χ^2 test for number of arrivals; — Mann-Whitney test for duration of stay; — P < 0.05]

Activity & conditions	Pool 10 m²		Foil 8 m²		Foil 1 m²
Duration of					
observation (min)					
sunshine	315		315		315
clouds	205		205		205
Arrivals per h					
(number of single values)					
sunshine	38 (198)	●	26 (135)	●	7 (35)
	●		✱		✱
clouds	26 (89)	✱	25 (86)	●	7 (25)
Duration of stay					
X̄ ± SD in s					
(number of single values)					
sunshine	13.5 ± 12.9 (177)	●	9.5 ± 9.2 (124)	●	1.9 ± 1.1 (35)
	●		●		✱
clouds	11.3 ± 9.5 (76)	●	16.9 ± 15.9 (75)	●	2.6 ± 1.5 (25)
range (*sunshine*)	1 - 77		1 - 37		1 - 5
range (*clouds*)	1 - 38		1 - 78		1 - 8
Number of fights per h					
(number of single values)					
sunshine	4.6 (29)		1.4 (9)		0.3 (2)
clouds	6.1 (20)		6.1 (20)		0.6 (2)

at the small foil (Mann-Whitney-test, P < 0.01).

(c) Sunshine vs cloud shade at pool and at the foils

In full sunshine the frequency of arrivals at the pool was significantly higher than in cloud shade (χ^2-test, P < 0.01). For the large foil no difference was recorded. The duration of stay became shorter at the pool when the sun was covered (Mann-Whitney-test, P < 0.01). At the large foil the opposite took place: the males stayed significantly longer at the foil after the sun was covered (Mann-Whitney-test, P < 0.01). At the small foil no differences were found either for the frequency of arrivals or for the duration of stay.

REACTIONS TOWARDS GROUPS OF SCATTERED FOIL AND CLOTH FRAGMENTS

At a site with dense vegetation and tiny hidden pools an area of 2 x 1 m was selected and marked out. In its vicinity 8 little boards covered with black plastic foil were scattered over an area of dry ground of 2 x 1 m. The same was done
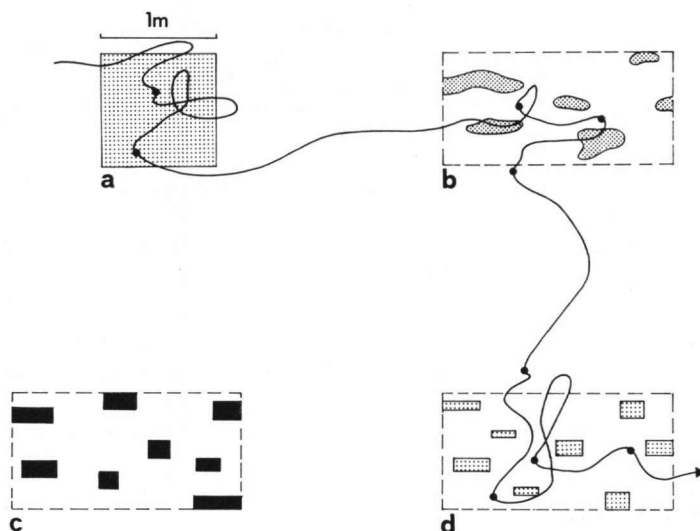
Fig. 6. Arrangement of dummies in vicinity of marked out area with scattered small pools (b): (a) black foil (1 m²); − (c) black cotton cloth fragments; − (d) black plastic foil fragments. − [Lines indicate an example of flight path (male) including sites of hovering (dots)].

with 8 appropriate fragments of black cotton cloth. In addition I mounted a black plastic foil of 1 m² in size (Fig. 6). Males chiefly stopped at the coherent foil, hovered and stayed for a while. Natural pools and foil fragments were only rarely visited, while non-shining cotton pieces did not release any reactions. Attempts at oviposition on foil fragments were observed only once. The female stayed ca 90 s at the site.

ATTRACTIVENESS OF DUMMIES ISOLATED FROM NATURAL OVIPOSITION SITES

In order to test if *A. juncea* would be attracted by dummies which were completely isolated from natural oviposition sites, 2 small black plastic foils, together with a large one, were placed between pine trees in a thin forest adjacent to a small bog in a clearing. The site was 30 m apart from the nearest pool. During the course of 90 min, under ideal weather conditions, only males visited the place, showing different reactions towards the dummies. Some individuals passed by while hunting insects and did not react, some flew over the foils slowly at low height and then moved on. Six males stayed between 5 and 50 s over the large foil, exhibiting the same behavioural pattern as at natural oviposition sites. However, the frequency of arrivals (incl. hovering) was significantly lower than at foils in the close vicinity of pools (χ^2-test, $P < 0.001$ for values from the same day at the same locality).

DISCUSSION

With respect to the quality of behaviour no differences were found between the responses towards natural and artificial oviposition sites. Over the foils males and females exhibited the complete repertoire of behavioural elements belonging to reproductive behaviour. From these responses it may be concluded that certain dummies which were used in the experiments emit the same or similar stimuli as do natural breeding places. The results of the multiple choice experiments revealed what cues were effective and which ones were not.

