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Analysis of developmental rates in field populations of Arctocorisa carinata (Sahlb.) and Callicorixa producta (Reut.) (Hemiptera, Corixidae) with the aid of developmental time axes

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The influence of environmental temperature on development in *Arctocorisa carinata* and *Callicorixa producta* was assessed by constructing developmental time scales from temperature records and temperature-specific developmental rates. The distances between successive stage occurrence curves in these scales suggested that at the start of recruitment, development in the field considerably exceeded the predicted rates. The discrepancy was largest and of longest duration in the first larval stage, diminishing steadily in later stages. Later, during the increase in population density, actual and predicted developmental rates were in close agreement. Increased interference by older individuals as an explanation. The rapid development of first individuals adds to the temporal heterogeneity and has a marked stabilizing effect in the populations.

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1. Introduction

Detailed information of the duration of development is an important prerequisite of the analysis of insect populations. Direct measurement by rearing only gives values under a certain set of environmental conditions, and is thus of limited value when analysing data covering extended periods. Another avenue of approach is to study effects of factors influencing development and to predict its progress on basis of available information about these factors under field conditions. One of the most important environmental factors is temperature. The idea of relating the progress of development to the thermal history experienced by individuals is old and heat unit summation techniques are frequently used in phenological studies. Although reference to this possibility was made by Ruesink (1975) and by Gilbert et al. (1976), no serious attempt to use the method in population analysis seems to have been published.

In the rock pool corixids *Arctocorisa carinata* (Sahlb.) and *Callicorixa producta* (Reut.) reproduction extends over three months. Daily as well as seasonal temperature fluctuations in the small rock pools are considerable (Pajunen & Jansson 1969), and thus direct estimation of the duration of development is impractical. For this reason the indirect approach was particularly attractive. No important subsidiary factors seem to exist in the aquatic habitat. Pajunen & Sundbäck (1973) determined the developmental rates of immature stages of the two species at several constant temperatures and used these data and daily time-temperature distributions based on field records to predict the daily progress of development. The results agreed satisfactorily with actual rates of development in field cultures in which feeding and handling techniques were the same as in the laboratory. In this paper the analysis will be extended to actual field populations.

2. Material and methods

The population data consist of successive estimates of numbers of active developmental stages of corixids in selected rock pools at alternating three and four-day intervals for most of the reproductive season. The material consists of 34 sets of data covering the whole reproductive season of populations in permanent rock pools, and 6 sets of data for the later part of the reproductive season in shallow temporary pools. These pools dried out in June before development of the larvae was complete. The field techniques and the method of estimation of numbers are described by Pajunen (1972). The description of the population data is given by Pajunen (1977).

Temperature was measured from some representative pools with Wallac 1000 Ω Ni resistors and Joens six-channel recorders or with Lambrecht mercury capillary thermographs. Measurements were accurate to within 0.5 °C. The thermal stratification in small rock pools is negligible. Temperatures were assessed at two-hour intervals from the continuous records, and daily time-temperature distributions were calculated by linear interpolation with 1 °C temperature intervals. The expected average daily progress of development for each developmental stage was then calculated as the sum of temperature-specific times weighted by the temperature-specific rates of development given by Pajunen & Sundbäck (1973). The intervals between successive sampling dates were expressed as sums of daily values, and the original time axes were thus transformed into developmental time units. For short periods for which temperature data were lacking, the daily progress of development was estimated with the aid of its linear regression on daily averages of standard meteorological temperature and cloudiness records.

No efficient method for comparing the predicted and actual development on the basis of stage occurrence data seems to exist. If the rate of development can be assumed to remain constant, the average developmental history of the population can be constructed (Ashford et al. 1970, Southwood et al. 1972). However, if this assumption appears too restictive, the only possibility is to measure the interval between two successive stage occurrence curves. For analysis, two successive stage occurrence curves or successive cumulative occurrence curves (daily numbers of individuals in a given stage and in all subsequent stages) were depicted on the developmental time scale of the first of the stages and the differences between recognizable points were measured. The comparison was facilitated by the characteristic irregularities in the curves and by their tendency to retain the same general form from stage to stage. Adult occurrence curves were often affected by dispersal, but the major part of recruitment could be observed in most cases. The method is open to subjective interpretation, and in many cases the information obtainable was not sufficient to allow detailed analysis. Pools showing prominent peaks of short duration were especially difficult to analyze.

