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SPATIAL INTERACTIONS BETWEEN CONSPECIFIC AND HETEROSPECIFIC *CALOPTERYX* LARVAE (ZYGOPTERA: CALOPTERYGIDAE)

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The locomotor responses of larval *C. splendens* and *C. virgo* were considered in interactions between conspecific and heterospecific individuals. Quantitative species-specific differences in the postures and movements of contacting individuals and qualitative species-specific differences in the application of these postures and movements in contacts with conspecific and heterospecific individuals were revealed. The results obtained give grounds for inferring a marked ability of the 2 spp. to discriminate conspecific from heterospecific individuals. The mechanism of this discrimination is not understood.

INTRODUCTION

During recent years interspecific and intraspecific competition of odonate larvae for space and food, and their aggressive interactions leading to inter-odonate predation and cannibalism have received much attention (ROWE, 1980, 1985, 1987; BAKER, 1986; ROBINSON & WELLBORN, 1987; CROWLEY et al., 1987; CONVEY, 1988; WISSINGER, 1988, 1989a, 1989b; VAN BUSKIRK, 1989). But some species show no competition or agonistic relationships between conspecific individuals (CHOWDHURY & CORBET, 1989), which gives grounds for believing that the relationship between odonate larvae are species-specific.

Our study of spatial interactions between the larvae of *Calopteryx splendens* Harris has demonstrated that they are characterized by territorial competition between older males, the competitors being distinguished in terms of sex, age and capacity for competition (RYAZANOVA & MAZOKHIN-PORSHNYAKOV, 1985, 1990). There are also age and sex dependent peculiarities in interactions leading to aggregation or isolation of individuals (RYAZANOVA & MAZOKHIN-PORSHNYAKOV, 1988). All such data suggest that dragonfly larvae can distinguish between competitors, including their species-specificity. However, there is no direct evidence available in the literature as to the discrimination by odonate larvae between conspecific individuals. A detailed study of individual interactions in space competition was performed by ROWE (1980, 1985, 1987), BAKER (1981), and SANT & NEW (1989). The available data indicate the presence of an entire set of display postures and movements used in agonistic interactions, and also of the differentiation by odonates of their competitors in terms of size. An ability of these species to identify conspecific individuals is postulated, though it has not been proved, since the peculiarity of the responses of dragonfly larvae to the larvae of insects of other orders exposed to them cannot be regarded as proof.

The present study is an attempt to answer the question as to whether odonate larvae have the ability to differentiate between conspecific and heterospecific individuals and whether heterospecific individuals are involved in competition in the samen way conspecifics are.

MATERIAL AND METHODS

The larval interactions of two sympatric species, *C. splendens* and *C. virgo* were studied. The experiments were performed in July-August 1989 in the Trans-Carpathian region, USSR. The larvae of *C. splendens* were collected in the Irshava River (instars F - F-3), those of *C. virgo* in the Clyazma River (instars F-4). The larvae (in groups of 6-7 individuals) were maintained in glass containers of about 9 litres, in tap water that had been allowed to stand, with forced aeration, with sand and water-plants. The containers were kept under natural temperature and light. The food, consisting of larvae of Culicidae, Chironomidae and Ephemeroptera, was always in abundance. For experiments 4-10 individuals, collected from different containers were placed in an empty vessel with a branch of forget-me-not (*Myosotis palustris* Lam.). There, the odonate community was formed anew, which ensured their active interactions, preceding the stable state of the community which once established showed very little mobility during the daytime. The behaviour of marked larvae was recorded visually and cinéfilmed until their active interactions discontinued.

The experiments were conducted during different times of the day. A total of 10 experiments were performed (34 hours of observations), during which 14 individuals of *C. splendens* (9 ♀, 5 ♂, of which 11 F and 3 F-1 - F-2) and 11 individuals of *C. virgo* (7 ♀, 4 ♂, i.e. 3 in F-1 - F-2 and 8 in F) were used. Since, in our previous studies, sex and age specificity of spatial behaviour in the larvae of *C. splendens* was established, the number of larvae of different sex and age for both species was equalized. Before the beginning of experiments the larvae were maintained in the laboratory for no less than two weeks.

RESULTS

Preliminary analysis of the behaviour of larvae of *C. splendens* and *C. virgo* in heterospecific and conspecific contacts has made it possible to distinguish over 20 postures and movements used in spatial interactions. Not a single species--specific movement or posture has been found. However, 7 movements showed

Table I

Comparison of the behaviour of larval *Calopteryx splendens* and *C. virgo* in conspecific and heterospecific interactions - [Heterospecific contacts 71; - conspecific contacts in *splendens* 33, - in *virgo* 28].

