COMPETITION, PREDATION AND MICROHABITAT SELECTION OF ZYGOPTERA LARVAE IN A LOWLAND RIVER

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The microdistribution of 4 lotic spp. was investigated in the field. Microhabitat selection of *Calopteryx splendens* and *Erythromma najas* was further examined in the laboratory, individually at different larval densities and in the presence of the other species and a predator. — *E. najas, Ischnura elegans* and *Platycnemis pennipes* showed significant preferences for particular aquatic macrophytes compared to others in the field, whereas *C. splendens* did not discriminate between the investigated plant species. Only limited spatial separation was apparent between the larvae of different species, as preferences for the same macrophyte species were found. — When kept separate and at low densities, larvae of *C. splendens* and *E. najas* inhabited significantly different microhabitats in the laboratory. At high intraspecific abundances, spatial overlap between the two species became apparent as both increasingly occupied less preferred substrata, which is in concurrence with the ideal free distribution model of habitat selection. *E. najas* showed no change in perch selection in the presence of *C. splendens* at high densities. — In this instance, intraspecific competition therefore appeared to be more important than interspecific competition with other Zygoptera in determining the microdistribution of *E. najas*. In the field, the niches of the two species may be more adequately separated on the basis of prey selection or hunting behaviour. *E. najas* also actively reacted to the presence of a predator, indicating some flexibility of response regarding perch selection.

INTRODUCTION

The larvae of Odonata families and especially those of the Anisoptera vary in physical appearance, adapting them to specific microhabitats. In contrast, most Zygoptera larvae are essentially weed-dwelling and differ only slightly in body shape, with differences mainly in body size and activity levels. In suitable sections of rivers a number of species of Zygoptera larvae often occur together in stands of aquatic macrophytes, but

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distinctions on a microhabitat level have seldom been investigated. A number of questions therefore remain. Does spatial separation, e.g on the basis of differential perch selection, play an important role in competitive avoidance? To what degree are innate preferences of microhabitat selection modified by intra- and interspecific competition for food and space, predation and prey distribution?

JOHANNSSON (1978) found spatial differences to be relatively more important than temporal separation based on life history traits, in separating the niches of *Coenagrion pulchellum, Ischnura elgans, Enallagma cyathigerum* and *Erythromma najas* in a lentic system. Each species occupied a more or less distinct microhabitat, i.e. lily-beds, reed-beds or open mud, and areas favoured by larvae did not necessarily correlate with adult oviposition site preferences and varied between different instars of the same species. Direct competitive interactions, as opposed to competitive avoidance due to innate preferences, have been demonstrated to affect larval community structure and distribution (BENKE et al., 1982; MERRILL & JOHNSON, 1984). Influences of interference competition on survival rates were shown in *Enallagma aspersum* (PIERCE et al., 1985) and *Celithemis elisa* (JOHNSON et al., 1985), whereas a shift in microhabitat selection of *Onychogomphus uncatus* occurred as a direct result of asymmetric interspecific interference, with increasing densities found in normally less preferred substrata (SUHLING, 1996). Interspecific competition can even result in complete exclusion of a species from potentially suitable habitats (CASTELLA, 1987).

Intraspecific interference, predominantly at high population densities, affects survival and growth rates (GRIBBIN & THOMPSON, 1990), as well as larval distribution, and even cannibalism has been suggested to occur in some odonates (CROWLEY et al., 1987).

The vulnerability of larvae to predation is correlated with microhabitat use of vegetated and unvegetated patches, which is often species- and habitat specific. Microhabitat selection may shift with the appearance of a predator, so that low-risk vegetated areas are preferentially occupied (PIERCE, 1988). Aquatic plants are utilised in a highly non--random fashion. Leaf-axial areas are preferred (WELLBORN & ROBINSON, 1987), as well as spatially heterogeneous macrophytes with complex leaf structures (LOMBARDO, 1997), where susceptibility to predation is diminished. LOMBARDO (1997) suggested that the presence of complex leafed plants may be responsible for the coexistence of otherwise mutually exclusive species, due to larger availability of microhabitats as refuges. Hiding behaviour has been shown to be conditional upon the type of vegetation providing habitat structure. Active 'hiding' as a form of antipredator behaviour is more common in macrophyte habitats of simple leaf structure (DIONNE et al., 1990). Interspecific differences with respect to activity patterns and ability to capture prey under varying levels of predation can be evoked to explain differences in the occurrence of Odonata species, e.g. between fish-containing and fishless ponds (PIERCE et al., 1985; JEFFRIES, 1990).

