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Quantitative analysis of competition between Arctocorisa carinata (Sahlb.) and Callicorixa producta (Reut.) (Hemiptera, Corixidae)[1]

V. Ilmari Pajunen

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The effect of mortality on the biomass ratio in late larval stages of *Arctocorisa carinata* and *Callicorixa producta* was studied by ratio diagram analysis. A typical frequency-independent change was detected. Difference equations describing the biomass changes and incorporating linear competition and a substantial time-lag to mimic the changes observed yielded competition coefficients of 1.45—1.50 per unit of biomass for *A. carinata* and 0.66—0.68 for *C. producta.*

V. Ilmari Pajunen, Department of Zoology, University of Helsinki, P. Rautatiekatu 13, SF-00100 Helsinki 10, Finland.

1. Introduction

Pajunen (1979) described competition between *Arctocorisa carinata* (Sahlb.) and *Callicorixa producta* (Reut.). These two species show complete habitat overlap and similar reproductive phenology. During the reproductive season the combined biomass of Corixidae in a rock pool often increased to a level at which signs of food shortage appeared. Estimates of stage-specific mortality during the later larval stages gave consistently higher values for the smaller *C. producta*, but no compensating factors could be found in adult mortality or reproductive rate. It was suggested, however, that *C. producta* was able to use small temporary pools more effectively and this might give it the necessary advantage to persist in face of the strong competition. Vepsäläinen (1978) has analysed the characteristics of the two species on the basis of the r — K selection theory.

The two rock pool corixids offer a rare opportunity for studying non-equilibrial competition. The intensity of this interaction varies rapidly and measurement of its effects is possible only for a limited period. This paper attempts a detailed analysis of the crucial part of the reproductive period.

2. Material and methods

The basic material consisted of estimates of stage-specific daily numbers made at regular intervals in selected pools throughout the reproductive season (Pajunen 1977). In spite of continuous oviposition, the numbers of larvae of a given developmental stage in a pool fluctuated regularly, and new large larvae appeared only after the previous batch had completed development. Typically, there were two distinct groups, one in June and the other in July — August, corresponding approximately to the reproductive efforts of overwintered and second generations. These groups, forming conspicuous peaks in the stage-specific daily numbers, served as natural study units and were also used in earlier papers (Pajunen 1977, 1979).

The numbers of individuals forming the groups were estimated from curves of stage-specific daily numbers by using developmental time-scales constructed from temperature records and temperature-specific developmental rates obtained from laboratory cultures. A linear relation was assumed between successive estimates of numbers. The estimates can be taken as measures of the numbers of individuals at the midpoints of the respective stages. The reliability of the time-scales was assessed from recognizable irregularities in the curves of daily numbers, and for short periods, when calculated and actual development did not correspond, appropriate corrections were made.

Only adults and the last three larval stages could be distinguished down to species level. The flight activity of adults interfered with attempts to estimate their total numbers, and thus the analysis could be applied only to late larval development.

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3. Ratio diagram analysis

Ratio diagrams were originally used in analysing results of cultivation experiments in which two plant species were sown in different densities but the overall density was kept constant (De Wit 1960). Although designed for analysing changes over a generation, the idea is applicable for shorter periods. The density of Corixidae naturally varied from pool to pool but, as the densities attained resulted in high mortality of larvae and in characteristic sudden decreases of biomass, it appeared reasonable to assume that these densit iesexceeded the carrying capacity of the respective pools and that the effective densities were thus roughly comparable.

The ratio of the biomasses of *C. producta* and *A. carinata* at the midpoints of the third and fifth stages were calculated from estimated numbers for the peaks, using the relative weights given by Pajunen (1977). Ratio diagrams were then constructed separately for early and late summer, the material from small temporary pools being included in the latter group. The analysis was also applied to the pooled data. The data points are depicted in Fig. 1.