Reaction types	Number of movements in conspecific contacts				Number of movements in heterospecific contacts				Differences between species in the total number of movements		Differences in the number of movements in conspecific and heterospecific contacts (χ^2, P)			
	splendens	*virgo*	χ^2	P	*splendens*	*virgo*	χ^2	P	χ^2	P	*splendens*		*virgo*	
Approaching the larvae	18	7	5.5	<0.05	3	10	15.1	<0.001	20.7	<0.001	1.1	>0.05	1.7	>0.05
Absence of response	12	15	1.8	>0.05	15	38	15.9	<0.001	16.1	<0.001	2.7	>0.05	0.00002	>0.005
Shifting	5	11	4.6	<0.05	7	22	9.8	<0.005	65.1	<0.001	0.6	>0.05	0.6	>0.05
Walking on larvae	12	3	5.4	<0.05	13	9	0.9	>0.05	4.8	<0.05	4.0	<0.05	0.07	>0.05
Quivering	4	0	3.6	>0.05	1	4	1.0	>0.05	0.1	>0.05	5.6	>0.05	1.6	>0.05
Throwing the mask	2	7	4.3	<0.05	5	0	5.2	<0.05	0.01	>0.05	0.03	>0.05	19.1	<0.001
Lashing	2	0	1.8	>0.05	1	8	5.8	<0.05	2.7	>0.05	1.7	>0.05	3.4	0.05

substantial species-specific frequency difference (Tab. I) and they alone will be discussed here.

It should be noted that an approach by individuals to a distance admitting tactile contact, or resulting in the escape of one of the individuals beforehand is regarded as a contact.

Table I presents the following types of larval responses.

(1) Approaching the partner. - The dragonfly comes up to an immobile or moving individual prior to establishing a contact.

(2) Shifting. - As another individual approaches, the larva curves its body to shift it without moving its legs, or it moves to the other side of the stalk.

(3) Standing still. - As another individual approaches, the larva does not change its posture.

(4) Walking on the partner. - The larva makes contact and climbs on its opponent, walking on it as if it were a common substrate, or lingering on its body despite resistance.

(5) Quivering. - Without moving its legs, the larva makes quick lateral movements with its entire body, like a dog shaking off water (2-3 movements). Numerous observations indicate that this movement is characteristic of an individual ready to fight.

(6) Throwing the mask. - In all cases the mask makes contact with the opponent, for less than a second. With one exception the movement was aimed at an immobile individual; normally, immobile prey are not caught by *Calopteryx*. The attacked individual usually slowly moves to another place, occasionally after 2-3 bites. This action can hardly be regarded as aggression.

(7) Lashing. - Curving the abdominal segments 1-3 with closed lamellae with sharp lateral strokes towards the opponent, with a preliminary swing to the

opposite side. In this way, the opponent is hit vigorously, occasionally several times. This movement had been previously observed by us a number of times in males of the last instar of *C. splendens* in their attempts to oust each other from a convenient territory.

The evidence presented in Table I indicates the presence of species-specific features in spatial interactions. The individuals of *C. splendens* significantly more often approach both con-specifics and heterospecifics, while those of *C. virgo* shift significantly more frquently from approaching larvae irrespective of their species. *C. virgo* more often show no response to the approach of a heterospecific individual, and presumably in these cases the larvae hide (keep quiet). The larvae of *C. splendens* more often walk on top of conspecific than heterospecific individuals, and in general they more often walk on competitors thans does *C. virgo*. In *C. splendens* quivering is significantly more frequent in the presence of conspecific individuals than in the presence of heterospecifics. Great differences were observed in throwing the mask, and in that case this movement is similarly frequently performed by both species. *C. virgo* aim at conspecific individuals only exceptionally, while *C. splendens* does so at both con- and heterospecific individuals. By contrast, *C. virgo* resort to lashing only in relation to heterospecifics, while *C. splendens* also lash the conspecific larvae.

DISCUSSION

The spatial interaction of individuals of two related species has revealed no qualitative differences in postures or movements, the differences being merely quantitative. However, the two species show qualitative differences in applying patterns of movemens of the same types. This concerns the throw of the mask and lashing. Of particular interest are such specific differences as the tendency of *C. splendens* to approach opponents and climb on their backs, and the tendency of *C. virgo* to move away and remain immobile. These observations indicate that despite the close similarity of movements and postures associated with spatial interactions of individuals, there are some species-specific features of behaviour. The presence of both qualitative and quantitative differences in behaviour between larvae of two different species is suggestive of their different responses to conspecific and heterospecific individuals and of their marked ability for individual discrimination between such individuals, although the mechanism of this discrimination is not yet understood. It appears that the *C. virgo* larvae are more specific in terms of their interactions with individuals of different species. For the imagines of three sympatric *Leucorrhinia* species, species-specificity in the ability to identify conspecific and heterospecific individuals in territorial competition has been reported by SINGER (1989). Presumably, the spatial behaviour in *Calopteryx* larvae is a spatial manifestation of the same phenomenon.

The results obtained are only tentative, since there are a number of problems to be solved. In particular, the temporal characteristics of all the reactions, their sequences, and variability as a function of sex and age of the participants remain to be understood. At the same time, the study of the factors mentioned above might reveal more species-specific behavioural features. A number of other factors capable of affecting larval behaviour have to be taken into account. In fact, it is known that the behaviour of dragonfly larvae is a function of their density (ANHOLT, 1990) and previous individual experience (BAKER, 1983; ROWE, 1985). Our method equalizes the conditions of the existence and individual experience of the larvae of different species. However, it should be kept in mind that individuals of different species can be influenced by identical conditions in different ways.

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