STERNBERG (1994) concluded that the observed microhabitat distribution of Odonata larvae at any point in time is the result of innate species-specific habitat preferences,

modified by competitive interactions that may change locally and seasonally.

The aims of this investigation were (a) to examine whether Zygoptera larvae are spatially separated at a lotic site, (b) to confirm innate microhabitat preferences in controlled laboratory experiments for some species and (c) to assess the effects of intra- and interspecific competition and predation on microhabitat preferences of these species.

METHODS

FIELD SURVEY. — Four 1-minute sweep samples were taken from each of the following pure macrophyte stands: *Phragmites australis, Rorippa nosturtium-aquaticum* and *Glyceria maxima* within a 20m section of the River Stour at Nayland in SE Britain (51°56'83"N and 1°17'88"E) in March 2000. The river in this section consists of two channels, an artificial channel, which was dug for flood prevention and takes the main water flow away from the settlement at Nayland, and the original river channel where flow is controlled by a weir. In this cut off section flow velocities were extremely low (<0.05ms⁻¹), and within the macrophyte stands, where the samples were taken velocities were below the detectable range of the flow meter. Each sample was taken from an area of 0.5m² of vegetation. Samples were sorted for penultimate and final instar Zygoptera larvae immediately upon return to the laboratory, identified and counted.

CHOICE CHAMBER EXPERIMENTS. — Choice chamber experiments were carried out to compliment field observations on microhabitat preferences of two of the species found in the river, *Calopteryx splendens* and *Erythromma najas*. These were chosen as they are weed-dwelling, occurred in relatively high numbers in the River Stour and co-existed at the sampled site. Their comparatively large size also allowed easier observation.

Three six-sided chambers (height = 29cm, base area = 412cm²) were divided into four equal sections, each containing only one species of aquatic vegetation. *Phragmites australis, Glyceria maxima, Rorippa nasturtium-aquaticum* and *Fontinalis* sp. were selected as they are frequently encountered along lowland rivers. Three of these species also occurred together in the sampled river section and are physiognomically very different from each other. Plant species were assigned to choice chamber sections using random numbers and individual specimen were arranged so as to cover similar areas. There were no physical barriers separating the sections and the four plant species were equally accessible to larvae from the centre of the chamber. The bottom was covered with gravel and neither prey species nor external oxygen was introduced. The chamber was filled to approximately 75% of its volume with tap water.

E. najas and *C. splendens* in particular are generally known to prefer flowing water. However, both *C. splendens* and *E. najas* larvae were found together in stagnant water within macrophyte stands at this and a number of other field sites along the River Stour. It was therefore considered adequate to utilise this experimental setup for the results to reflect the field conditions encountered at these stagnant riverine sites within plant stands. A flow chamber, which is generally considered to be more suitable to mimic lotic conditions in the river channel, was also less suitable to allow easy observation of larval settlement. The results are therefore limited to the described field conditions and cannot be used to make inferences about faster flowing river sites.

Table I

Species, number of individuals and replicates used in each experimental treatment

Treatment No.	*Erythromma najas*	*Calopteryx splendens*	*Gasterosteus aculeatus*	No. of replicates
1	-	1	-	20
2	-	15	-	5
3	-	30	-	5
4	1	-	-	20
5	12	-	-	5
6	24	-	-	5
7	12	12	-	5
8	12	24	-	5
9	12	-	1	5

Larvae of *C. splendens* and *E. najas* were kept in separate tanks on gravel only and fed on *Daphnia* and chironomid larvae. A total of 243 *C. splendens* and 176 *E. najas*, penultimate and final instar larvae of comparable sizes, were available for the experiments. All had been taken from the River Stour.

