Ann. Zool. Fennici 16: 138—143. 1979

Competition between rock pool corixids[1]

V. ILMARI PAJUNEN

Pajunen, V. I. 1979: Competition between rock pool corixids. — Ann. Zool. Fennici 16: 138—143.

Life histories and population data of two corixid species living in temporary rock pools were investigated for evidence of interspecific competition. The evidence found included similar reproductive phenology, total qualitative habitat overlap and frequent occurrence of harmfully high densities during the reproductive period. As adult winter mortality and reproductive rates are the same in the two species, but the smaller *Callicorixa producta* suffers from higher larval mortality, its exclusion by *Arctocorisa carinata* would be expected in a stable environment. In the unpredictable rock pool environment its inferiority is offset by its ability to disperse rapidly into refilled pools after the termination of rainless periods. This behavioural difference between the species leads to quantitative differences in habitat utilization late in the reproductive season.

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

1. Introduction

Demonstration of strong interspecific competition between field populations is difficult. The evidence available is nearly always indirect, and considerable disagreement still exists about what amounts to sufficient proof. Attempts to establish general rules (Reynoldson & Bellamy 1972) have not been very successful. At present, much research is concerned with the analysis of resource use by coexisting species, but the relation between niche overlap and competition is far from clear (Colwell & Futuyma 1971, Pianka 1974, Sale 1974). Studies aimed at the detection of effects of competition on population parameters (Williamson 1972) are badly needed.

The scarcity of well-established cases of strong interspecific competition in natural conditions is in fact consistent with theoretical considerations. These suggest that interactions of this type are labile; they lead either to exclusion of the competitively inferior species or to the evolution of factors decreasing competition to acceptable levels, as studies of resource partition between coexisting species seem to show (Schoener 1974). Consequently, strong competition can be studied only when the adverse effects are counterbalanced by other factors, so that non-equilibrial populations can be maintained for longer periods. Such factors include environmental changes sufficiently frequent to give a competitive advantage alternately to each competing species, and strong environmental heterogeneity allowing each to survive in local refuges (Hutchinson 1953, Broadhead & Wapshere 1966).

The rock pools of the outer archipelago of southern Finland are an example of a fragmented habitat characterized by rapid and unpredictable changes. These pools are inhabited by two corixids, *Arctocorisa carinata* (Sahlb.) and *Callicorixa producta* (Reut.). The two species are very similar in their ecology, and show a total habitat overlap. These insects and their environment may form a system in which strong competition is maintained by environmental heterogeneity. In this paper the data available will be analysed in an attempt to discover evidence for such interactions.

---

[1] Report no. 602 from Tvärminne Zoological Station, University of Helsinki.

2. Habitat

The ecology of the two species was studied at Tvärminne Zoological Station in 1963—77. The main features of the habitat have been described in Pajunen & Jansson (1969b). Rock pools typically form where rain water and brackish sea-water collect in shallow depressions in the bedrock. Most pools are 10—50 cm deep. The shallower pools regularly dry up during bouts of dry weather; those deeper than 25 cm normally retain their water troughout the summer. However, most pools freeze totally during the winter, and large, deep pools suitable for overwintering are rare and often separated by distances of several kilometres.

The pools vary considerably in characteristics. As a result of gradual land upheaval new pools are formed and those already existing come to lie farther from the sea. Bottom sediment gradually accumulates, but in the pools near the sea this sediment is frequently washed away by waves. In the older, more sheltered pools sedimentation can continue undisturbed. Then plants invade, and the pools ultimately silt up.

The two corixid species occur in most types of pools, avoiding only those nearest the sea. For reproduction, the most important aspect of a pool is its permanence. Shallow pools are liable to dry up before the development of Corixidae can be completed, but during years with frequent rain they form a significant proportion of the total reproductive habitat available. The depth and thus the permanence of a pool is correlated with its surface area. The habitat selection of arriving adults seems to depend directly on the size of the pools, at least during the autumn dispersal (Pajunen & Jansson 1969b). The surface area can thus be taken as the basic environmental factor reflecting the usefulness of the pools for reproduction.

As detailed data were not included in earlier papers, an example of the abundance of pools of different sizes is given in Table 1. The data include the pools on the islands of Brännskär, Granboskan, Gulkobben and Mellanskär, as representative of the Tvärminne study area. Those pools were excluded that lose water rapidly through fractures in the rock and are thus useless as reproductive habitats. The frequency of rainy periods can be ascertained from the precipitation data for the southern archipelago in Finland (Pajunen 1972). Nowadays, late May and June are relatively rainfree months, after which the probability of longer dry periods clearly diminishes, but local variation in this general pattern is pronounced.