The main results were similar in the two sets of data. The mean values showed that during the period considered the ratio of the biomasses changed by factors of 0.586 and 0.724 in early and late summer, respectively. For the pooled material this factor was 0.648. The corresponding change in the ratio of weights of individuals was only 0.894. The regressions of the logarithm of biomass ratio in the fifth stage on that in the third stage had slopes slightly below but not significantly different from unity. We may thus conclude that, within the range of values represented (Fig. 1), the ratio of biomasses changes during late larval development in favour of A. *carinata* by a constant factor. The result is typical of two species using the same resources but, when sympatric, with differing success.

The pronounced scatter of the data points suggests that the assumption of the same effective density in the pools was not wholly correct. The pools characterized by high density but

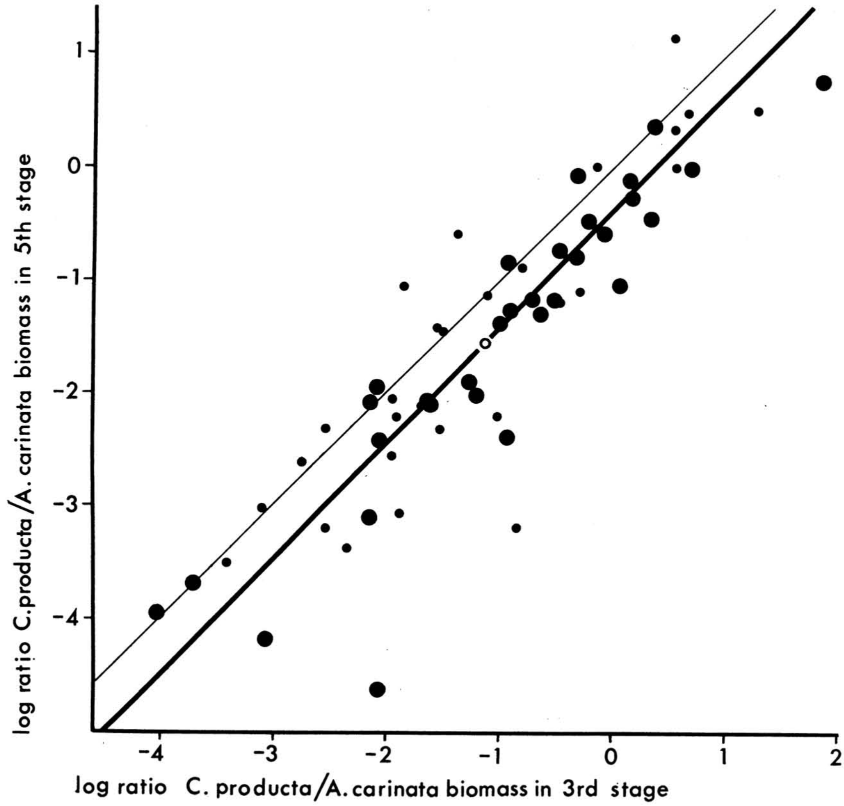

Fig. 1. The ratio diagram of the combined material. Symbols: large dots = early summer peaks; small dots = late summer peaks. The mean value is indicated by an open circle, and the heavy line gives the ratio change corresponding to the parameter values calculated. The thin line is $y = x$.

with a pronounced decrease of biomass after the maximal values had ratio changes above the average. Also, variation was increased by inclusion in the material of small pools with small numbers of individuals. The difference between the early- and late-season groups resulted mainly from a few deviant values from small pools, and the pooling of the data is justified. As mortality was heavier in both species late in the season (Pajunen 1979), the similarity of the two sets and the direction of the difference was unexpected. The increase in mortality may thus depend on factors which are not relevant in early summer, and affect the larvae of the two species similarly. Several factors may contribute to the difference; for example, the numbers of adults increase and the rates of development decrease towards autumn.

4. Estimation of competition coefficients

The construction of equations around the linear competition functions of Lotka - Volterra type to represent the results obtained is at least of some value for pedagogic purposes. As the system is unstable when both populations are present, we must estimate population growth rates in addition to carrying capacities and competition coefficients. Changes in numbers of larvae are too complex for elementary analysis, but simple calculations are possible if populations are measured in terms of biomass. Let us assume that the combined populations consist of individuals of the same age, the contribution of the adult parents being negligible. Any change in biomass is then due to two factors, the increasing size of individuals and mortality; the latter can be assumed to depend on the availability of food and include competition effects.