All experiments were carried out in the open, at ambient temperature and light. The position of the chambers was changed after each treatment to alter the incidence of light, which may affect larval settlement choices. Nine different competitive treatments were carried out (Tab. I). Within each treatment new individuals were used for each replicate. Due to insufficient numbers of larvae, particularly of *E. najas*, individuals were reused in different treatments.

Larvae were introduced into the chamber by placing them onto the gravel in the middle section. The position of each individual was noted on either of the four plant species or gravel after a period of 1 hour in treatments 1 and 4, and 24 hours in all other treatments. The longer time period allowed competitive interactions to develop and affect larval distributions before their position was recorded. The final treatment included the presence of a predator, a three-spined stickleback, *Gasterosteus aculeatus*.

DATA ANALYSIS. — The microdistribution of larvae, as established by the field survey, was compared using a χ^2 contingency table, as well as Kruskal-Wallis single factor analysis of variance by rank, appropriate for small sample sizes (ZAR, 1999).

Within-treatment choice chamber results were analysed using χ^2 and Friedman's analysis of variance by ranks. Corrections were computed for tied ranks (ZAR, 1999). Different treatments were compared using χ^2 contingency tables. Replicates were pooled where appropriate following analysis of heterogeneity.

RESULTS

FIELD SURVEY

The larvae of *C. splendens*, *I. elegans* and *E. najas* had significantly different microdistributions with respect to the three aquatic macrophytes sampled ($\chi^2 = 36.43$, d.f. = 4, p < 0.01). *I. elegans* was found in greatest numbers on *G. maxima*, with few on *P. australis* (Fig. 1). Comparing ranked densities, the difference is significant (Kruskal-Wallis test, H = 8.171, d.f. = 3, p < 0.05). *E. najas* was found in equal abundance on *P. australis* and

G. maxima, but numbers were significantly lower on *R. nasturtium-aquaticum* (H = 7.765, d.f. = 3, p < 0.05). *Platycnemis pennipes* occurred mainly on *G. maxima* and was not found on *R. nasturtium-aquaticum* or *P. australis* (H = 8.518, d.f. = 3, p < 0.05). No preference could be detected in the distribution of *C. splendens*.
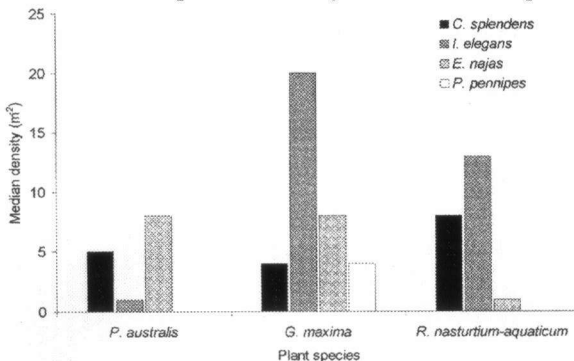
Fig. 1. Median number (m⁻²) of *Calopteryx splendens*, *Ischnura elegans*, *Erythromma najas* and *Platycnemis pennipes* larvae on three aquatic macrophytes (n = 5).

CHOICE CHAMBER EXPERIMENTS

In experiments with species tested individually, the distribution of *C. splendens* and *E. najas* differed significantly between the five substratum types at all larval densities, with the exception of one treatment (*E. najas* at 24 individuals) (Fig. 2).

C. splendens showed a preference for *Fontinalis* in all experimental treatments. Fifty percent of individuals were on average found on the moss at low larval densities (Fig. 2a). This figure decreased to 31% at high densities, whilst proportions on *R. nasturtium-aquaticum* and *P. australis* increased from 7% to 21% and from 1% to 13% respectively. Larval density had a significant effect on the microdistribution of *C. splendens* individuals ($\chi^2 = 18.04$, d.f. = 4, p < 0.01).