3. Results

The stage-specific developmental time axes allow a standardized comparison of average development under field conditions. When the data collected from the representative pools between the beginning of June and the middle of September were used, the relative durations of successive stages (inverse values of the relative lengths of the axes) were as follows:

Larval stages:	1st	2nd	3th	4th	5th
A. carinata	1	0.85	0.87	0.97	1.63
C. producta	1	0.86	0.82	0.97	1.54

The range of the three-year variation was 0.03 for the 2nd to 4th stages and 0.06 for the 5th stages. The distribution of the total development time between the different stages is thus remarkably similar in the two species. This pattern may represent a general corixid feature, but it is also possible that the duration of the stages is optimized to give the shortest possible total development time. In the unpredictable environment of rock pools, selection against slow development must be intense. From the point of view of analysis, most of the stages are of sufficiently similar duration to preclude distortion of the stage occurrence curves. Only the longer duration of the 5th stage can cause appreciable changes, such as heightening and translocation of the maximum values.

The differences between corresponding stages of the two species were also small. When the average of stage-specific developmental rates was used instead of the species-specific rates, the difference for longer periods in no case exceeded 5 %. For small pools, therefore, the material for the two species can be pooled and an average stage-specific time scale employed without fear of unacceptable error. Average developmental rates were always used for the first two larval stages, which were not distinguishable in the species in the field.

Examination of pairs of successive stage occurrence curves showed that the calculation of actual developmental rates generally agreed satisfactorily, but certain differences were consistently observed. In all 40 sets of data, the actual development was faster than predicted at the start of recruitment, but this difference gradually disappeared. The difference was greatest in the 1st larval stage, and diminished steadily in later stages. Furthermore, the length of the affected period grew shorter. Occasionally, at periods of high density, actual development tended to lag slightly behind the calculated values.

The details varied from pool to pool; examples are given in Figs. 1 and 2. The first individuals of the 2nd stage always appeared after about one half of the predicted duration of the 1st stage. The rates of recruitment were initially the same, which suggested high survival at this time. Then, after 2—3 sampling intervals (7—10 days) there was an appreciable shift in the 2nd stage curve, suggesting a slowing down of the rate of development and increasing mortality, and after 14—17 days the difference between comparable points on the curves approached the predicted duration of the 1st stage. The same general pattern was then repeated in subsequent stages but with smaller differences. Adults and the first 5th stage larvae usually appeared after 75 % of the predicted duration of the

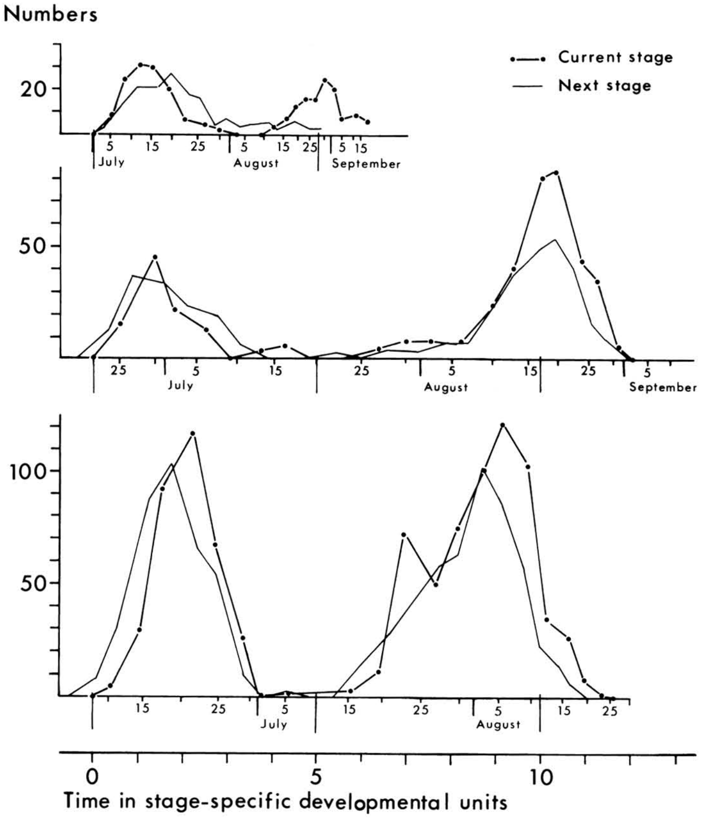

Fig. 1. An example of the analysis. The dotted line gives a stage occurrence curve depicted on its developmental time scale, using one stage duration as the time unit. The original time scale is included to show its distortion. The continuous line gives the occurrence curve of the next stage, displaced to the left by one stage duration. Graphs: from below, 1st and 2nd-stage larvae; 3rd and 4th-stage larvae of *A. carinata;* 5th-stage larvae and adults of *A. carinata.* This pool (B 48 c in 1966, Pajunen 1977) shows the two-peaked occurrence pattern characteristic of two-thirds of the permanent pools studied. Note the greater discrepancy in early summer peaks, and its gradual disappearance in later developmental stages.

previous stage, and the discrepancy took 7—10 days to disappear.

