

## The effect of age-dependent interference on larval development in *Callicorixa producta* (Reut.) (Hemiptera, Corixidae)

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Pajunen, V. I. 1982: The effect of age-dependent interference on larval development in *Callicorixa producta* (Reut.) (Hemiptera, Corixidae). — Ann. Zool. Fennici 19: 221-224.

The influence of later-stage larvae and adults on the development of 1st and 2nd-stage larvae of *Callicorixa producta* was studied in laboratory cultures. The presence of large individuals lengthened the developmental time by 20 %, and the moulting 3rd-stage larvae were 5 % smaller than the controls. The effect could be largely eliminated by providing refuges for the small larvae. Direct interference with feeding and resting of small larvae is assumed to be the main mechanism involved.

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### 1. Introduction

The development of insects is flexible and individuals can respond to adverse conditions, such as high population density or food shortage by retarded development and by changes in the size attained (Beddington et. al. 1976, Peters & Barbosa 1977). Pajunen (1977) noted that the later-stage larvae of rock pool corixids which developed during high population density were smaller than those which developed during low density. Pajunen (1981) showed that there were considerable differences in developmental rates. The first larvae, enjoying the low initial population density of a newly invaded pool, developed more rapidly than later larvae. One of the reasons for this intra-generation variation was obviously resource depletion by rapidly growing populations. However, the changes in the developmental rate and in the size attained were quite rapid and started even before any food shortage was evident. It was assumed that some type of interference by older and larger individuals on small larvae was an additional factor. This paper describes the results of laboratory experiments aimed at detecting this type of interaction.

### 2. Material and methods

Adult corixids were collected in late autumn from rock pools in the vicinity of Tvärminne Zoological Station. They were kept in the laboratory in aquaria at 4°C in a short-day light

rhythm. Laboratory cultures were established as described by Pajunen & Sundbäck (1973). Frozen chironomid larvae were given as food. Experiments were carried out in plastic containers with a bottom area of 17 x 25 cm. Each container was filled with two litres of charcoal-filtered tap water. Sieved pool detritus was added to form a 1 mm layer at the bottom. A gentle flow of air was passed through the upper layer of the water to prevent the formation of bacterial film. Five small stones were provided as resting places. In one experiment five 3 x 6 cm pieces of plastic netting (1.3 x 1.8 mm mesh) were placed on the sediment for additional support and refuges for the small larvae. The containers were kept in a 18 : 6 (L : D) light rhythm at 22,5°C (range of variation 1°C).

At the beginning of each experiment, ten newly-moulted 1st-stage larvae were placed in each container. The experimental (interference) containers also received five 3rd or 4th-stage larvae, or adults. During the course of the experiment dead larger individuals were replaced. At the end of the experiments the large larvae were in the 5th stage. When the small larvae attained the 3rd stage, they were removed and kept in separate 250 ml glass jars for one day. Their total length, from the front edge of the frons to the tip of the abdomen, was then measured under a stereo-microscope with a micrometer eyepiece.

A single experiment consisted of 5-9 replicate containers in each of the interference and control groups. Two experiments were carried out with adults as interference animals. The experiments with 3rd-stage and 4th-stage larvae were performed simultaneously and had a common control group.

### 3. Results

In all experiments more small larvae died in interference containers than in controls. Variation between containers as well as between experiments was considerable, and in some interference containers all small larvae died. In the pooled material mortality in the interference and control containers was  $56 \pm 5$  % and  $29 \pm 7$  %

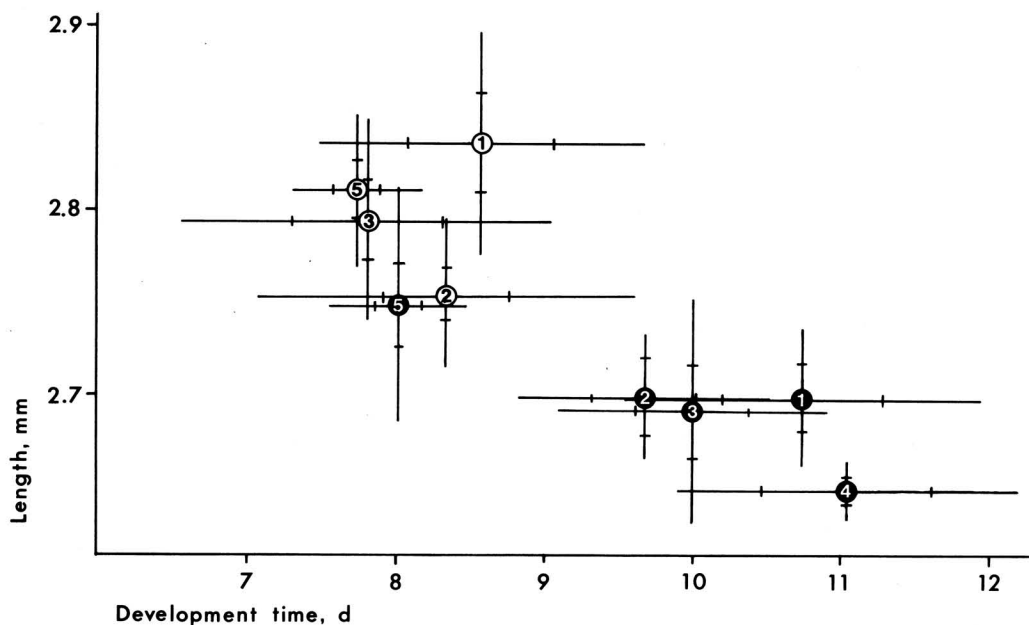


Fig. 1. Mean values of the time taken to complete the first two larval stages and the total length at the beginning of the 3rd stage of control (black symbols) and interference (white symbols) groups. The numbers identify the experiments as follows: 1 and 2, adults; 3, 4th-stage larvae; 4, 3rd-stage larvae with the same control group as 3; 5, adults and refuges for small larvae. The lines give  $\pm$  standard deviations and standard errors of distributions of container means. Standard deviations of within-container variation for experiments 1-4 were 0.91 (development time) and 0.08 (length), and those for experiment 5, 0.67 and 0.07, respectively.