A. Biomass changes in the pools

Examples of daily changes in biomass in representative pools were given by Pajunen (1977). The developing groups of larvae have a notable influence. The total biomass increases rapidly and typically attains maximal values when the majority of the larvae are in the fifth stage. The biomass then decreases rapidly, indicating a sudden increase in mortality. In early summer the numbers of adults are low but later their presence causes a considerable fluctuation in biomass, which tends to obscure the effect of growing larvae, at least in the permanent pools.

The relation between biomass change and the average progress of development of batches of larvae was studied from 11 early-season peaks of permanent pools and 3 late-season peaks of temporary pools. Peaks with large numbers of adults were excluded, and so were those for which the occurrence of larvae was temporally too heterogeneous. Rates of development were assessed as follows. Daily estimates of stage-specific numbers of the two species were combined and depicted on average developmental time-scales. Points corresponding to the accumulation of half the areas under the curves were estimated graphically from cumulative curves, and the corresponding dates used as midpoints of the respective stages. Biomasses were then calculated for the dates by assuming a linear relation between successive daily estimates.

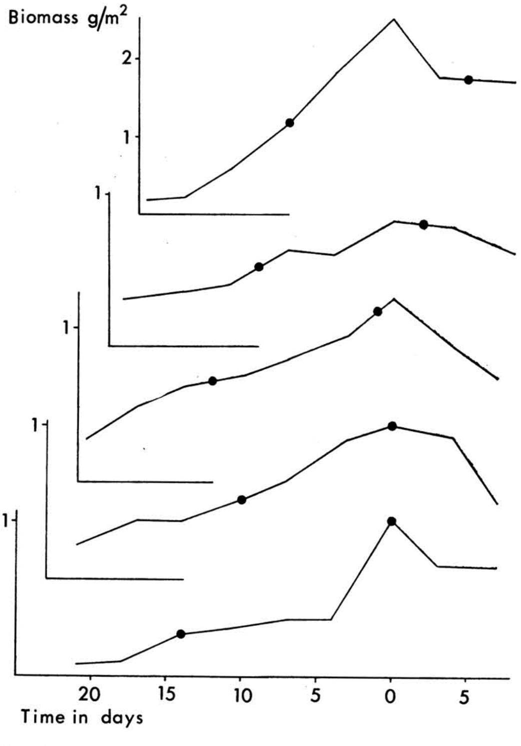

Fig. 2. Examples of the change in combined corixid biomass and its timing in the pools. The dots denote the midpoints of third- and fifth-stage larvae. Three average results and the two most extreme cases of the material are given.

The changes varied considerably from pool to pool. The only useful landmark was the maximal biomass value. The difference between this and the date of the midpoint of fifth-stage larvae was mostly small, the mean difference being — 0.36 ± 1.00 days. The difference between the dates for third- and fifth-stage larvae varied considerably, depending on the prevailing temperature and on the proportion of larvae developing during the more favourable initial period when density was low. The biomass at the third stage ranged from 0.3 to 0.8 of that at the fifth stage, the mean being 0.55±0.04. Examples of biomass changes in relation to dates of the midpoints of two larval stages are given in Fig. 2.

Some care should be exercised in comparing a temporally heterogenous group with a cohort of equal-aged individuals. In the field mortality is probably higher in the younger individuals and, if so, will be more effective in curtailing the increase of biomass near the maximal values.

B. Competition equations

In larvae, the fresh weight changes stepwise at moultings, but for a group of individuals of a species the daily increase in weight may be derived from the difference equation relating biomass, B, on successive days (t) as

$$B_{t+1} = (1 + g) B_t \qquad (1)$$

where g is the species-specific growth parameter. The biomass is also affected by mortality. In the pools the biomass tends to increase to a peak and then to decrease; hence mortality should depend on the limited resources with a substantial additional time-lag (m days). A simple equation giving the required result is

$$B_{t+1} = B_t \, [1 + gk^{-1} (k - B_{t-m})],$$

where k is the equilibrium biomass that the environment can maintain. Under assumption of linear competition between two species (i and j) with similar requirements, species i will grow according to the equation

$$B_{i,\,t+1} = B_{i,\,t} \, [1 + g_i k_i^{-1} (k_i - B_{i,\,t-m} - a_{ji} \, B_{i,\,t-m})]$$

where a_{ji} is the competition coefficient describing the effect of species j on species i.