3. Life history data

The life histories of the two species are similar. The adults overwinter in deep pools and disperse in May to shallow pools, the intense flight activity ensuring efficient use of the habitats available. Oviposition starts in late May and the first new adults appear in late June. These produce a second generation, but most of the later-emerging females remain callow and overwinter. The last fifth-stage larvae are found in late September. In the autum the flights of the adults result in their concentrating into the large, deep pools.

The overwintered adults are few in number and the proportions of the two species vary considerably from pool to pool. In small-sized pools, the proportion of *C. producta* among the larvae tends to be higher, but typically both species are present. The data of Pajunen (1977) are in good accord with the general field experiences of 1963—77. As the shallow pools tend to dry up in early summer, and the adults are forced to concentrate in the deeper and larger pools, the possibility of a quantitative difference in habitat selection between the species disappears.

When the shallow pools are refilled, typically in early July, they are rapidly recolonized by *C. producta.* This species is more apt to take wing, as the frequency of take-off of marked adults was estimated by Pajunen & Jansson (1969b) to be 0.1— 0.6 per adult per day, about twice that of *A. carinata.* It is also possible that *C. producta* actively selects small-sized pools, or reacts to high densities in large pools by increased dispersal. As a result, its proportion in the permanently filled pools may diminish and it becomes the dominant species in shallow refilled pools. The data of Pajunen (1977) again correspond with the extensive field experiences. In 1977 even the smallest pools contained water permanently, and in early August they contained larvae of *C. producta.* The larvae were significantly younger than in the larger shallow pools, which suggests that oviposition in them had started later. This seems to indicate that the selection

Table 1. The distribution of rock pools of different size and depth classes on the islands of Brännskär, Granboskan, Gulkobben and Mellanskär in the Tvärminne study area.

Class limit (maximal surface area in m²)	Class limit (maximal depth in cm)									
	4	6	9	12	15	18	21	25	30	40
0.10	11	10	4	1	–	1				
0.13	7	–	4	2	1	1				
0.16	9	2	5	–	1	–				
0.20	12	10	1	–	–	1				
0.25	18	14	6	3	4	–				
0.32	9	11	8	1	–	–				
0.40	7	12	10	5	–	2	1			
0.50	10	13	12	8	4	2	–	2		
0.63	6	18	7	4	2	–	–	–		
0.79	6	13	8	3	5	3	1	1		
1.0	5	6	8	4	4	1	2	1	2	
1.3	2	7	8	2	3	2	3	4	–	
1.6	4	1	4	3	4	3	2	1	4	
2.0	1	2	4	3	7	4	2	–	2	
2.5	2	2	3	2	4	1	2	–	–	
3.2	–	2	2	1	4	1	4	–	2	
4.0	–	–	4	2	1	3	3	1	3	
5.0	–	1	–	3	1	4	2	3	4	1
6.3	–	–	3	1	1	1	4	2	1	1
7.9	–	–	–	–	–	1	1	2	1	1
10.0	–	–	–	1	–	1	3	–	2	–
12.6	–	–	–	–	–	–	–	1	–	–
15.9								1	–	1
20.0							1	–	–	1
25.1							–	–	1	–
31.6									–	–
									1	–

of oviposition sites is dependent both on pool size and on the local density of Corixidae.

Egg development is slightly more rapid in *C. producta*, but no appreciable differences seem to exist in the rate of larval development (Pajunen & Sundbäck 1973). The rate of development falls with increasing density, and the first larvae take about 30 % less time to develop. The older larvae, presumably being cannibals, interfere with the younger ones, and in spite of continuous oviposition, a regular fluctuation of numbers results (Pajunen 1977). Typically, a pool permanently filled with water produces two cohorts in a summer. In spite of the elimination of small larvae, the mortality of large larvae is often heavy. This is particularly evident in the changes of total biomass, which attains maximal values at the peak numbers of fifth-stage larvae and then abruptly decreases. Pajunen (1977) attributed these changes to depletion of food. Feeding experiments support this interpretation, as densities of large larvae and adults could be increased two- to three-fold by adding food.

4. Competition

The following facts suggest that competition occurs between *A. carinata* and *C. producta* in rock pools.