In contrast, the highest mean percentage of *E. najas* was found on *P. australis* at all abundance levels (40% at low density) (Fig. 2b). With increasing density, a greater proportion of larvae was found on *R. nasturtium--aquaticum* (increase from 8% to 11%) and particularly *G. maxima* (increase from 2% to 22%). Again the effect was significant ($\chi^2 = 13.76$, d.f. = 4, p < 0.01). In both species a rise in density led to a more even spread of individuals over the five substratum types. At low densities the distributions of the two species differed significantly from each other ($\chi^2 = 43.70$, d.f. = 4, p < 0.01).

Neither of the two competitive levels (5 or 12 individual of *C. splendens*) had an effect on the distribution of *E. najas* compared to the control (Fig. 3). Highest mean proportions were found on *P. australis* in all three treatments.

In the presence of *G. aculeatus* at the same larval density (12 individuals) the
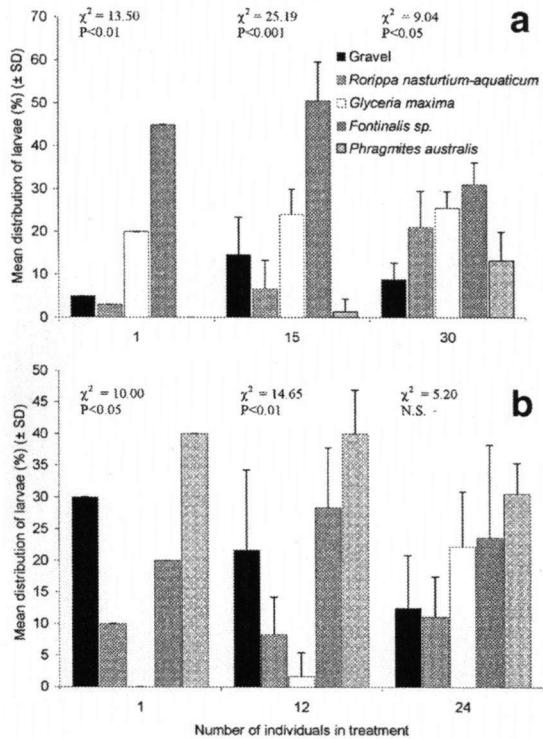

Fig. 2. Proportionate microdistribution (%) of (a) *Calopteryx splendens* and (b) *Erythromma najas* larvae on five substratum types at three experimental densities, choice after one hour for experiments run with one individual (n = 20), mean number (±SD) after 24 hours for block experiments (n = 5). Significance was tested with χ^2 for frequencies and Friedman test for block experiments (d.f. = 4).

mean proportion of *E. najas* occupying *G. maxima* and *R. nasturtium-aquaticum* increased from 2% to 5% and from 8% to 23% respectively, whilst only 5% of larvae remained on gravel. Differences in the distribution of *E. najas* with and without predator (control) were significant ($\chi^2 = 11.63$, d.f. = 4, $p < 0.05$).

DISCUSSION

MICRODISTRIBUTION IN THE FIELD

The results of the field investigation indicated that the four Zygoptera species differed significantly from each other in distribution, with respect to the three aquatic plants sampled. With the exception of *C. splendens*, each species occurred in significantly higher proportions on some of the macrophyte species compared to the others. *I. elegans* seemed to avoid *P. australis*, but was found on both *G. maxima* and *R. nasturtium-aquaticum*. In contrast, *E. najas* was rarely present on *R. nasturtium-aquaticum*, occupying mainly *P. australis* and *G. maxima*. *P. pennipes* was absent from *R. nasturtium-aquaticum*.