For estimation of the parameters a suitable time-scale is necessary. In the field, developmental times vary considerably from pool to pool and between different parts of the reproductive season. For calculations, the correct relative durations of larval stages are important, the step length being mainly determined by the time-scale used. For these reasons, the duration of each stage was assessed directly from uncorrected stage- and species-specific developmental time-scales by averaging the daily progress of development between mid-June and mid-August. The resulting values in days were as follows:

	A. carinata	*C. producta*
3rd stage	5.58	5.92
4th stage	6.54	6.94
5th stage	10.92	10.73

For both species the distance between the midpoints of the third and fifth stages was 15 days. Assuming that the weights given by Pajunen (1977) represent those at the midpoints of the respective stages and assuming constant growth according to equation (1), the following daily growth coefficients (g) were obtained:

A. carinata	*C. producta*
0.127	0.118

The carrying capacities of the two species are not known. The ratio diagram, however, is typical of two species replacing each other, with a fixed total biomass. Data for apparently similar pools also suggest that the maximal biomass attained is the same irrespective of the ratio of the two species. The smaller size of *C. producta* may be energetically disadvantageous, but as regards the great overall similarity of the species it is permissible to assume identical efficiency and put $k_i = k_j$. This naturally only applies to the late larval stages; the allocation of energy is quite different in the adults, *C. producta* investing more on dispersal.

Competition coefficients (a) indicate the effect on biomass increase of one biomass unit of another species in relation to one conspecific unit. In competition, cannibalism and the energy loss incurred by smaller individuals in avoiding reactions may be important, in addition to differences in feeding efficiencies. An increase in the influence of one species causes a corresponding decrease in that of the other. We may accordingly assume that $a_{ij} \times a_{ji} = 1$.

Fig. 3 gives biomass changes for the two species in ratios approximating to the average field material. Calculations were started from a combined biomass of 0.1 *k*, the necessary lower values being derived from equation (1). Trials with different values of parameter *m* showed that time-lags corresponding to the average duration of one larval stage were necessary to give maxima rising sufficiently above the equilibrium. With still longer values for the time-lag the peak was progressively higher. As the time-lag was introduced to mimic the overuse of resources, long intervals are not acceptable. Values of 7—9 days are still realistic.

The shape of the calculated curves is quite insensitive to moderate changes in competition coefficients. On the other hand, the difference in growth parameters introduces a slight frequency-dependent effect (p. 00). With increasing proportion of *C. producta* the increase in total biomass is slower and the peak values are lower; in consequence the intensity of competition decreases.

The curves in Fig. 3 show a satisfactory resemblance to the actual pool data. However, there are two discrepancies. The field information would position the midpoint of the fifth stage, the end point of the 15-day segment of the curve under consideration, at the peak value. The biomass at the midpoint of the third stage would then be 47—52 % of this maximal value, appreciably lower than the average pool value. This difference can be eliminated by shifting the end point beyond the peak.

In the permanent pools survival rates for *A. carinata* between the midpoints of the third and fifth stages were 0.53 in early summer and 0.39 in late summer (Pajunen 1979). For the calculated curves the corresponding survival rates vary from 0.36 to 0.40, depending on the time-lag, when the end point of the 15-day segment lies at the peak. These rates are unrealistically low, but can be increased by shifting the end point before the peak.

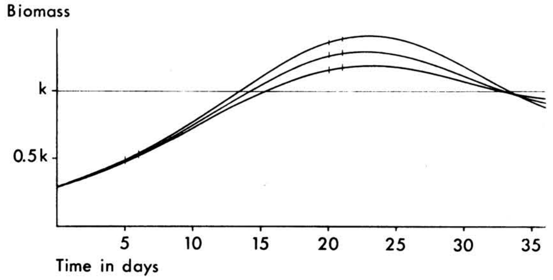

Fig. 3. Changes in the total biomass of the two competing populations for time-lags *m* ranging from 7 days (lowest curve) to 9 days.