White non-reflecting areas had no positiv effect on *A. juncea*. This is in contrast to the reactions of males of *A. caerulea* which regularly settle upon white cotton. They do it in order to take up heat, as demonstrated by STERNBERG (1990). *Leucorrhinia dubia* is also attracted by white areas (STEINER, 1948). This again is a thermoregulatory reaction and not a behavioural element concerning breeding habitat selection as Steiner claimed (cf. SCHIEMENZ, 1954). Males of *A. juncea* searching females avoid pools if they are enclosed by bright mats (STERNBERG, 1990). In connection with habitat finding white areas may have a repellent effect on bog dwellers in general, as *Somatochlora alpestris* does not react to white cotton cloth either (pers. observation). On the other hand, males of *A. juncea* are attracted by pools which are bordered by dark brown or green mats (STERN-BERG, 1990). Black non-shining cotton cloth alone, as shown in the present study, however, evokes hardly any positive reaction, even if it is covered with reflecting glass splinters.

The reactions towards tulle were ambiguous. Only in one of four experiments could clear responses be recorded (13% of the number of arrivals; Tab. III). This relatively high number of stops at tulle might be due to the arrangement of the dummy elements; both of the tulle areas were situated between black plastic foils (Fig. 5b). As there was frequently some wind blowing during the experiment from the large foil over to the dummy arrangement, individuals hovering over the edge of the large foil were possibly slightly shifted by the wind to the adjacent dummy elements. But this does not explain the difference in the number of responses between the tulle areas. The loose meshed transparent tissue, covered with glass splinters, which imitated the light reflections of tiny puddles hidden in emergent vegetation, was definitely preferred to tulle without glass (10% against 3% of the total number of arrivals; χ^2-test, P < 0.001). The positive reactions towards this dummy element might have come from the same individuals which were looking for females at oviposition sites in dense vegetation, with a definite search pattern in mind.

Black plastic foil with a shining surface proved highly attractive to *A. juncea*. In 4 multiple choice experiments with 9 dummy elements 83-95% of the number of arrivals were recorded at the black foils. Among the black foils of various sizes the largest one was definitely preferred by the males. Similar results were

obtained with only 3 dummy elements which were placed in the vicinity of a natural pool. The findings correspond to the observation that males prefer larger pools to small pools in natural situations. Glass splinters did not clearly enhance the attractiveness of black foil. Only in one of four experiments was the number of arrivals significantly higher. This corresponds to the findings in experiments with *Somatochlora arctica* (WILDERMUTH & SPINNER, 1991), another species which dwells in small shallow pools of bogs.

From all these experiments it may be concluded that the stimulus which is efficacious in feigning an oviposition site consists of a relatively coarse mosaic of light reflections on dark ground, produced by the uneven surface of the plastic foil. In this connection polarized UV-light might play an important role, as demonstrated for the water bug *Notonecta glauca* and other water insects (SCHWIND, 1983, 1991). In *Sympetrum rubicundulum* MEINERTZHAGEN et al. (1983) found orange receptors (λ_{max} at 623 nm) in the ventral eye which are highly sensitive to polarized light. Additionally the vertical structures of the emergent vegetation within or at the margin of a pool may also be a part of the recognition pattern of the oviposition site. According to STERNBERG (1990) *A. juncea* shows a high affinity to *Carex* sp. On the other hand male and female individuals also visit pools which are at least partly surrounded by peat free of vegetation (WILDERMUTH, 1992a).

It may be assumed that the duration of stay of the adults is a measure of the attractiveness of a real or fictitious breeding place. On the average, males stayed 23.3 s (n = 218) over a natural and 15.3 s (n = 118) over an artificial oviposition site of about the same size. Although the mean duration of stay does not differ greatly between both types of sites, the results are not directly comparable, as the data originate from different localities, days and individuals. As shown by KAISER (1976) and POETHKE (1988) for *A. juncea* and *A. cyanea* the duration of stay of an individual male at the pool may depend on the frequency of arrivals and on male density conditions. This may explain the remarkable differences of the mean values within the same type of site (Tabs I, II). From the fact that males stayed up to 140 s over a foil it may be concluded that dummies appear like natural breeding sites to them.

Do the animals prefer natural or dummy sites? From choice experiments in which pool and dummies were offered side by side no definite answer could be obtained. The differences with respect to the number of arrivals and the duration of stay were not in all experiments significant (Tabs IV, V). This might be due to the fact that the light conditions varied during the course of these experiments. In full sunshine the pool was clearly preferred (Tab. VI). As soon as the sun was covered by a cloud this difference disappeared and the animals stayed longer over the foil, possibly because the nature of the light reflections had changed.

As shown by observations at undisturbed sites and by dummy experiments *A. juncea* also accepts areas with tiny scattered puddles hidden in vegetation. If

males and females have the choice, however, they prefer pools or larger foil areas respectively. This corresponds to the findings that *A. juncea* prefers pools with relatively deep water thereby avoiding larval habitats which easily dry up or freeze through (STERNBERG, 1990). This is in contrast to the findings in *Somatochlora arctica* which prefers small and shallow pools (STERNBERG, 1985; WILDERMUTH, 1986). However, this species may tolerate freezing and resist draining out of the larval habitat as does *S. alpestris* (STERNBERG, 1985; JOHANSSON & NILSSON, 1991).

If black foils are mounted at areas where adult dragonflies normally hunt (and not breed) only few of the individuals present are attracted by pool dummies. All others, corresponding to their hunting mood, do not notice them and continue foraging. If they come into reproductive mood they visit places which they already know. Marked individuals of *A. juncea* and *A. cyanea* regularly frequent the same sites on many subsequent days (KAISER, 1974, 1975). For *Leucorrhinia dubia* it was shown that adults remember exactly specific breeding localities (STERNBERG, 1990).

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