1) The habitats of the two species overlap. The quantitative differences in the use of pools of different sizes occur only for part of the reproductive season.

2) The species are similar in reproductive phenology.

3) The structure of the pool habitat is simple, and the pools are small in relation of the swimming powers of even the smallest larvae. The active developmental stages form a succession of overlapping size classes (Pajunen 1977). Hence no detailed differentiation in the use of resources is possible.

4) The density of the combined populations rises repeatedly during the reproductive season to levels causing high mortality, presumably by depletion of food.

In these conditions the individuals can have effects on coexisting populations which are comparable to their effects on their own populations. In the absence of the other species each could attain higher peak densities and presumably enjoy greater reproductive success.

An attempt was made to analyse the data of Pajunen (1977) by plotting population characteristics of one species (maximal density, numbers and total biomass of final stage larvae alive at the midpoint of the stage) against the corresponding values of the other. A negative relation was evident in the distribution of the data points, but the pronounced scatter hampered the detailed analysis. However, the general course of competition can be ascertained from information available on natality and mortality. Winter mortality among the adults is heavy, and all but those in the few winter pools perish. The data available (Pajunen & Jansson 1969b) suggest that the two species select the same winter habitats. In these winter pools, the proportions of the two species seem to remain unchanged from autumn to spring. Precise information is available for one pool (Br 1 in Pajunen & Jansson 1969b). Catches (217—389 individuals) comprising about half the number of adults present were marked during late autum. The mean proportion of *C. producta* was then 0.60 ± 0.01. The following spring two catches of 163 and 217 individuals gave the proportion of *C. producta* as 0.53 and 0.60, respectively. Additional information can be gleaned from changes in the sex ratio during the winter (Pajunen & Jansson 1969a). The change from an even ratio indicates a higher mortality among the males. In most years these changes were similar in the two species, which suggests the same overall mortality.

Oviposition rates were measured by confining females with the outward appearance of mature females in plastic enclosures in which small stones were provided for resting and oviposition. In June — July the rates were 8.45 and 9.44 eggs per female per day for *A. carinata* and *C. producta*, respectively. However, only 78 % of the 350 *A. carinata* females oviposited, whereas in *C. producta* this proportion was 89 % of 225 females tested. The values per ovipositing female, 10.9 (*A. carinata*) and 10.6 (*C. producta*), are roughly equal. The smaller *C. producta* females may suffer a somewhat higher mortality, but in conditions characterized by strong interactions between larvae of different ages, the reproductive effort is only of importance during limited periods. Even in years of moderate adult density, larval densities rise rapidly to high levels, and the larvae hatching from late-oviposited eggs are eliminated while in the early stages. Thus a comparison between the species can be based on daily oviposition rates.

In late summer the numbers of mature females and their contribution to reproduction are very difficult to assess. Egg production is largely controlled by the availability of food. Egg cannibalism may also be significant late in the season. In the oviposition studies, losses due to cannibalism by females rose from nil in early June to 20—50 % in late July, the values for *A. carinata* being about twice those for *C. producta*. Mortality of eggs placed in pools varied from pool to pool, but no differences could be found between the species.

Survival of larger larvae can be assessed from successive estimates of daily stage-specific numbers, stage-specific developmental rates and temperature records. By combining the 3-year data of Pajunen (1977) into groups representing the early- and late-summer conditions in the permanent pools (G 3, M 1, M 2, M 3, B 48 c, B 48 d and B 82) and the late summer conditions in refilled temporary pools, values for average survival between midpoints of the last three larval stages (Table 2) were obtained. Although the data cover only part of development, this part is presumably important as regards competitive interactions. Naturally, care should be exercised when using average values for a parameter changing conspicuously with time, as the first larvae to hatch probably enjoy advantages over those moulting from later eggs. Mortality at the end of the fifth stage and during early adult life may be expected to be heavier than appears from the estimates. The species-specific survival of small larvae is not known, but the species are unlikely to differ in this respect. In laboratory cultures, when individuals were maintained in groups of the same age in optimal conditions, the two species had the same mortality throughout development (Pajunen & Sundbäck 1973).

The estimates of survival clearly show that in all pool types *C. producta* is less successful, and the difference between this species and *A. carinata* increases with the increase in mortality. Even its numerical dominance in temporary pools does not compensate for its inferiority. As food shortage and possibly also cannibalism are significant mortality factors a part, at least, of the difference can be attributed to competition.