For the reasons given in section A, the first of these two conflicting requirements is less compelling and can be given less weight. A shift of the 15-day segment backwards by 2 days brings survival rates to 0.41—0.46 and the proportion of third-stage biomass is still 40—44 % of the fifth-stage values. A 3-day backward shift yields survival rates of 0.44—0.50, the ratio between the biomasses being 37—41 %.

It is now possible to estimate the competition coefficients that cause the ratio of the biomasses of *C. producta* and *A. carinata* to change by a factor of 0.648 between the third and fifth stages. The values for *A. carinata* are as follows;

m	2-day shift	3-day shift
7	1.432	1.470
8	1.456	1.500
9	1.487	1.536

The results are strongly influenced not only by the position of the end point but also by the magnitude of the time-lag. Combining the results we may place the competition coefficients between the values:

A. carinata	*C. producta*
1.45—1.50	0.66—0.68

These express the effect of one biomass unit of one species on the biomass of the other. As the weight of one *A. carinata* fourth-stage larva is 1.73 times that of *C. producta*, the equivalence of one individual to individuals of the other species is accordingly:

A. carinata	*C. producta*
2.51—2.59	0.38—0.40

These results were calculated from the ratio corresponding to the average. If we retain the timing in relation to the peak biomass, an increase in the proportion of *C. producta* will lead to smaller changes in the ratio. Thus the lines of the ratio diagram consistent with the various parameter values used have slopes slightly greater than unity, but this difference falls within the confidence limits of the original data.

In spite of the stabilizing influence of the interaction between older and younger larvae, the biomass of the third-stage larvae in the actual material is not a constant proportion of the equilibrium value (k). This variation can be incorporated in the model by allowing shifts of the beginning and end points of the segments of the curves. This generates a corresponding variation in the change in ratio.

For both species the growth parameters used give weights at the end of larval development that are slightly too large. The results of extrapolation outside the period studied should therefore be interpreted with care. If the competition process is followed for a further 5 days, only 62—66 % of *A. carinata* and 40—46 % of *C. producta* individuals attaining the middle of the fifth stage are still alive. The difference corresponds to a further change in ratio by a factor of 0.74—0.77. The heavy mortality is consistent with these calculations (Pajunen 1977).

5. Discussion

The results suggest that the competition process is similar in all pools and the simple linear model is an adequate approximation. In such a rapidly fluctuating system by far the best unit for use in analyses is biomass. Although several untested assumptions had to be made, field experience suggests that they are realistic. The analysis was based on population effects, and much indirect reasoning was thus avoided.

The intensity of competition depends on the difference between carrying capacity and use of resources. The first individuals to develop thus have a considerable advantage, and the existing temporal heterogeneity contributes to the stability of the system. In late summer, *C. producta* gains from its earlier arrival in temporary pools, although the high mortality in this type of habitat lowers the average production to the level of the other pools. The unpredictable environment of rock pools naturally favours rapid production, and no notable differences in reproductive capacity can exist between the species.

Strong competitive interactions are labile and therefore short-lived. Two outcomes are possible. Either one of the species is excluded, or both species adapt until competition weakens sufficiently to permit continuous coexistence. Thus strong competition can be detected in the field only when some factors shelter it from these outcomes, and such cases must be rare. To some extent, however, this apparent rarity may depend on the way ecologists select their objects of study. Nowadays, much effort is directed towards the study of guilds of coexisting species, which are known to represent equilibrium cases. More studies should be made in temporally and spatially heterogeneous environments and habitats with rapidly varying resource availability. These factors have been suggested to act as agents decreasing the effects of competition on community structure (Wiens 1977), but they may also protect strong competitive interactions from exclusion or selection.

The study of communities typically centres around the determination of niche overlap, and in cases of equilibrial competition the different overlap coefficients probably approximate satisfactorily to the actual competition coefficients. However, they cannot be used to describe strong competitive interactions, and new methods are necessary.

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