When the numbers of 1st stage larvae again started to increase in late summer, the corresponding increase in 2nd stage larvae tended to start when 75 % of the predicted duration had passed, but the difference generally disappeared after one sampling interval. Curves of later stages had a comparable pattern.

The periods of retarded development were characterized by high mortality. Maximally, actual development seemed to exceed the predicted values by 20 %.

As the rapid development occurred early in the season when the numbers of larvae were increasing, but was less evident in late season, when the pools in question had already produced one cohort of adults, it is assumed that the observed differences between actual and predicted progress of development express the effect of population density on the rate of development. The temperature-specific developmental rates used were determined in cultures, which necessarily had relatively high densities. Although food was available in greater amounts than required, the presence of several individuals in small containers can be expected to affect development to some degree. The same considerations apply to the field cultures which were used to test the laboratory data. In the rock pools, on the other hand, the first small larvae developed under optimum conditions, but during the rapid increase in numbers the situation soon approached that of the cultures, and the difference in the progress of development accordingly disappeared. At more advanced developmental stages, the period during which the first moulted larvae can enjoy low population densities shortens rapidly, and thus diminution of the discrepancy between actual and predicted development and shortening of the affected period can be expected. When the late season increase in small larvae started, there were still sufficient older individuals to cause interference.

However, this is not the sole explanation. In the cultures produced by Pajunen & Sundbäck (1973) at naturally varying temperatures, considerable variation was observed in the time needed to complete a given stage. The frequency distributions