Whilst these species-specific differences ensured a certain degree of spatial separation, some overlap was apparent and different zygopterans essentially coexisted in the same microhabitat, e.g. all species were found on *Glyceria maxima*. The observed microdistribution may be explained on the basis of innate preferences for particular plant species, modified by intra- and interspecific interactions. The severity and outcome of competition differs between plants (SUHLING, 1996), as perch availability changes in line with varying leaf and structural complexity, and also between Odonata species, dependent upon the size of the competitors. Competitive interactions are reduced where perch availability is higher (GRIBBIN & THOMPSON, 1990) and in more heterogeneous microhabitats (complex-leaf versus simple leaf structures) (LOMBARDO, 1997). Innate species-specific preferences may be related to size differences between larval Odonata of the same instar, making particular aquatic plants more suitable as perches than others. Differential selection of perches of different diameter on the basis of
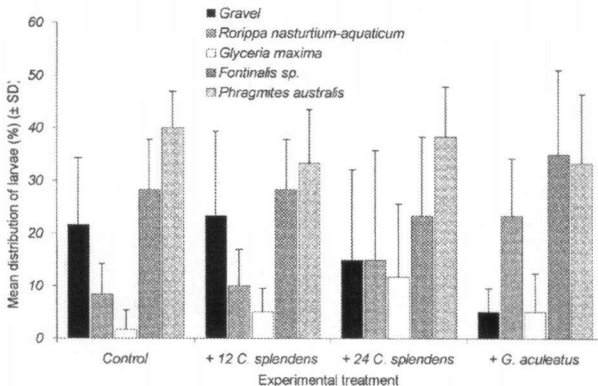
Fig. 3. Proportionate distribution (%, ±SD) of *Erythromma najas* (12 individuals, n = 5) per substratum type, when kept separately (control), at low levels (12 individuals) and high levels (24 individuals) of competition for perches with *Calopteryx splendens* and in presence of a predator, *Gasterosteus aculeatus* (1 individual).

certain body dimensions (eye spacing) was demonstrated by ASKEW (1982) in adult Odonata. If a similar principle applies to larvae, it could explain why the two smallest species (*I. elegans* and *P. pennipes*) were rare on *P. australis* stems, which have a comparatively greater diameter.

Where species coexist, e.g. on *G. maxima*, size differences between larvae may allow niche separation on the basis of prey selection, a factor also evoked to be partially responsible for the separation of different instars of the same and different species (CROWLEY & JOHNSON, 1982).

On a cumulative basis, most Zygoptera larvae were found on *G. maxima*, least on *P. australis*. Differences in structural complexity between plant species may be responsible for larval preferences. *Phragmites* has a relatively simple structure, offering limited perch space per plant in only one dimension (vertical stems). Concealment from predators is limited compared to macrophytes with more complex leaf structures. *G. maxima* has vertical and horizontal structural components for larvae to occupy. Leaves are fairly simple (linear), but may form dense floating mats (PRESTON & CROFT, 1997), which increases perch availability per plant and effectiveness as refuge. *R. nasturtium-aquaticum* is structurally the most complex of the three macrophytes. However, leaves are oval-shaped and may be less suitable for occupancy by some larvae, a possibility that requires further investigation. Selection of microhabitat on the basis of predator avoidance has been repeatedly suggested (THOMPSON, 1987; CONVEY, 1988; PIERCE, 1988; JOHNSON, 1991). Preference for complex leaf habitats and particular parts of a plant has been observed (WELLBORN & ROBINSON, 1987; DIONNE et al., 1990, LOMBARDO, 1997) and greater prey availability in addition to concealment from predation has been proposed as possible reason.

CHOICE CHAMBER EXPERIMENTS

In the field, many environmental factors may influence the perch selection by Zygoptera larvae, including water temperature, competition and predation. The observed microdistribution at any point in time is the result of the combined effect of all of these on larval communities (STERNBERG, 1994). Controlled laboratory experiments can help to identify 'true' larval choices and illustrate how these may change when other influences are added.