(mean  $\pm$  SE), respectively. The difference is significant.

The developmental variables investigated were the time taken to complete the first two larval stages and the length at the beginning of the 3rd stage. The mean values of the interference and control groups are given in Fig 1. The presence of older individuals seems to have a marked effect on both variables, the length in interference groups being about 5 % smaller and developmental time 20 % longer than in the controls. Mortality differences and total elimination of individuals in some containers strongly influenced the availability of data and thus only a nested analysis of variance was carried out. The distribution of developmental time appeared to be sufficiently symmetrical to warrant a parametric test. The analysis disclosed significant differences between the interference and control treatments, at the 5 % level for size and the 1 % level for developmental time. In both cases the between-container mean square was significantly (0.1 % level) greater than the within-container variance, and for size but not for developmental time the between-experiment mean square was significantly greater (5 % level) than the between-container mean square. The

great between-container variation clearly shows the difficulties involved in the standardization of even a relatively simple experimental environment. Both within-replicate and between-replicate variation was of the same magnitude in the control and interference groups. This indicates that mortality differences did not influence the results.

The interference can be based on two mechanisms. Either the larger individuals contaminate the limited environment with metabolic wastes or by specific agents, or they interfere with the feeding and resting of small larvae and thus diminish their intake of food or cause additional energy requirements. Adults and larger larvae of rock pool corixids are cannibals, and under field conditions small larvae avoid approaching larger individuals.

A modified experimental plan was used to test the alternatives. The plastic netting placed at the bottom increased the safe resting places for small larvae and allowed them to consume prey laying on the netting without interference. The results of the experiment consisting of 8 interference and 7 control replicates are included in Fig 1. Again, a significant between-replicate difference was

detected, and the two groups differed significantly (5 % level) for size but not for developmental time. As the modification could be expected to reduce interference by disturbance, but not the effect of contamination, the results suggest that much of the effect of large individuals can be accounted for by the disturbance. Mortality in the modified experiment was remarkably low, 30 % in the control and 25 % in the interference group.

#### 4. Discussion

The results show that large individuals can retard the development of small corixid larvae even when food is available in sufficient quantities. The mechanism is probably direct disturbance, resulting in decreased feeding time or increased energy requirements for avoidance. In the interference containers the bottom sediment was soft and loose, whereas in the control containers the particles in the sediment had a tendency to adhere, forming a cohesive layer. This suggests that the movements of larger individuals have a considerable mechanical effect on the bottom sediment and also on smaller individuals moving on it.

The density of 10 individuals per container equals 240 individuals per m<sup>2</sup>. In small larvae, comparable densities occur often under natural conditions. The density of large larvae was high but this density has often been observed at times of maximum numbers in the field (Pajunen 1977). The results can thus be generalized. The main difference from field conditions was the limited bottom area and lack of depth differences. Although the rock pools are very homogeneous habitats when compared to larger bodies of water, the shallow shore area allows some size-dependent habitat segregation. In addition, pools with a thick layer of bottom sediment, containing decaying vegetable matter may offer refuges for small larvae. On the other hand, in the field, food shortage forms an additional hazard, increasing the effects of even moderate interference.

The changes in the two developmental variables are compensatory. However, no definite correlation can be expected between the size of an individual and the time taken to complete development. Furthermore, the average change in size was not as extreme as under field conditions.

Pajunen & Sundbäck (1973) measured stage-

specific rates of development by using median developmental times of corixid larvae in different constant temperature regimes. The data give 10.9 d as the average developmental time over the first two stages at 22.5°C. The development in control cultures was noticeably shorter but in interference cultures almost the same. However, Pajunen & Sundbäck (1973) suggested that slow development in one stage may be compensated by rapid development in another. Direct summation may thus give biased results. The variances of the developmental time distributions in the present material (1st and 2nd stages combined) are in fact relatively small, 1.50 for pooled control and 1.96 for pooled interference groups. They are only slightly larger than values for single stages in the earlier material, in which average variances for 22°C and 24°C experiments were 1.17 for 1st stage and 1.06 for 2nd stage larvae. Assuming independent development, the variance of developmental time over the two stages would then be 2.23. There is thus some indication of the existence of compensatory development. The experimental procedures were so different that no precise analysis is possible.

The negative effect of larger individuals on the development of smaller conspecific individuals is known in several aquatic animals (Rose 1960). The only account concerning aquatic Hemiptera is by Murdoch & Sih (1978). They detected that the rate of prey capture decreases with density in *Notonecta hoffmanni* (Hungerford), and that the effect of larger individuals is more pronounced. In the presence of larger individuals the smaller larvae tend to avoid the favourable border habitats and their success in prey capture decreases. This interference has also been observed under field conditions. In *Notonecta*, the rate of prey capture is known to affect the size as well as rate of development (Fox & Murdoch 1978).

The interference by larger individuals has important consequences. It considerably influences the performance of the predator population. The total predatory pressure cannot simply be inferred from the performance of single individuals (Murdoch & Sih 1978). The interference also increases the social inequality of members of the population, and is thus a significant factor in population limitation and stabilization (Pajunen 1977, 1981).

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Received 8.I.1982

Printed 10.XII.1982