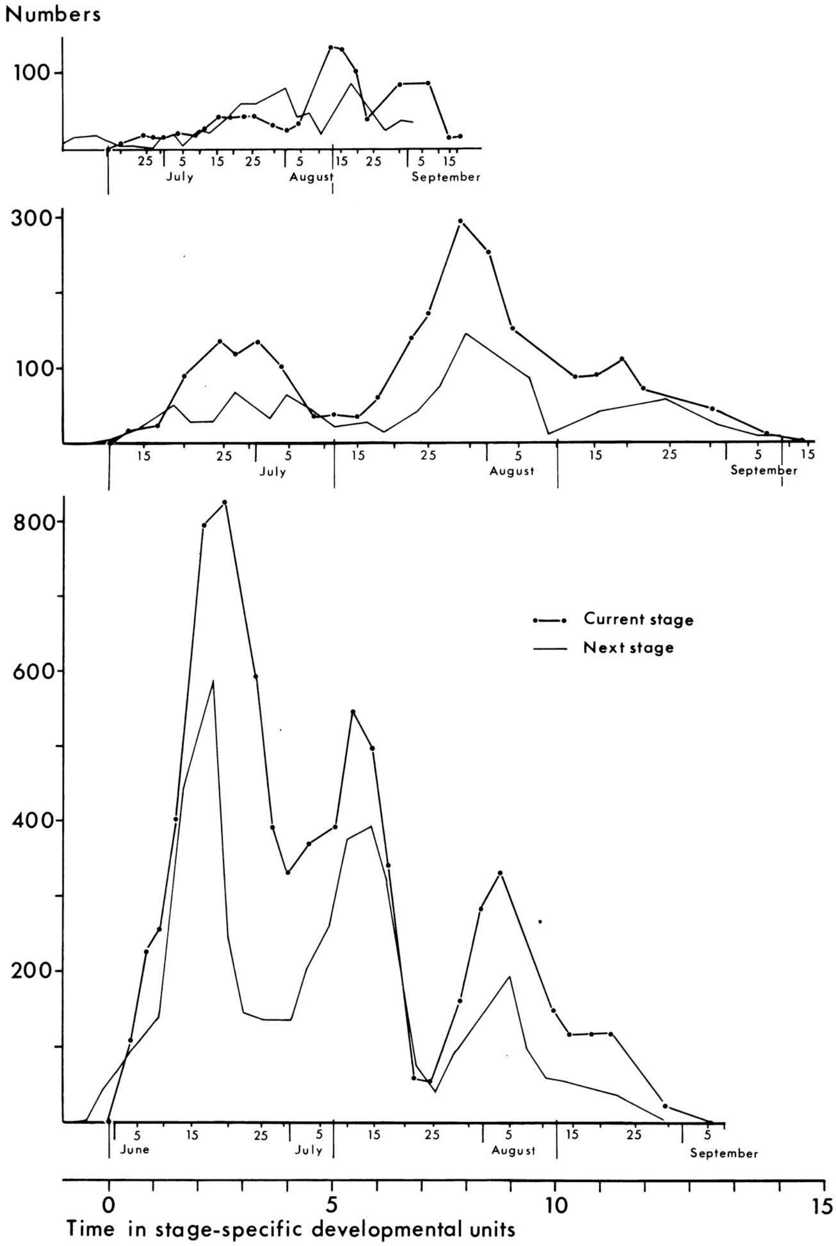

Fig. 2. An example of data from large rock pools (G 3 in 1968). Symbols as in Fig. 1. Graphs: from below, 1st and 2nd-stage larvae; 3rd and 4th-stage larvae of *A. carinata;* 5th-stage larvae and adults of *A. carinata.* Even in 1st-stage larvae the discrepancy between calculated and real development is slight and of short duration, and for most of the season the curves are in close agreement. In large pools the numbers of adults often varied erratically, making analysis more difficult.

of developmental times were skew, with extended tails towards long values, but in both species 2—3 % of the individuals completed their development in less than half of the median values. During the periods of increasing rate of recruitment, as in the beginning of the season, the more rapidly developing individuals predominate over the more slowly developing individuals and thus largely determine the recruitment to the next stage and the form of the stage occurrence curves, causing an apparent shortening in the observed development time. Thus a part of the observed, early, accelerated development over predicted rates can be explained by the normal variation of developmental rates. On the other hand, during periods of diminishing rate of recruitment, the more slowly developing individuals form the majority. Assuming constant mortality, comparable apparent retardation would be observed later. There is, however, reason to expect that the stage-specific mortality increases with increasing density. The mortality then has a greater effect on later-developing larvae and thus on those developing more slowly, and, accordingly, the average rate of development is shorter than expected.

The differences between actual and predicted rates of development are thus the results of two interacting factors whose effects cannot be clearly separated. Simulation studies suggested that the variation in the length of development, comparable to that given by Pajunen & Sundbäck (1973), could not wholly explain the discrepancies. The difference between early and late-season peaks evidently shows the effect of population density on development.

Time axes which accurately depict the progress of development in the field are useful in population analysis. Such transformations directly relate the areas of stage occurrence curves to the numbers present in the population and greatly simplify survival calculations. However, the effect of changing population density on developmental rates introduces a bias, the extent of which naturally depends on the proportion of individuals affected. In the rock pools characterized by continuous recruitment, only a relatively small proportion of individuals were affected by the early, accelerated development. On the other hand, in prominent peaks of short duration, often half of the individuals were in this category.

The periods of retarded development were short and of little importance, and it is thus certain that the calculated axes underestimate the actual progress of development. They can thus be used, at least for less affected, later developmental stages, when the results are interpreted with care. An attempt was made to assess the extent of the bias by lengthening or shortening the deviant time intervals, using the observed discrepancies as guiding values. For the rock pools in which the correspondence between two successive stage occurrence curves was difficult to estimate, the results from other sets of data were applied. For the initial build-up of numbers, the rates of accumulation of areas under the stage occurrence curves were also compared. Slight deviations (distances of more than 0.75 of calculated stage duration for the first interval with the total disappearance of discrepancy after three intervals) were assumed to be the result of inter-individual variation in development, and these were not corrected. The effect of manipulation of time axes was assessed by comparing the changes in the areas under the peaks of stage occurrence curves.

Only the last three larval stages were included in the analysis. As expected, the effects of changing the time intervals varied considerably. The average percentage increase in areas under the peaks (early season peaks of permanent pools and late season peaks of temporary pools in Pajunen 1977) were as follows:

Larval stages:	3rd	4th	5th
A. carinata	14	8	0.5
C. producta	15	9	2

No correction was necessary for the secondary (late summer) peaks. The average change was not great, although large values were occasionally noted. The highest correction amounted to 48 %, 32 % and 7 % for *C. producta* and 43 %, 25 % and 0 % for *S. carinata.* Much greater changes were necessary for the first two larval stages, and no analysis was attempted as it was felt that sufficient reliability could not be expected from such a degree of data manipulation.