Assuming that mortality in the callow adults before overwintering is the same in the two species, the proportion of *C. producta* would rapidly diminish in a habitat consisting solely of pools deeper than 25 cm. Both species would reproduce at the same rate, but the difference in survival would result in fewer adults per female in *C. producta*. Between reproductive seasons the proportions would remain unchanged. A typical competitive exclusion would ultimately result, although *C. producta* could survive in small numbers for considerable periods by taking advantage of the better survival of the very first larvae of the season.

Table 2. Survival rates of larvae of *Arctocorisa carinata* (A. c.) and *Callicorixa producta* (C. p.) for periods between midpoints of the last three larval stages.

Pools	3rd – 4th		4th – 5th		3rd – 5th	
	A.c.	C.p.	A.c.	C.p.	A.c.	C.p.
Permanent, early summer	0.81	0.69	0.66	0.57	0.53	0.40
Permanent, late summer	0.58	0.59	0.68	0.52	0.39	0.30
Temporary, late summer	0.56	0.57	0.51	0.35	0.29	0.20

The factor that apparently gives the rapidly dispersing *C. producta* sufficient advantage to escape elimination is the availability of refilled pools in late summer. Its earlier arrival in the refilled pools allows it to start reproduction sooner, and thus attain more advanced larval stages in relation to *A. carinata*. This advantage is evident in the survival data, as the values from the third to the fourth stage are similar in the two species, but later *C. producta* again suffers from higher mortality.

The advantage of temporary pools is probably due to many factors. In comparing two habitats, the rates of egg production need not be taken as equal. The temporary pools probably contain more food, and this would increase egg production, which may be hampered by several factors in the permanent pools. Also the less severe egg cannibalism can be assumed to favour reproduction in the temporary pools, and the small larvae can at first develop without interference by larger larvae. Reproductive success can thus be expected to be better in the temporary pools and *C. producta*, forming the bulk of individuals, gains this advantage.

The significance of the refilled temporary pools in late-summer reproduction is evident from the great increase in the numbers of *C. producta* adults arriving in autumn in the large pools (Pajunen & Jansson 1969b). However, the unpredictability of this increase necessitates sufficient reproduction in the permanent pools. At least during the prevailing type of weather, the reproductive effort expended in the small pools in early summer is largely wasted.

5. Discussion

For rock pool corixids, information on the life history is sufficient to allow inferences about the results of interspecific interactions. However, even here much relevant information is unobtainable. In particular, the availability of food and its use could not be measured directly, and indirect reasoning was necessary. The evidence of overuse of resources consisted of characteristic changes in biomass, high mortality, reduction in the size of developing larvae, and cannibalism. This overall picture corresponds closely to the results of Istock (1967) on Gyrinidae and of Fox (1975a, 1975b) on *Notonecta hoffmanni*. Both suggested population limitation by cannibalism at the period of limited availability of prey.

Insect populations can be maintained for considerable periods at a low level of biomass, the main food demand often being limited to a short reproductive season. This allows for temporal segregation of species that would otherwise be in competition. In Corixidae this mechanism has been suggested by Hutchinson (1959) and Istock (1973). No such differences exist between the two rock-pool species.

Size differences between coexisting species have generally been interpreted as leading to differences in resource utilization, but since Hutchinson's (1959) paper the additional problem of the simultaneous presence of several developmental stages in hemimetabolous insects has not been discussed. The relative size differences between successive stages in the two rock pool species are smaller than the Hutchinsonian distance, and *A. carinata* seems to be the superior competitor. Although not much is actually known about the diet, in the simple environment of a rock pool the two species presumably take the same type of food, and larger individuals are probably more efficient feeders. The considerations of Wilson (1975) are obviously applicable to the present case. Larger individuals can consume a wider range of food, and their large size is energetically more efficient, especially as small larvae seem to use much energy in avoiding larger individuals, i.e. potential cannibals. The more rapid growth of *A. carinata* contributes to lessening the effects of cannibalism.

The term fugitive species was introduced by Hutchinson (1951) for a species inferior to its competitors but superior in dispersal and able to exist when sufficiently frequent changes of environment provide empty local habitats which it can reach before the others. In the rock pools, *C. producta* fits this definition, relying mainly on its ability to disperse effectively. As regards the total Palaearctic corixid fauna, both species are inhabitants of typical marginal habitats, which other species do not occupy. It is tempting to assume that they are inferior competitors. On the other hand, they are best adapted to unstable environments requiring frequent repopulation, and are thus able to use environments that may be too demanding for other species.