In experiments carried out with individual species, it became apparent that *C. splendens* larvae favoured *Fontinalis* moss over any of the macrophytes and that this preference persisted as larval densities increased. Unfortunately this could not be compared to field results, as *Fontinalis* was found at too low a quantity to be sampled in the river section. However, based on field results from another river, ZAHNER (1959) proposed that *C. splendens* avoided *Fontinalis* due to its dense growth. These differences in observation may be an indication of how perch choice is modified in the field. Increased flow velocity at some riverine sites may render *Fontinalis* unsuitable for larval occupancy, as the moss has no support tissue to withstand flow. Where there is no flow as was the

case at the site sampled in this study, *Fontinalis* can offer a structurally heterogeneous habitat, enabling concealment from predators and conspecifics. An innate preference for the most complex perch substratum, offering effective concealment, may exist irrespective of the presence of a predator.

Increased larval densities led to more larvae starting to colonise less preferred substrata, in order to limit intraspecific interference, conforming with the 'ideal free distribution' model of habitat selection, which states that overcrowding reduces the suitability of the most preferred habitat, increasing that of intermediate habitats where densities rise accordingly (FRETWELL, 1972). Similar observations were made by SUHLING (1996) regarding *Onychogomphus uncatus* larvae. Aggressive interactions and perch defence behaviour are known to occur in Zygoptera larvae (JOHNSON, 1991). This may imply that competitively inferior individuals are forced to occupy microhabitats that are less suitable (e.g. gravel) and may confer further disadvantages (e.g. greater vulnerability to predation, limited prey availability) (BEGON et al., 1996). It appears that larval densities in conjunction with intraspecific interference competition affect the microhabitat selection of *C. splendens* larvae.

The microdistribution of *E. najas* differed significantly from that of *C. splendens* at low larval densities. *E. najas* larvae preferentially occupied *Phragmites* stems, but were also found at high proportions on *Fontinalis* and gravel. In contrast to field observations, *E. najas* larvae avoided *G. maxima* in the choice chamber.

The decision criteria with respect to perch selection may vary between species, dependent on ecological differences, e.g. differential level of intraspecific interference (including cannibalism). Also, subject to life style (e.g. active versus passive hunting), microhabitat selection may be evolutionary fixed or flexible (PIERCE, 1988).

Similar to *C. splendens*, microdistribution of *E. najas* changed as larval densities increased, with larvae more evenly spread over all substratum types. At the same time the degree of spatial overlap between the two species increased, so that the differences became non-significant. This may be a more realistic representation of the field situation, where densities are higher.

The microdistribution of *E. najas* changed significantly in the presence of a predator. The main observations were a decrease in proportional occupancy of gravel and *Phragmites* and an increase in relative abundance of larvae on *Fontinalis* and *Rorippa*. Complex macrophytes that offer suitable refuges were therefore increasingly selected, as suggested by LOMBARDO (1997). High-risk habitats, such as gravel, were largely avoided. Perch selection in *E. najas* was therefore flexible to suit a changing environment.

It may be surprising, in the first instance, that the introduction of *C. splendens* larvae did not have a significant effect on *E. najas* microdistribution in the competition experiments. The results discussed above suggest that the two species avoid intense competition by limiting spatial niche overlap at low intraspecific larval densities. When intraspecific competition is low, innate perch selection preferences, e.g. based on physical characteristics of the larvae, may be more easily realised.

In conclusion, intraspecific competition appears to be more important than interspecific

competition with other Zygoptera in determining the microdistribution of *C. splendens* and *E. najas* in marginal macrophyte stands with diminished flow. The species showed different preferences with respect to perch substratum. However, dependent on larval densities, spatial separation was limited, as intraspecific interference caused individuals to increasingly occupy less preferred substrata. The niches of the two species may be more adequately separated on the basis of prey selection or hunting behaviour. *C. splendens* individuals of the same instar are on average larger than *E. najas* larvae and may consume larger prey. *E. najas* also use a more active hunting method, whereas *C. splendens* are essentially sit-and-wait predators and are more active at night (BROOKS, 1999). *E. najas* also actively reacted to the presence of a predator, indicating flexibility of response regarding perch selection.

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