A definite association existed between the larval stages. When the change in the 3rd stage was above average in a particular pool, the same was also true for later stages. The changes also seemed to reflect the general well-being of populations. Considerable correction was necessary in several eutrophic pools, which were also characterized by high population densities during later larval stages. On the other hand, almost no correction was needed in temporary, oligotrophic pools in late summer. These pools acquired considerable numbers of small larvae, which then suffered from high mortality.

In most pools the two species reacted differently, the earlier arrival naturally causing greater change. Thus indiscriminate use of uncorrected time axes can considerably affect between-species comparison. Although it was not possible to assess the reliability of the correction method, it was felt that the corrected axes reflect the reality better than the original axes and those for large larvae have been used in the analysis, e.g. in the calculation of average stage-specific mortality (Pajunen 1979a) or stage-specific numbers (Pajunen 1979b).

4. Discussion

The idea of heat-unit summation is old (Wang 1960), but progress in the field of insect ecology after Shelford (1927) has been slow. Attempts to develop detailed and theoretically sound models describing the effect of temperature on the rate of development and attempts to test these models have resulted in many publications, but they have seldom led to field applications, such as those described in Andrewartha (1944) or Pradham (1946). Now that complicated methods are applicable, current opinion (Gilbert et al. 1976) maintains that difficulties involved in the measurement of the temperature of insects in the field largely defeat the day-degree summation. Besides, secondary factors, such as humidity tend to interfere. The experience with rock pool corixids presents population density as one such factor. Although the physiological time scales give the analysis a certain sophistication, difficulties often seem to ensue. This possibly explains the scarcity of published results since the early paper by Hughes (1963). Simulation studies have been one promising area. With the use of proper time scales, comparison of results with field data is greatly facilitated, and the mere labelling of the time axis of computed results as physiological time can be regarded as an expression of faith to the method.

The present results suggest that the rate of development in corixids is strongly affected by population density, especially by the presence of older individuals. Shortage of food can hardly be the major disturbing factor and thus direct interference or comparable mechanisms are probably responsible. In the rock pools the larvae developing from the first eggs of females arriving in a hitherto unoccupied habitat pass the first larval stages in half the time and complete development in at least three-quarters of the time needed by later larvae. This is a clear advantage in an unpredictable environment. The first larvae then affect the development of later larvae, and also strongly dominate the population. The dynamics of population structure in rock pool corixids depends largely on the interaction of individuals of different size classes (Pajunen 1977). Later laboratory studies have verified the importance of cannibalism. The difference in the developmental rates of first and later larvae is thus significant in causing a marked heterogeneity in the population.

These results have wider implications. Much of the general thinking in insect population ecology uses the generation as the basic unit. This is partly derived from its methods, such as *k*-factor analysis. Construction of simple population models can be listed as another source. These models are based on generation parameters, which are assumed to reflect average properties of individuals. These simplifying assumptions are necessary to keep the models manageable. However, much relevant information is lost when working in terms of generations. For example, the temporal heterogeneity caused by short-term changes in developmental rates, together with the social superiority of older individuals form one of the processes stabilizing the populations of corixids: there are always more favoured individuals which are able to survive even at the expense of other members of the population. These short-term processes contribute to the stability, but become obscured when generations are used as time units. Nevertheless, these are in reality the processes that cause the parameters of the models, when estimated, to lie within the acceptable region of the parameter range.

In stable environments, competition between the two rock pool corixids is clearly nonequilibrial (Pajunen 1979 a, b), but the rapid environmental changes, spatial heterogeneity and the intense dispersal of the weaker competitor stabilize the process. The species arriving first in an unoccupied pool gains a considerable advantage. Its larvae are able to develop in a noncompetitive environment and can complete development regardless of later interactions. The temporal heterogeneity thus forms an additional stabilizing factor.

The differences in development rates also cause a further type of heterogeneity. The first and more rapidly developing larvae also tend to attain a larger size than later individuals. The size differences can probably be correlated with stronger competitive ability and possibly with superior fecundity. These differences contribute to the unequal resource use in the population and form a basis for further stabilizing processes (Łomnicki 1978). These results suggest that more effort should be made in the analysis of short-term changes in insect populations. Inter-generation processes are largely reflections of several interacting short-term processes.

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