In models of competition between fugitive species (Skellam 1951, Cohen 1970, Levins & Culver 1971, Slatkin 1974) the environment is assumed to consist of discrete patches and competition acts in changing the probabilities of colonization and extinction of local populations. These models, in which the species typically do not occupy all the available patches at equilibrium, are not directly applicable to the case in which all patches are occupied by both species within a period shorter than one generation time.

Acknowledgements. I wish to express my thanks to Dr. Kari Vepsäläinen for valuable criticism of the manuscript, and to Mrs. Jean Margaret Perttunen B.Sc. (Hons.) for revision of the English text. The study was supported by grant no. 413—2 551—3 01087722—1 from the National Research Council for Sciences.

References

Broadhead, E. & Wapshere, A. J. 1966: Mesopsocus populations on larch in England — the distribution and dynamics of two closely - related coexisting species of Psocoptera sharing the same food resource. — Ecol. Monogr. 36 (4): 327—388.

Cohen, J. E. 1970: A Markov contingency-table model for replicated Lotka-Volterra systems near equilibrium. — Amer. Nat. 104: 547—560.

Colwell, R. K. & Futuyma, D. J. 1971: On the measurement of niche breadth and overlap. — Ecology 52: 567—576.

Fox, L. R. 1975a: Some demographic consequences of food shortage for the predator, Notonecta hoffmanni. — Ecology 56: 868—880.

—»— 1975b: Factors influencing cannibalism, a mechanism of population limitation in the predator Notonecta hoffmanni. – Ecology 56: 933—941.

Hutchinson, G. E. 1951: Copepodology for the ornithologist. — Ecology 32:571—577.

—»— 1953: The concept of pattern in ecology. — Proc. Acad. Nat. Sci. Philadelphia 105:1—12.

—»— 1959: Hommage to Santa Rosalia or why are there so many kinds of animals. — Amer. Nat. 93:145—159.

Istock, C. A. 1966: Distribution, coexistence, and competition of whirligig beetles. — Evolution 20: 211—234.

—»— 1972: Population characteristics of a species ensemble of waterboatmen (Corixidae). — Ecology 54:535—544.

Levins, R. & Culver, D. 1971: Regional coexistence of species and competition between rare species. — Proc. Nat. Acad. Sci. USA 68: 1246—1248.

Pajunen, V. I. 1972: Adaptation of Arctocorisa carinata (Sahlb.) and Callicorixa producta (Reut.) populations to a rock pool environment. — Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek, 1970): 148—158.

—»— 1977: Population structure in rock-pool Corixids (Hemiptera, Corixidae) during the reproductive season. — Ann. Zool. Fennici 14: 26—47.

Pajunen, V. I. & Jansson, A. 1969a: Seasonal changes in the sex ratio of rock pool corixids (Heteroptera, Corixidae). — Ann. Zool. Fennici 6: 219—226.

—»— 1969b: Dispersal of the rock pool corixids Arctocorisa carinata (Sahlb.) and Callicorixa producta (Reut.) (Hemiptera, Corixidae). — Ann. Zool. Fennici 6: 391—427.

Pajunen, V. I. & Sundbäck, E. 1973: Effect of temperature on the development of Arctocorisa carinata (Sahlb.) and Callicorixa producta (Reut.) (Hemiptera, Corixidae). — Ann. Zool. Fennici 10:372—377.

Pianka, E. R. 1974: Niche overlap and diffuse competition. — Proc. Nat. Acad. Sci. USA 71:2141—2145.

Reynoldson, T. B. & Bellamy, L. S. 1972: The establishment of interspecific competition in field populations with an example of competition in action between Polycelis nigra (Mull.) and P. tenuis (Ijima) (Turbellaria, Tricladida). — Proc. Adv. Study Inst. Dynamics Numbers Popul. (Oosterbeek, 1970):282—297.

Schoener, T. W. 1974: Resource partitioning in ecological communities. — Science 185:27—39.

Skellam, J. G. 1951: Random dispersal in theoretical populations. — Biometrica 38:196—218.

Slatkin, M. 1974: Competition and regional coexistence. — Ecology 55:128—134.

Williamson, M. 1972: The analysis of biological populations. — 180 pp. London.

Wilson, D. S. 1975: The adequacy of body size as niche difference. — Amer. Nat. 109: 769—784.

Received 20. XI. 1978
Printed 14. IX. 1979